Facilitation cascade drives positive relationship between native biodiversity and invasion success

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Abstract. The pervasive impact of invasive species has motivated considerable research to understand how characteristics of invaded communities, such as native species diversity, affect the establishment of invasive species. Efforts to identify general mechanisms that limit invasion success, however, have been frustrated by disagreement between landscape-scale observations that generally find a positive relationship between native diversity and invasibility and smaller-scale experiments that consistently reveal competitive interactions that generate the opposite relationship. Here we experimentally elucidate the mechanism explaining the large-scale positive associations between invasion success and native intertidal diversity revealed in our landscape-scale surveys of New England shorelines. Experimental manipulations revealed this large-scale pattern is driven by a facilitation cascade where ecosystem-engineering species interact nonlinearly to enhance native diversity and invasion success by alleviating thermal stress and substrate instability. Our findings reveal that large-scale diversity–invasion relationships can be explained by small-scale positive interactions that commonly occur across multiple trophic levels and functional groups. We argue that facilitation has played an important but unrecognized role in the invasion of other well studied systems, and will be of increasing importance with anticipated climate change.

Key words: *biodiversity; ecosystem engineer; facilitation cascade; foundation species; invasion paradox; invasive species; marine conservation; nonlinear ecological interactions.*

Introduction

The pervasive impact of invasive species has motivated considerable research to understand how characteristics of invaded communities, such as native species diversity, affect the success of invasive species establishment (Elton 1958, Vitousek et al. 1997, Levine and D'Antonio 1999, Tilman 1999, Millennium Ecosystem Assessment 2005). Efforts to identify general mechanisms that limit invasion success, however, have been frustrated by the conflict between large-scale patterns and small-scale experimental results (Shea and Chesson 2002, Fridley et al. 2007). Whereas landscape-scale observations generally find a positive relationship between native diversity and invasibility (e.g., Lonsdale 1999, Stohlgren et al. 1999, 2003, Sax et al. 2002, Brown and Peet 2003, Davies et al. 2005), smaller-scale experiments consistently reveal competitive interactions that generate the opposite relationship (e.g., Knops et al. 1999, Stachowicz et al. 1999, Tilman 1999, Kennedy et al. 2002). This disagreement between observational and manipulative studies is described as an invasion paradox (Fridley et al. 2007), and it suggests that fundamental

ecological interactions other than competition contribute to the relationship between native and invasive species in natural ecosystems, and that they have yet to be experimentally identified and tested (Bulleri et al. 2008).

Recent conceptual models and observational studies suggest positive interactions generate positive relationships between native diversity and invasibility in natural systems that should be detectable at scales amenable to experimental manipulations (Simberloff 1986, Levine and D'Antonio 1999, Richardson et al. 2000, Dunstan and Johnson 2004, Stachowicz and Byrnes 2006, Bulleri et al. 2008). Facilitation is a widespread and fundamental driver of community structure in natural systems (Bertness and Callaway 1994, Stachowicz 2001, Bruno et al. 2003), and experiments have revealed that native species can facilitate either native diversity (Witman 1985, Callaway 1995, Hacker and Bertness 1999) or the success of invasive species (Smith et al. 2004, Zabin and Altieri 2007, Bulleri and Benedetti-Cecchi 2008). Experimental evidence for facilitative interactions resolving the invasion paradox by generating a positive relationship between native diversity and invasibility, however, is lacking (Bulleri et al. 2008), perhaps because modeling and experimental studies have simply failed to provide conditions for them to occur (Shea and Chesson 2002).

Here we present results from manipulative field experiments that uncover facilitative interactions as the

mechanism underlying the positive relationship between native diversity (species richness) and invasion success of the Asian shore crab (*Hemigrapsus sanguineus*) across the intertidal landscape of southern New England cobble beaches. Over the past 20 years, the Asian shore crab has become a dominant shallow water species and conservation concern in the northeastern United States because of its high abundance and voracious omnivorous diet (McDermott 1998, Lohrer et al. 2000, Lohrer 2001, Tyrrell et al. 2006). Crab densities within New England rival or exceed those in their native Asia, particularly on shorelines where Atlantic cordgrass (*Spartina alterniflora*) is a conspicuous component of the cobble beach landscape (McDermott 1998, Bruno and Bertness 2001, Lohrer 2001). Cordgrass is a foundation species (sensu Dayton 1972) widely recognized for its facilitation of vascular plant communities (Redfield 1965, Bruno and Bertness 2001), and it is also known to enhance the abundances of native algae and invertebrates on New England cobble beaches through the indirect positive interactions of a facilitation cascade: cordgrass ameliorates solar stress and provides an attachment surface for ribbed mussels (*Guekensia demissa*) which, in turn, provide stable hard substrate and crevice space for other organisms (Altieri et al. 2007). We hypothesized that native biodiversity and invasion success also benefit from this ecosystem engineering (sensu Jones et al. 1997) by cordgrass and mussels, leading to their large-scale positive association. Understanding how attributes of the native community have aided the establishment of introduced species can help resolve the invasion paradox, and also has immediate practical importance for conservation of invaded ecosystems.

MATERIALS AND METHODS

Study system

Research was conducted on cobble beaches in Narragansett Bay, Rhode Island, USA, a well-mixed estuary with near oceanic salinity (28–31 ppt) and semidiurnal tides ranging from 0.8 to 2.0 m. Narragansett Bay is representative of sheltered bays and sounds in Southern New England where shorelines are typically cobble beaches composed of substrate deposited by receding glaciers. Manipulative experiments were conducted May 2003–September 2004, and tethering experiment in August 2004 on beaches within the Narragansett Bay National Estuarine Research Reserve (NB-NERR).

Landscape-scale surveys

Surveys of Asian shore crab (*Hemigrapsus sanguineus*) populations and native species richness were conducted in 2004 at 14 mid-intertidal sites (0.6–0.8 m above mean lower low water, >500 m apart) spanning 30 km of cobble beach coastline in Brown University's Haffenreffer Reserve in Bristol (41°41′ N, 71°14′ W), Colt State Park in Bristol (41°41′ N, 71°18′ W), and the Narragansett Bay National Estuarine Research Reserve (NB-

NERR) on Prudence (41°39′ N, 71°21′ W) and Patience (41°39′ N, 71°22′ W) Islands. Native species richness was quantified by sampling the number of macroinvertebrate and algal species (observable with unaided eye) within ten 70 × 70 cm quadrats per site. Densities of Asian shore crab were quantified by sampling the number of crabs in eight 25 × 25 cm quadrats per site. To examine the large-scale relationship between native richness and crab density, the total number of native species per site and the average crab density in the high-intertidal zone at each site were used as the response variables in the linear least squares regression analysis. Sites with and without cordgrass were interspersed with one another to account for large-scale environmental gradients.

Based on our observation that the most diverse and heavily invaded sites had cordgrass, and in accordance with recent conceptual and observational studies suggesting the potential importance of positive interactions for the correlated success of native and invasive species (Simberloff 1986, Levine and D'Antonio 1999, Richardson et al. 2000, Stachowicz and Byrnes 2006, Bulleri et al. 2008), we conducted the following three experiments on the shores of the NB-NERR to test the hypothesis that a facilitation cascade (sensu Altieri et al. 2007) in cordgrass beds enhances both native diversity and invader abundance, leading to their large-scale association.

Cordgrass bed manipulation experiment

We manipulated the presence of ribbed mussels (*Geukensia demissa*) and the cordgrass (*Spartina alterniflora*) canopy within existing cordgrass beds to examine their separate and interactive effect on densities of Asian shore crabs and the species richness of native organisms. In a fully factorial design, 1-m^2 plots (>1 m apart) were randomly assigned one level of cordgrass canopy manipulation (aboveground biomass removed or unmanipulated control) and one level of ribbed mussels manipulation (removed or unmanipulated control; $n = 12$ plots per treatment, $n = 48$ total). The cordgrass canopy was removed by clipping, and ribbed mussels removed manually, and both maintained as needed. The experiment was initiated in spring 2003, and at the end of the experiment in fall 2004, the density of Asian shore crabs and the presence of all native macro-organisms (observable with unaided eye) were quantified in a 25 × 25 cm area centrally located within each plot. Cordgrass and ribbed mussels were not included in the census of native organisms because they were directly manipulated in the experiment. Data for this and the following experiments were analyzed by two-factor (fixed) ANOVA. Data were transformed ($\log_{10}x + 1$) to meet ANOVA assumptions, and all post hoc analyses were by Tukey's hsd test.

Abiotic stress measurements

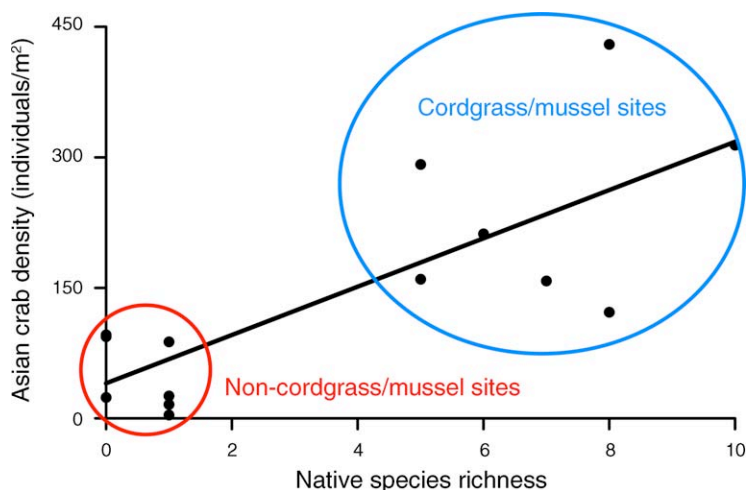To quantify how abiotic stress varied between cordgrass beds and cobbles outside cordgrass beds,

Fig. 1.   Landscape-scale positive relationship between native diversity and invasibilty of intertidal shorelines. Native species richness and Asian shore crab density were positively correlated across intertidal cobble beach sites in southern New England. Subsequent characterization of the survey sites revealed that those with cordgrass were consistently the most diverse and invaded, suggesting that cordgrass beds facilitate the success of both native and invasive species.

solar stress and substrate instability were measured in July 2004 by three methods. (1) Desiccation stress was measured with moistened cube-shaped sponges (8 cm³ volume) placed in either cordgrass beds among mussels, or open stretches of cobble beach among cobbles, for 2 hours at low tide ($n = 10$ sponges per habitat). Evaporative water loss was recorded and analyzed as percent change in sponge mass with a one-way ANOVA. (2) Thermal stress was measured with a thermocouple (Omega model #HH508; Omega Engineering, Stamford, Connecticut, USA) at survey sites in 2004. Five replicate temperature measurements were recorded in the interstitial space (among ribbed mussels within cordgrass beds or among cobbles on beaches without cordgrass beds) commonly inhabited by Asian shore crabs. Temperature data were analyzed by nested ANOVA to account for the replicate temperature readings within replicate cordgrass bed or non-cordgrass bed sites. (3) Substrate instability was measured by the distance that marked cobbles (5–7 cm diameter) moved when placed in either cordgrass beds or open stretches of cobble beach. Within each habitat type, five cobbles were initially placed in each of five replicate plots. This design was duplicated on both an east- and west-facing coastline to account for potential differences in wind-generated wave exposure, however there was no main or interactive effect of coastline orientation in an initial nested design ANOVA, so the data from the two coastlines were pooled for analysis.

Cobble manipulation experiment

We manipulated solar stress and substrate instability in high-intertidal cobbles to test whether the effect of cordgrass and ribbed mussels on native species richness and Asian shore crab populations could be explained by amelioration of those stresses. In a fully factorial design,

0.4-m² plots (>1 m apart) were randomly assigned one level of cobble stabilization (stabilized or unmanipulated control) and one level of shade (shaded or unmanipulated control) in a fully factorial design ($n = 8$ plots per treatment, $n = 32$ total). Cobbles were stabilized by securing vinyl-coated steel mesh (2.5 cm mesh size) across cobbles with rebar corner stakes (Bruno 2000). Plots were shaded by erecting a canopy of double-layer black plastic mesh (mesh size 5 mm) 30 cm above the plot (Bertness and Leonard 1997). The experiment was initiated in spring 2002, and at the end of the experiment in fall 2004, we sampled the density of Asian shore crabs and the presence of all native macro-organisms on and among cobbles in a 25 × 25 cm area centrally located within each plot.

Crab tethering experiment

The direct effects of solar stress, substrate instability, and other potential causes of mortality on Asian shore crabs were measured in August 2004 by tethering crabs to galvanized steel nails pushed flush with the primary substrate in either cordgrass beds or open stretches of cobble beach ($n = 25$ crabs per habitat) for two tidal cycles (24 hours). The proportion of live and dead crabs in each habitat was recorded at the end of the deployment, and the difference in crab survivorship between habitats was examined with chi-square analysis.

RESULTS

Our 14-site survey revealed a landscape-scale positive correlation between the diversity (richness) of native intertidal organisms and the invasion success (abundance) of Asian shore crabs ($R^2 = 0.6099$, $P = 0.001$; Fig. 1).

We tested the hypothesis that this relationship between native diversity and invasion success of Asian shore crabs is the product of a facilitation cascade within
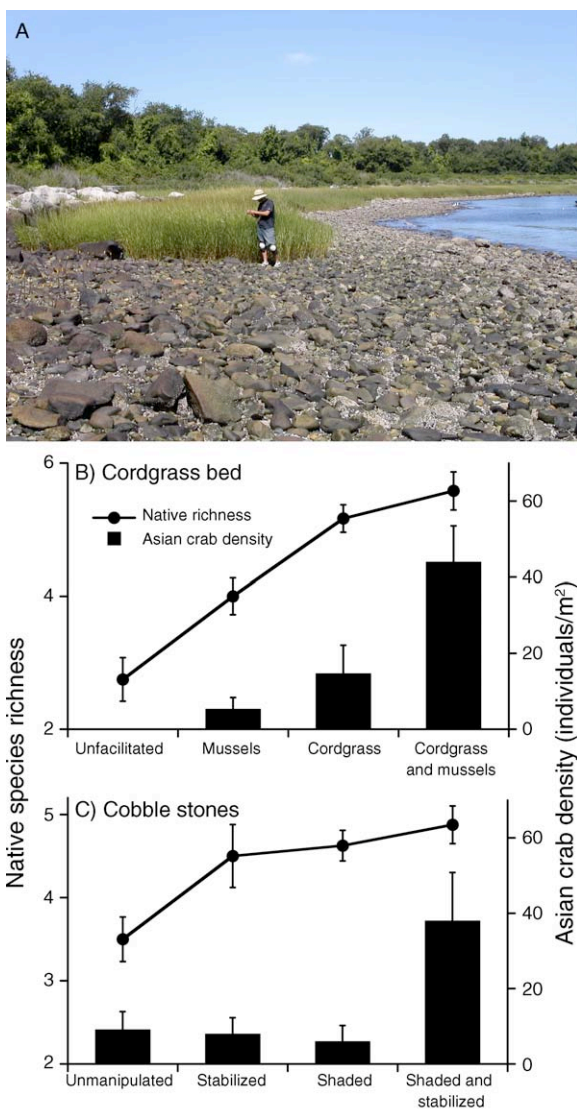
FIG. 2. (A) Photo of a typical intertidal cordgrass bed. (B, C) Experimental evidence for the role of positive interactions driving a positive relationship between native diversity and invader abundance: intertidal cordgrass beds facilitate both native species richness and invasive Asian shore crab densities from (B) experimental manipulations of mussel and cordgrass canopy presence within cordgrass beds and (C) experimental addition of substrate stabilization that mimicked mussels and shading that mimicked the cordgrass canopy. Crab densities were highest when both mussels and cordgrass canopy were present within cordgrass beds and in plots with both stabilization and shading in cobbles. Likewise, the highest native species richness values were observed when both mussels and cordgrass were present within cordgrass beds and when cobbles were both stabilized and shaded. Data shown are means and SE.

cordgrass beds (Fig. 2A) and found that crab density (two-way ANOVA, mussels × cordgrass; mussels $F_{1,44} = 10.34$, $P < 0.05$, cordgrass $F_{1,44} = 21.45$, $P < 0.0001$) and native species richness (mussels × cordgrass $F_{1,44} = 4.30$, $P < 0.05$) were highest where both cordgrass and

mussels were present relative to other treatments where one or both of those foundation species were removed (Fig. 2B).

We further hypothesized that cordgrass beds had this facilitative effect on native species and invasive Asian shore crabs by buffering solar stress and substrate instability based on observations that evaporation rates ($F_{1,18} = 509.42$, $P < 0.0001$), substrate temperature ($F_{1,96} = 693.37$, $P < 0.0001$), and cobble mobility ($F_{1,96} = 55.32$, $P < 0.0001$) were all lower inside cordgrass beds than outside among cobbles. In the second experiment, we tested this hypothesis by experimentally shading and/ or stabilizing cobbles outside cordgrass beds, and found that experimentally mimicking cordgrass effects on solar stress and mussel effects on substrate stability had results similar to our cordgrass beds experiment: the density of crabs (two-way ANOVA, stabilization × shading; $F_{1,28} = 5.18$, $P < 0.05$) and the diversity of native organisms (stabilization $F_{1,28} = 5.46$, $P < 0.05$; shading $F_{1,28} = 9.14$, $P < 0.01$) were highest when cobbles were both shaded and stabilized (Fig. 2C). Notably, shading and stabilization of cobble promoted Asian shore crab densities that were quantitatively very similar to those observed within the cordgrass bed when both the cordgrass canopy and mussels were present (Fig. 2).

In the third experiment, we examined the short-term fate of crabs tethered either inside cordgrass beds or among cobbles outside cordgrass beds, and found that survivorship was over seven times higher in cordgrass (92%) than in cobbles (12%) after 24 hours ($\chi^2 = 32.05$, $P < 0.0001$). Dead crabs in both habitats were intact but crushed by cobbles or desiccated, and there was no evidence of predation (e.g., broken tethers, severed carapace remains) indicating that survivorship is primarily limited by abiotic stress on these beaches (though crabs may also benefit secondarily from increased trophic resources in less stressful cordgrass beds).

DISCUSSION

We found general agreement between small-scale experiments and landscape-scale observations of a positive relationship between native diversity and invasion success of the Asian shore crab on New England cobble beaches. Results from our three complementary experiments reveal that cordgrass and ribbed mussels trigger a facilitation cascade that enhances both native diversity and Asian shore crab populations by ameliorating the harsh sun and wave stresses that otherwise limit intertidal organisms (see Plate 1). The patchy nature of cordgrass/mussel beds across the intertidal landscape thus creates areas where extrinsic factors are modified by facilitative beds and native diversity and invader abundance are higher, and more stressful areas without stress amelioration by beds where diversity and invader abundance are lower. As a consequence, facilitation detected at the experimental-scale contributes to the heterogeneity at the landscape-

PLATE 1. Cordgrass facilitates ribbed mussels and other intertidal organisms by ameliorating thermal and desiccation stress. Ribbed mussels, in turn, facilitate other species by providing a hard settlement substrate for species including barnacles and crevice space for mobile species such as littorine snails and the invasive Asian shore crab (inset). This facilitation cascade thus enhances both native diversity and the success of invasive species. Photo credit: A. H. Altieri.

scale that can drive broader positive diversity-invasibility relationships (Shea and Chesson 2002, Huston 2004). Our findings thus answer affirmatively the fundamental questions of whether facilitative interactions affect the relationship between native and invasive species, and whether they do so on a scale detectable by experiments (Bulleri et al. 2008).

While cordgrass and mussels together had a less than additive effect on native diversity relative to their separate effects, we observed a sharply more than additive effect on invasive crab densities (Fig. 2). Thus, native species and invasive crabs both responded nonlinearly to the presence of both foundation species, and this effect was strongly multiplicative on the invasive species. These results introduce the ability of such synergistic foundation species, acting through a facilitation cascade, to drive patterns of *biodiversity*, *invasive species*, and the *diversity–invasion relationship*. This novel insight builds on previous work that introduced the facilitation cascade concept by demonstrating its importance for the *abundances* of native cobble beach species (Altieri et al. 2007). Although Asian shore crabs potentially have significant impacts on basal trophic levels (Lohrer et al. 2000, Bourdeau and O'Connor 2003, Brousseau and Baglivo 2005, Tyrrell et al. 2006) and other consumers (Griffen and Byers 2006, Kraemer et al. 2007), the positive association of the crab populations and native diversity indicates the primary importance of positive interactions in this system.

Our findings suggest that previous experimental designs that precluded the role of foundation species and facilitation have contributed to the consistent opposition between large-scale observations and small-scale experiments underlying the "invasion paradox." Prior experiments identified competitive interactions among native and invasive species by focusing primarily on constructed assemblages within a single functional group where relevant positive interactions may have been overlooked (Shea and Chesson 2002), and were thus unable to explain large-scale positive relationships between native diversity and invasibility (Fridley et al. 2007). By elucidating the importance of positive interactions, our study increases the power to explain the invasibility of natural ecosystems by demonstrating that the mechanism of stress amelioration by foundation species that we identified at the experimental-scale is sufficient to explain landscape-scale associations between diversity and the abundance of invasive species.

We argue that facilitation has played an important but unrecognized role in the natural systems that provided the context for landmark experimental studies where competition purportedly dominates the relationship between native biodiversity and invasiveness. For example, Levine (2000a) focused on native–invasive competitive interactions within a riparian plant community that was dependent on a plant generated tussock habitat for colonization and survival (Levine 2000b,

Reports

2001). Similarly, Tilman and colleagues (Tilman 1997, Kennedy et al. 2002) developed models of biodiversity resistance to invasion in prairie grasslands where C_4 grasses enhance diversity and the success of both experimental "invaders" (Tilman 1997) and exotic species (Smith et al. 2004). Stachowicz found competition for space to be a mechanism underlying a negative relationship between biodiversity and invasion resistance within an assembled marine fouling community (Stachowicz et al. 1999), but subsequent observational studies with an entire fouling community containing additional functional groups revealed that habitat creation by a sessile fouling species can drive the opposite relationship (Stachowicz and Byrnes 2006). Revisiting these experimental systems, in combination with the present study, suggests that facilitation driving positive associations between native diversity and invasibility is a general mechanism. Further experimental study of biodiversity-invasibility relationships needs to consider this hierarchical community organization concept in which negative interactions (e.g., competition and predation) commonly occur within a community that is itself dependent on facilitation by habitat modifying species (Bruno and Bertness 2001, Altieri et al. 2007).

Our results emphasize that experimental studies must extend their perspective beyond a single guild, trophic level, or taxonomic assemblage (Simberloff 1986, Mooney and Drake 1989). On New England cobble beaches, cordgrass (i.e., plant/primary producer) and mussels (i.e., animal/consumer) act synergistically to facilitate a suite of native and invasive species comprised of both invertebrates and algae. Had we limited our experimental perspective to a single trophic level, our ability to address the "invasion paradox" would have been hampered by the predominance of competitive interactions among plants and suppression of native plant diversity within cordgrass beds (van de Koppel et al. 2006).

Recognizing the importance of positive interactions in driving diversity-invasibility relationships as a mechanism of "biotic acceptance" (Stohlgren et al. 2006) is particularly urgent since they will likely play an increasingly important role as environmental stresses become more severe with predicted climate change (Bertness and Callaway 1994, Bruno et al. 2003). Some studies have already documented apparent native facilitation of invasion success following disturbances (e.g., fire and flooding) that are expected to worsen with climate change (Smith et al. 2004, Von Holle 2005). Future research should prioritize conservation efforts by identifying the foundation species that mediate large-scale patterns of community diversity and invasibility in natural ecosystems, and will contribute to our understanding of how facilitation allows species to overcome limiting conditions outside their native range.

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Reports