# LETTER

# Scale-dependent interactions and community structure on cobble beaches

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## Abstract

Recent theory suggests that scale-dependent interaction between facilitation and competition can generate spatial structure in ecological communities. The application of this hypothesis, however, has been limited to systems with little underlying heterogeneity. We evaluated this prediction in a plant community along an intertidal stress gradient on cobble beaches in Rhode Island, USA. Prior studies have shown that *Spartina alterniflora* facilitates a forb-dominated community higher in the intertidal by modifying the shoreline environment. We tested the hypothesis that, at a smaller scale, *Spartina* competitively excludes forb species, explaining their marked absence within the lower *Spartina* zone. Transplant experiments showed forb species grow significantly better in the *Spartina* zone when neighbours were removed. Removal of the *Spartina* canopy led to a massive emergence of annual forbs, showing that competition limits local occupation. These findings indicate that interaction of large-scale facilitation and small-scale competition drives plant zonation on cobble beaches. This study is the first to provide empirical evidence of scale-dependent interactions between facilitation and competition spatially structuring communities in heterogeneous environments.

## INTRODUCTION

A dominant theme in ecological research is to explain the mechanisms underlying spatial distribution of species and resulting patterning of ecological communities. Classical approaches emphasize that differences in adaptation to environmental stress, predation and competition lead to species zonation along gradients of environmental stress (Stephenson & Stephenson 1949; Chapman 1974; Whittaker 1975). The patterning observed in ecological communities would hence reflect the spatial structure of the underlying abiotic substrate. This notion is particularly dominant in intertidal ecology, as many studies have related species zonation in intertidal systems to gradients in physical stresses that characterize intertidal habitats (Stephenson & Stephenson 1949; Connell 1961; Menge & Sutherland 1987).

Recently, a number of papers have emphasized the occurrence of spatial patterning in ecosystems that have little underlying abiotic heterogeneity (see Rietkerk *et al.*

2004a for a review). Vegetation occurring in arid ecosystems (Klausmeier 1999; Leprun 1999; Valentin & d'Herbes 1999), savanna woodlands (Lejeune *et al.* 2002) and boreal peatlands (Rietkerk *et al.* 2004b) was shown to be strongly patterned, and there was little evidence that these patterns were caused by environmental heterogeneity and the resulting physical adaptation of plants. Similar spatial patterns were observed in intertidal mussel beds and microbial mats on relatively homogeneous intertidal flats (de Brouwer *et al.* 2000; Van de Koppel *et al.* 2005). The spatial patterns have been explained by self-organization (e.g. caused by the interactions within the ecosystem), resulting from the interaction between large-scale facilitation and small-scale competition between individuals (Couteron & Lejeune 2001; Rietkerk *et al.* 2004a; Van de Koppel *et al.* 2005). For instance, short-range facilitation (< 10 m range) through improved local infiltration of water around establish plants, in combination with long-range competition for surface water (> 10 m range), was proposed to

explain the formation of banded patterns in so-called tiger bush (Couteron & Lejeune 2001; Rietkerk *et al.* 2002). These results, with those of a large body of similar studies (see Rohani *et al.* 1997; Rietkerk *et al.* 2004a; Pascual & Guichard 2005 for reviews), demonstrate the potential capacity of scale-dependent ecological interactions to produce heterogeneous landscapes in otherwise homogeneous environments, largely independent of preexisting environmental stress gradients. However, the importance of scale-dependent ecological interactions in structuring communities characterized by gradients in physical conditions, such as those found in many intertidal communities, is poorly understood.

Over the past 15 years, many studies have revealed the importance of facilitation in determining community structure in intertidal communities (Bertness 1991; Bertness & Callaway 1994; Bertness & Hacker 1994; Bruno *et al.* 2003). Salt marsh plants were shown to strongly benefit from indirect facilitative interactions by mediation of physical stress (Bertness & Hacker 1994). On cobble beaches, dense stands of *Spartina alterniflora* occupying the lower intertidal zone were found to facilitate an entire plant community dominated by annual and perennial forbs occurring behind the *Spartina* zone by buffering them from intense wave action (Bruno 2000). Bruno (2000) determined the importance of facilitation by *Spartina* in five life-history stages. His manipulative experiments showed that facilitative effects were particularly strong at the seedling stage, as forb seedlings could only survive when the substrate was stabilized by *Spartina*. Moreover, forb occupation and diversity was found to correlate with the size of the *Spartina* beds (Bruno & Kennedy 2000; Bruno 2002). Despite strong facilitative effects of *Spartina* on plants in the upper intertidal zone, the *Spartina* zone itself is a near-monoculture, suggesting that either biotic (competition) or abiotic factors (recruitment failure, for instance because of increased inundation) limits forb establishment or survival within the *Spartina* zone. This would imply that facilitation prevails only at a certain distance, whereas other factors determine forb growth close-by. However, little is known about the relative importance of facilitative and competitive interactions at different spatial scales on cobble beaches.

In this paper, we investigate the hypothesis that *Suaeda linearis*, *Salicornia europaea* and *Limonium nashii*, three of the most abundant cobble beach forbs, are excluded from the *Spartina* zone due to aboveground competition with *Spartina alterniflora*, using two manipulative experiments. We tested the importance of aboveground competition in limiting the growth of (1) forbs transplanted into the *Spartina* zone, and (2) forb seedlings that emerge naturally in the *Spartina* zone. We discuss the implications of our results for current theories on the effects of spatial scale of ecological interactions on community organization.

## MATERIALS AND METHODS

### The New England cobble beaches

Our study was performed on the cobble beaches of Prudence Island, within the Narragansett Bay National Estuarine Research Reserve, Rhode Island, USA (coordinates: 41.67°N, 71.34°W). The Narragansett Bay cobble beaches consist of a mixture of glacially deposited cobbles, gravel and sediment. The main physical stress to plants apart from tidal inundation is the exposure to wind-driven waves, which destabilize sediment and can prevent seedling emergence (Bruno 2000, 2002). The plant community that inhabits cobble beaches consists at the sea-side of a monospecific zone of *Spartina alterniflora*. *Spartina alterniflora* beds significantly attenuate waves energy, and have a stabilizing effect on cobble sediment. Reduced wave exposure facilitates establishment and growth of a number of forb species such as *Salicornia europea*, *Suaeda linearis* and *Limonium nashii*, that occur as a second zone almost exclusively behind *Spartina* beds. *Spartina alterniflora* is virtually absent from this forb-dominated zone. Although many forb seedlings emerge within *Spartina* beds early in the growing season, nearly all die before reaching maturity. For a detailed description of Narragansett bay cobble beach plant communities, see Bruno (2000) and Kennedy & Bruno (2000).

### Transplant experiment

We tested whether competition limited growth of the forbs *Suaeda linearis*, *Salicornia europaea* and *Limonium nashii* within both the *Spartina* zone and the native zone of the forbs behind the *Spartina* beds. We established 12 experimental sites along the cobble beach, each *c.* 30 m apart. Within each site, we haphazardly placed four treatment plots, two in the lower *Spartina* zone, and two in the higher, forb-dominated zone. In each zone, we created a no-competition treatment by cutting away all aboveground vegetation in one of the two plots. Regrowth was prevented using root cloth (industrial grade weed block), which was fastened in place with vinyl-coated wire mesh (Aquamesh, 2 inch mesh size; Riverdale Mills Corporation, Northbridge, MA, USA). In each zone, we used the second plot, with an unmanipulated canopy of either *Spartina* in the lower zone or forbs in the upper zone, as a control with full aboveground competition. The experiment was hence set-up as a randomized block design, with zone and competition as fixed treatments, and site as the blocking factor.

Small seedlings of *Salicornia* were obtained from a near-by salt marsh, as they were unavailable early in the season on the cobble beach, and transplanted in cylindrical pots (15 × 15 cm diameter × height) by extracting peat sods. All sods contained at least 10 *Salicornia* seedlings. Seedlings of *Suaeda* were extracted from the cobble beach, and planted

into pots filled with peat sods. Each pot contained 12 *Suaeda* seedlings. Small adult *Limonium* plants, all having three to four leaves, were obtained from the cobble beach, and planted into pots using a mix of local soil and cobbles. The transplant pots were randomly assigned to each of the treatment plots. During the summer months, all emerging vegetation (apart from the transplants) was removed from the no-competition treatments at 1-month intervals. The aboveground portion of transplants were harvested on the 9th of September, counted and dried for 4 days at 60 °C.

### Seedling emergence experiment

To test whether seedling dispersal, rather than competition with *Spartina*, limited seedling emergence within the *Spartina* zone, we experimentally removed the *Spartina* canopy at the edge of the *Spartina* and forb-dominated zones. Within sites selected for transplant experiments, we established two 50 × 50 cm plots in the upper *Spartina* zone, on 8 May 2004. In one plot, we carefully clipped away all *Spartina* stems without damaging emerging seedlings, and left the second as an unmanipulated control. The plots were monitored once a month, during which re-emerging *Spartina* shoots were cut away. All aboveground vegetation was harvested on 9 September, after which plants were sorted into species and dried for 4 days by 60 °C. We measured light intensity levels in all experimental plots on the19th of July 2004, using a Quantum Light Meter (Apogee Instruments, Inc., Logan, UT, USA), which integrates across 5 points the rate of photon flux ($\mu$mol m$^{-2}$ s$^{-1}$) in photosynthetic wavelengths. We used analysis of variance to analyse both experiments, with zone (only for the transplant experiment) and competition as fixed factors (for both), and site as a random factor. All data were log or square-root transformed if necessary to meet the assumptions of ANOVA with regard to the homogeneity of variances. We applied the Mann–Whitney *U*-test if transformation failed in satisfying the assumptions of homogeneity of variances. The Kruskal–Wallis test with Bonferroni corrections was applied in case of multiple comparisons.

### RESULTS

The results of both the transplant (Fig. 1) and the seedling-emergence experiments (Fig. 2) revealed a clear negative effect of competition by *Spartina* on the growth of forbs species. For both *Suaeda linearis* and *Salicornia europea*, we found a significant effect of competition by *Spartina* on transplant biomass (SL: ANOVA, $F_{11,48} = 5.19$, $P = 0.044$; SE: ANOVA, $F_{11,48} = 71.69$, $P < 0.001$). There was a significant interaction between competition and zone in the case of *Salicornia* (ANOVA, $F_{11,48} = 7.08$, $P < 0.022$), indicating competition was stronger in *Spartina* beds than in
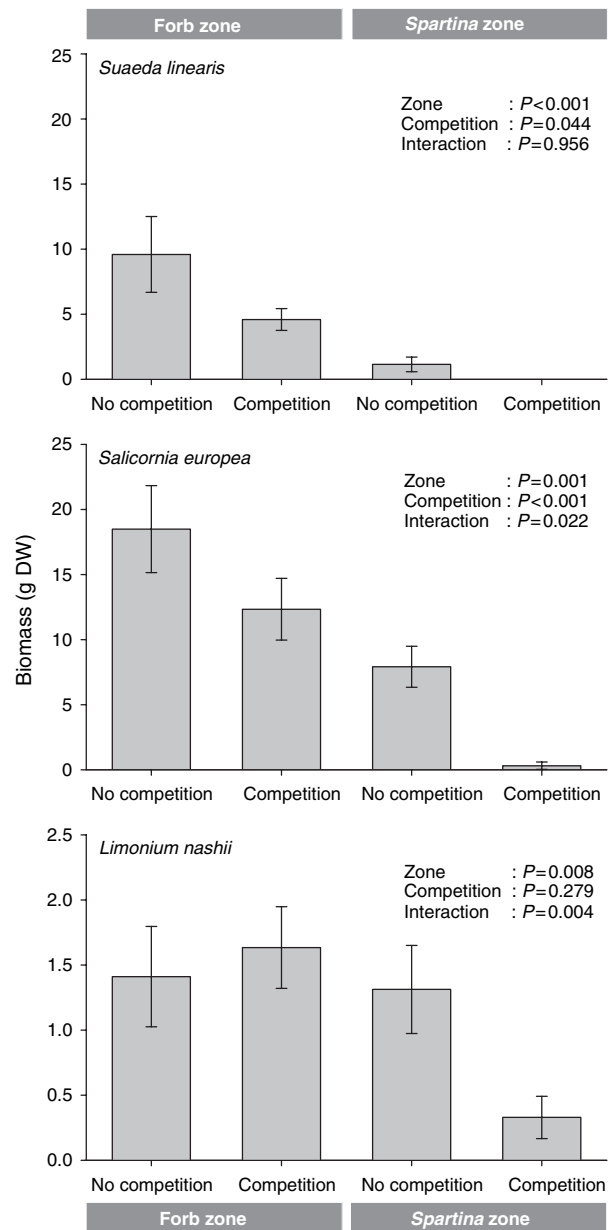


**Figure 1** Results of the transplantation experiment in which juveniles of the forbs *Suaeda linearis*, *Salicornea europea* and *Limonium nashii* were transplanted into the zone dominated by *Spartina alterniflora* and into their own native zone, with and without competition from neighbouring plants. For each treatment, the mean of 12 replicates is given.

the forb zone. Similarly, we found a significant interaction between zone and competition in the case of *Limonium nashii* (ANOVA, $F_{11,48} = 12.76$, $P = 0.004$), indicating competition strongly affected growth of *Limonium* in the *Spartina* zone, but not in the forb zone. For all species, zone (*Spartina* zone vs. forbs zone) strongly affected growth (SL: ANOVA, $F_{11,48} = 26.88$, $P < 0.001$; SE: ANOVA, $F_{11,48} = 19.34$,
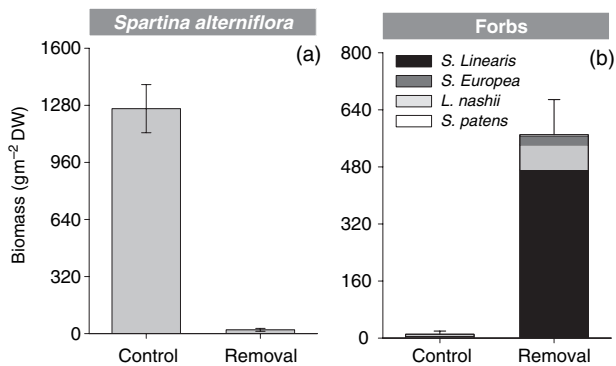
**Figure 2** Results of the seedling emergence experiment, in which we removed the *Spartina alterniflora* canopy in plots at the upper edge of the *Spartina* zone. (a) Effects of the experimental removal of *Spartina* on *Spartina* standing crop in the experimental plot relative to the control. (b) Seedling emergence in the experimental plot relative to the control. For each treatment, the mean of eleven replicates is given.

$P < 0.001$; LN: ANOVA, $F_{11,48} = 10.42$, $P = 0.008$), revealing that a portion of the forb growth reduction in the *Spartina* zone was due to physical constraints. No significant effects were found for the blocking factor (site), for any of the transplanted species (SL: ANOVA, $F_{11,48} = 0.60$, $P = 0.790$; SE: ANOVA, $F_{11,48} = 0.70$, $P = 0.710$; LN: ANOVA, $F_{11,48} = 0.97$, $P = 0.542$).

The most striking results were obtained in the Seedling emergence experiment. Monthly removal of *Spartina* canopy reduced *Spartina* standing crop by well over an order of magnitude at the end of the season (Fig. 2a, Mann–Whitney *U*-test, $U < 0.000$, $P < 0.001$). Release from aboveground competition allowed massive emergence of forb species: the biomass of *Suaeda*, *Salicornia* and *Limonium* were one to two orders of magnitude higher when *Spartina* had been removed (Fig. 2b, Mann–Whitney *U*-tests, SL: $U = 8.50$, $P = 0.001$; SE: $U = 22.00$, $P = 0.010$; LN: $U = 27.50$, $P < 0.028$, total biomass: $U = 2.00$, $P < 0.001$). Forbs emerged in both treatments at the beginning of the season but were largely shaded out in control plots by the end of the season.

Results from both experiments can in part be explained by the effect *Spartina* has on availability of photosynthetically active light. In both the transplantation and seedling emergence experiments, light availability on a sunny day was reduced by *Spartina* from c. 1400 to 450 μmol m$^{-2}$ s$^{-1}$ (Fig. 3; Mann–Whitney *U*-tests, TE: $U = 1.00$, $P < 0.001$; RE: $U = 2.00$, $P < 0.001$). In the forbs zone, the natural forb cover reduced light from c. 1600 to 1250 μmol m$^{-2}$ s$^{-1}$ (Mann–Whitney *U*-tests, RE: $U = 14.00$, $P < 0.002$).

## DISCUSSION

Our experimental results demonstrate competition with *Spartina alterniflora* limits both establishment and growth of the cobble beach forbs *Suaeda linearis*, *Salicornia europaea* and *Limonium nashii* in the lower, *Spartina*-dominated zone. Removal of *Spartina* canopy at the upper edge of the *Spartina* zone led to a massive emergence of forb seedlings. Moreover, transplants of *Suaeda*, *Salicornia* and *Limonium* grew better in the *Spartina* zone when the *Spartina* canopy was removed, when compared with the full *Spartina* matrix. Our results, in combination with those obtained by Bruno (2000), show that the nature of interaction between *Spartina* and the forb species depends strongly on spatial scale (or distance): facilitation dominates at larger range (behind the bed – Bruno 2000), while competition dominates at smaller range (within the bed). The interplay of facilitation and competition at different scales segregates the cobble beach community into a forb-dominated community in the upper zone that persists in the wake of a competitively dominant monoculture of *Spartina* in the lower zone. Hence, our results suggest plant zonation on New England cobble beaches results from a localized, scale-dependent interaction between facilitation and competition between species, rather than being a direct reflection of the underlying gradient of physical stress.

Our results are in apparent disagreement with zonation theory on how physical stress gradients structure intertidal plant communities. Classical intertidal studies showed that in salt marsh plant assemblages, competition limits the upper distribution of plants, while physical factors limit the
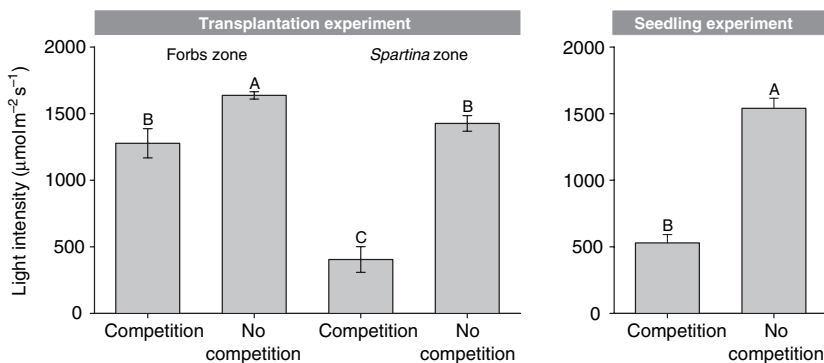


**Figure 3** Light intensities in both the transplantation experiment and the seedling emergence experiment. Light levels were determined on 19 July 2004. The letters on top of the bars denote significant differences between the treatments, for each experiment separately. For each treatment, the mean of 11 replicates is given.

lower distribution (see Bertness 1999 for an overview). In our study, we observed the opposite: forbs were limited by competition at the lower edge of their distribution. Moreover, a previous study has shown that physical stress limits forbs at the upper edge (Kennedy & Bruno 2000). A likely reason for this mismatch between our observations and traditional zonation concepts is strong modification of the gradient in wave energy by *Spartina Spartina* is very efficient in reducing wave impacts and thereby protects forb plant communities on the lea side from wave stress and substrate instability, in particularly affecting seedling survival (Bruno & Kennedy 2000). This effect is local, however, as wave-induced substrate instability again limits plant growth at the upper edge of the forb community (Kennedy & Bruno 2000). This pattern illustrates that the local gradient of physical stresses is completely determined, and even reversed, by the habitat modifying characteristics of *Spartina alterniflora*, rather than imposed by the landscape. As a consequence, biotic interactions set the low-stress, lower boundary of the forbs zone, while physical limitations limit forb growth the high-stress upper boundary, in agreement with classical zonation concepts for salt-marsh plants.

In the past decade, a significant body of research has emerged emphasizing importance of facilitative interactions in communities where competition and predation were formerly thought to be primary structuring forces (see Bruno *et al.* 2003 for a review). Examples stem from rocky shores (Bertness *et al.* 1999), salt-marsh ecosystem (Bertness & Hacker 1994), mussel beds (Bertness & Grosholz 1985; Hunt & Scheibling 2001, 2002), arid ecosystems (Maestre & Cortina 2004), boreal peatlands (Rietkerk *et al.* 2004b) and alpine ecosystems (Callaway *et al.* 2002). Despite the abundance of studies on facilitation, most have focused on the relative importance of positive and negative interaction, and their significance in structuring natural communities. Our findings suggest that a hierarchical perspective, as proposed by Bruno & Bertness (2000) and Stachowicz (2001), might be more appropriate: facilitation by a foundation species opens up a potential niche for many species, while competition determines the final species sorting. On the cobble beach, strong modification of the physical environment by *Spartina* facilitates survival of a host of species along the cobble beach gradient (A.H. Altieri *et al.* unpublished data), while local competition determines the spatial arrangement of species in zones (this paper). Key in understanding how facilitation and competition determine the final cobble beach zonation is their scale-dependence, rather than their relative importance.

Our results have important implications for the concept of the ecological niche. Current theory predicts that only a limited number of species can coexist at equilibrium, determined by the number of factors that limits the growth of the involved species, such resource availability or predation (see e.g. Chase & Leibold 2003). In this view, regional coexistence of many species can only be explained by assuming environmental heterogeneity at the landscape level. Our results, however, show that scale-dependent ecological interactions can generate spatially heterogeneous communities, as some organisms generate environmental gradients themselves (by attenuation of waves in case of *Spartina*). Hence, interactions between organisms and their environment may result in coexistence of competing species in spatially heterogeneous communities, even when coexistence at small spatial scales is impossible. Key in understanding species coexistence in our cobble beach plant community is what limits *Spartina* from occupying the entire intertidal gradient. No conclusive evidence has been obtained so-far on this question. A recent study on the interaction between the ribbed mussel (sp) and *Spartina*, however, indicated that nutrient availability is an important factor limiting the establishment of *Spartina* on open cobble beach (A.H. Altieri *et al.* unpublished data). It is therefore possible that nutrient limitation, possibly in combination with nutrient competition, limits the upper distribution of *Spartina*, allowing the persistence of a forb community above the *Spartina* zone. More research is required to elucidate coexistence mechanisms on the cobble beach.

Complexity theory proposes that complex structures in ecosystems can emerge from localized ecological interactions between the ecosystem's components (see Bascompte & Sole 1995 for a review). This principle has been applied to a wide variety of ecosystems to explain the occurrence of regular (Klausmeier 1999; Von Hardenberg *et al.* 2001; Rietkerk *et al.* 2004a; Van de Koppel *et al.* 2005) or scale invariant spatial patterning (Pascual & Guichard 2005). A typical property of these ecosystems and of the models used to explain their patterning is the absence of heterogeneity in the underlying environment (e.g. they are characterized by a flat soil or sediment surface). In this study, we showed that a localized, scale-dependent interaction between facilitation and competition strongly affects the spatial structure and composition of cobble beach communities, a system characterized by a strong environmental gradient. Hence, our study stresses that complexity theory principles can explain spatial patterning across a potentially much larger range of ecosystems, even those in which environmental variability seems to play an overruling role.

## ACKNOWLEDGEMENTS

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