Original article

Interactions between ecosystem engineers: A native species indirectly facilitates a non-native one

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ABSTRACT

The positive impact that native species have on the survival, persistence and/or range-expansion of invasive species, is receiving increasing attention from ecologists and land managers trying to better understand and predict future invasions worldwide. Ecosystem engineers are among the best-known model organisms for such studies. The austral cordgrass *Spartina densiflora* is an ecosystem engineer native to South America coast, where it colonizes rocky shores that were recently successfully invaded by the acorn barnacle *Balanus glandula*. We conducted a field experiment combining living *Spartina* transplants and artificial model plants in order to address the following questions: Does the native ecosystem engineer *S. densiflora* facilitate the invasion of rocky shores by *B. glandula*? If so, how much of this facilitation is caused by its physical structure alone? We found that *S. densiflora* had a positive effect on the invasive barnacle by trapping among its stems, the mussels, shells and gravels where *B. glandula* settles. Dislodged mussels, cobbles, and small shells covered and agglutinated by living barnacles were retained within the aboveground structures of *S. densiflora* while the control plots (without living or artificial plant structures) remained mostly bare throughout the experiment, showing how plant structures speed the colonization process. Moreover, transplanting living *Spartina* and artificial *Spartina* models led to a maximum increase in the area covered by barnacles of more than 1700% relative to the unvegetated control plots. Our study clearly shows how a native ecosystem engineers can enhance the success of invasive species and facilitate their local spread.

1. Introduction

Many studies have evaluated the direct impacts of non-indigenous species on native biota, encompassing changes in ecosystem processes (Hoffmeister et al., 2005), loss of biodiversity (Clavero and García-Berthou, 2005), increase of pests and diseases (Prenter et al., 2004) or alteration of community structure through negative and positive interactions (Grosholz et al., 2000; Rodriguez, 2006). The positive impact that native species may have on the survival, persistence and/or range-expansion of the invasive species, has received less attention (but see Maron and Connors, 1996; Badano et al., 2007; Altieri et al., 2010; Cushman et al., 2011). Native organisms able to ameliorate key physical stressors can also facilitate the colonization and survival of a variety of other organisms (Michalet et al., 2006; Altieri et al., 2007; Cavieres and Badano, 2009), including invasive species (Maron and Connors, 1996; Cavieres et al., 2005; Badano et al., 2007; Altieri et al., 2010). When these positive interactions involve the facilitation of non-native species invasions, it is likely that they affect native communities by at least altering the composition and relative abundances of local species. Ecosystem engineers are, by far, the best-known example of this type of facilitating organisms, since they can create suitable habitats for several other organisms through non-trophic alterations of biotic and abiotic materials (Crain and Bertness, 2006; Wright and Jones, 2006).

The austral cordgrass *Spartina densiflora* Brong. is an ecosystem engineer native to South America (Bortolus, 2006; Fortuné et al., 2008). This species is commonly found on soft substrates as well as on a variety of rocky shores along the Pacific and Atlantic coasts of the Americas, and also in other regions (Bortolus, 2006; Bortolus et al., 2009). As an autogenic engineer (*sensu* Jones et al., 1997) *S. densiflora* can modify its abiotic environment through its physical structure, for example, by enhancing the sedimentation rate, reducing soil-surface temperature and desiccation stress, and

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providing a surface for attachment and shelter to many invertebrates (Bortolus et al., 2002; Sueiro et al., 2012). Nevertheless, biological characteristics of these plants may also be important to the associated fauna. For example, they may exude chemicals that attract or repel larvae of marine invertebrates or stimulate settlement (Pawlik, 1990). In addition these cordgrasses are an important food resource for benthic invertebrates (Silliman and Bortolus, 2003; Bortolus et al., 2004) and a source of detritus and litter for the environment (Vera et al., 2009). Thus, two different mechanisms may influence faunal pattern within S. densiflora patches, those generated by its biological properties and those caused or mediated by the physical structure supplied by them.

In the Patagonian rocky salt marshes (sensu Bortolus et al., 2009), this halophyte creates highly heterogenous intertidal habitats occupied by several invertebrate species, including the invasive barnacle Balanus glandula Darwin 1854 (Schwindt et al., 2009; Sueiro et al., 2011). This barnacle, native to the rocky shores of the Pacific coast of North America, was introduced to Argentina more than 40 years ago and has spread over 17 latitudinal degrees southward up to Tierra del Fuego Island (Schwindt, 2007). B. glandula has established along most of the Argentine coast showing a remarkable versatility in recruitment, colonizing not only in typical rocky shores but also soft-bottom salt marshes (Schwindt, 2007; Schwindt et al., 2009; Mendez et al., 2013). In rocky shores, the highest density of adults and recruits occurred on sedimentary substratum (Savoya and Schwindt, 2010). In salt marshes, barnacles utilize more than 10 different types of substrata to recruit, by settling on salt marsh plants and exploiting additional hard substrata like stones, cobbles, trash, mussels and other organisms present (Schwindt et al., 2009; Mendez et al., 2013). This barnacle is also considered an autogenic engineer species, capable of drastically change the physical structure, complexity, and heterogeneity of the environment (review in Barnes, 2000). A large variety of organisms use the micro-habitats generated by barnacles to settle and/or avoid predation and desiccation (Farrell, 1991; Schubart et al., 1995; Barnes, 2000; Harley, 2006). In Patagonian salt marshes, B. glandula groups together to form three-dimensional structures of large sizes (aggregates) which are used by the rest of the macrofauna to avoid thermal stress and predation (Mendez et al., 2012).

In the Patagonian rocky salt marshes, B. glandula is often co-dominant, in terms of relative cover, with native mussels and S. densiflora (Sueiro et al., 2011). This intertidal system offers an excellent opportunity to study the impact of a native ecosystem engineer organism on a non-native one. Thus, in this study we address the following specific questions: Does the native ecosystem engineer S. densiflora facilitate the invasion of rocky marshes by B. glandula? If so, how much of this facilitation is caused by its physical structure alone?

2. Materials and methods

2.1. Study system

Our fieldwork was carried out in Ambrosetti rocky salt marsh (42°50′S, 64°50′W, Patagonia, Argentina). Rocky salt marshes develop on top of wave-cut platforms of sedimentary rock and are dominated by a dwarf ecotype of the austral cordgrass Spartina densiflora (the Patagonian ecotype; see Bortolus, 2006; Fortuné et al., 2008; Bortolus et al., 2009). In Ambrosetti, S. densiflora occupies the middle-high intertidal (~3.50 m above the Argentine hydrographic zero) along a fringe approximately 30 m wide and 370 m long, and covers about 40% of the substrate. The density of S. densiflora is 14 stems·100 cm^{-2} (SD ± 2). Its compact mat of roots and rhizomes has an average thickness of 6.2 cm (SD ± 0.7), and is covered by a dense bed of the small native mussels Brachidontes purpuratus (Lamarck, 1819) and Brachidontes rodriguezii (d'Orbigny, 1846). This habitat engineered by S. densiflora is also occupied by several other invertebrate species, including the invasive acorn barnacle B. glandula (Sueiro et al., 2010). The climate in the region is mostly arid (precipitation < 200 mm yr^{-1}), annual temperatures ranging from −7.5 °C to 39 °C, and strong, cold winds predominantly from the southwest with a mean annual speed of 22 km h^{-1} and gusts that may exceed 100 km h^{-1} (Frumento and Contrera, 2011).

2.2. Experimental design

We established a set of cordgrass manipulation and control plots in the rocky salt marsh to determine whether the native ecosystem engineer Spartina densiflora is able to facilitate the invasion of rocky marshes by another ecosystem engineer, the acorn barnacle B. glandula, and to quantify the effect caused by the plant's physical structure, as opposed to its biological properties. We randomly positioned plots of transplanted cordgrass, artificial cordgrass, and controls across the study site. Plots were 25 × 25 cm and placed in the middle-high intertidal with a minimum distance of 20 m between them, covering all the extension of the rocky salt marsh. For transplanted cordgrass treatments (hereafter "Spartina transplant", Fig. 1A) ten clumps of S. densiflora were removed from the marsh and carefully defaunated by hand under dissecting magnifier and keeping the plants always wet at the laboratory. All clumps were then transplanted back to the marsh and pinned down with stakes of 10 cm in plots from which macrofauna had been removed using a metal scraping tool. Artificial cordgrass treatments (hereafter "Spartina mimic", Fig. 1B) were inert plastic models (n = 10) resembling the physical structure of S. densiflora. Each Spartina mimic was constructed on a 25 × 25 cm rigid plastic grid (mesh size = 2 × 2 cm). Over this grid, a plastic cable of 0.5 cm diameter
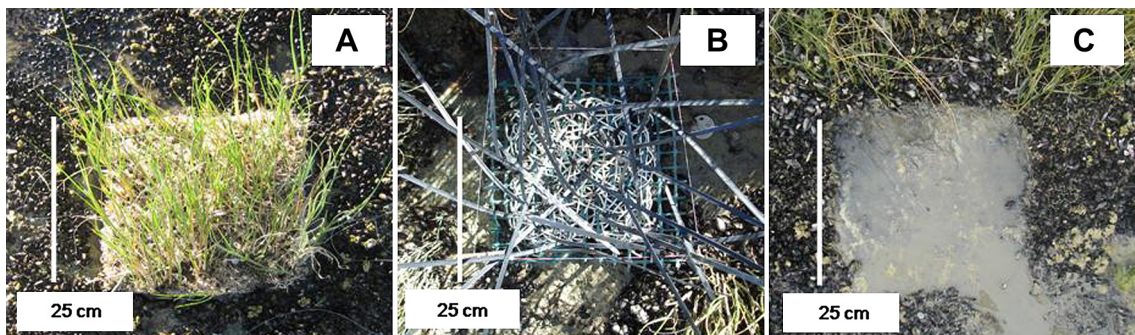

Fig. 1. Treatments plots placed in the rocky salt marsh at the beginning of the experiment (A) Spartina transplant (B) Spartina mimic and (C) control plots.

was interwoven simulating the thick and compact mat of *S. densiflora* roots and rhizomes. Forty plastic leaf-like structures (40 cm height, 0.5 cm width) were then attached around the mimics to recreate *S. densiflora*'s physiognomy. The *Spartina* mimics were pinned down with stakes to parcels of substratum previously scraped clean, as described above. Control plots were ten parcels (25 × 25 cm each, Fig. 1C) scraped clean as described above. After one year, all treatment plots were removed and transported to the laboratory. *Spartina* transplant and *Spartina* mimic were collected and control plots were removed by scraping the substrate. Additionally, ten *Spartina* samples (25 × 25 cm each; hereafter "natural *Spartina*") were collected at random from the marsh in order to quantify and compare the similarity between the experimental and the natural scenarios.

2.3. Sample and data analysis

At the laboratory we registered barnacle density; barnacle size, size frequency distribution and the percentage of barnacles attached on different types of substrate. For barnacle density, we counted the number of barnacles per plot under a stereomicroscope (80×). For barnacle size, barnacles were randomly chosen from treatments and we measured the orifice length along the carinal and rostral plates with digital caliper (precision ± 0.01) ($n = 200$ for each treatment, excepting controls where a total of 184 barnacles were found). In order to estimate the percentage of barnacles attached on different types of substrate, we identified the type of primary substrate where each barnacle was attached.

One-way fixed ANOVAs were used to test for differences among treatments in mean total abundance of barnacles. Normality and homogeneity of variance assumptions were evaluated with Kolmogorov–Smirnov and Levene tests, respectively. Significant results were analyzed a posteriori with the Unequal N HSD (Zar, 1999). On the other hand, given that variances were heterogenous and could not be stabilized after different transformations, the nonparametric Kruskal–Wallis was used to test for differences among treatments in mean size of barnacles and significant results were analyzed with multiple comparisons of mean ranks (Zar, 1999). Considering the potential undesirable consequences of taxonomic misidentifications (Bortolus, 2008), we requested the assistance of taxonomic specialists for each taxon. A voucher of each specimen collected was deposited in the CENPAT invertebrate collection (http://www.cenpat.edu.ar).

3. Results

After one year, all the treatments in the experiment were colonized by the barnacle *B. glandula,* by forming aggregates of densely packed individuals. The maximum mean density was found in natural *Spartina* plots (273 ± 191 individuals per plot); while the minimum was observed in control plots (without *Spartina*) (19 ± 27 individuals per plot). These results show that plant structures led to a maximum increment of more than 1700% relative to the nonvegetated plots. The mean density was significantly different among treatments (ln [$x + 1$] transformed, $F = 23.78$, $df = 3$, $P < 0.001$, Fig. 2A). *Spartina* transplant, *Spartina* mimic, and natural *Spartina* plots showed higher densities than control plots (Unequal N HSD test, $P < 0.001$, Fig. 2A) while no differences in barnacle density were observed among the treatments containing *Spartina* (i.e., transplant, mimic or natural; Unequal N HSD test, $P > 0.05$ Fig. 2A).

Considering barnacles from all treatments, the mean size was 2.5 ± 1.3 mm with a minimum of 0.37 mm and a maximum of 6.86 mm. The size frequency distribution of *B. glandula* indicated that, in the *Spartina* transplant and mimic treatments, barnacles
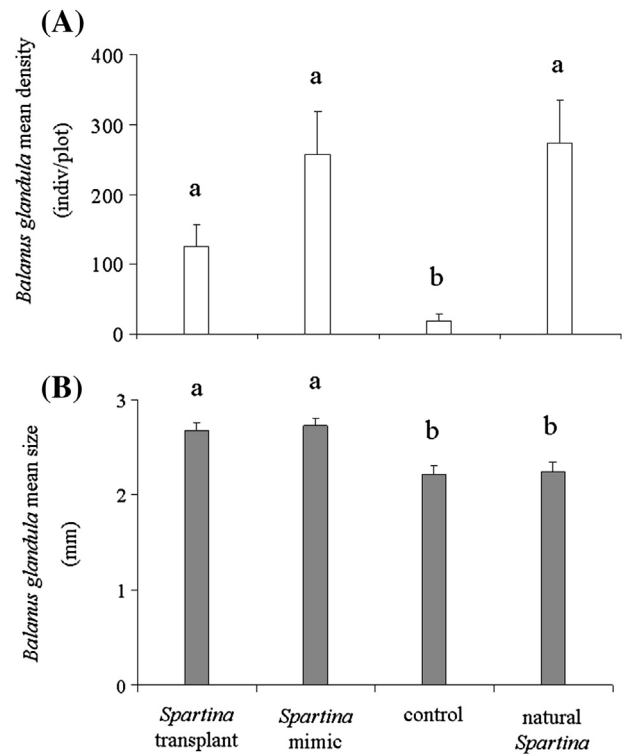

Fig. 2. (A) Mean density (+SE) and (B) mean size (+SE) of *Balanus glandula* found on the different treatments. Different letters above bars indicate significant differences among treatments (Unequal N HSD test or multiple comparisons of mean ranks $P < 0.05$).

tended to be represented by individuals of medium size while in the control and natural *Spartina* plots they were relatively smaller (Fig. 3). The mean size of barnacles was significantly different among treatments ($H = 32.08$, $df = 3$, $P < 0.001$; Fig. 2B). The multiple comparisons of mean ranks showed that *Spartina* mimic and *Spartina* transplant plots had a larger mean size of barnacles living within them than natural *Spartina* and control plots ($P < 0.001$; Fig. 2B).

We identified the following types of primary substrate where barnacles were attached: mussels, shells (which include shells of the blue mussel *Mytilus edulis* Linnaeus, 1758, native mussels *Brachidontes purpuratus* and *B. rodriguezii*), gravels, roots and bare rock. Due to the experimental design, bare rock was only available in control treatments. For all treatments, we found that over 50% of barnacles were attached to mussels and also found a large percentage on other shells (Fig. 4). Finally, among the treatments with *Spartina,* only in transplant plots we found a small percentage of barnacles (28%) attached to its roots (Fig. 4).

4. Discussion

Understanding what facilitates the invasion of non-native organisms is an important theoretical and practical goal (Carlton, 1999). The better we know the ecological processes underlying a given invasion, the better our chances of predicting where and when the invasion is likely to happen again locally or globally. In this work we examined if a native ecosystem engineer (the austral cordgrass *Spartina densiflora*) facilitates the invasion of a marine intertidal invertebrate (*B. glandula*) and we found that the presence of *Spartina*, indeed, promotes the colonization by the invasive *B. glandula*. Moreover, we observed that the nature of this positive
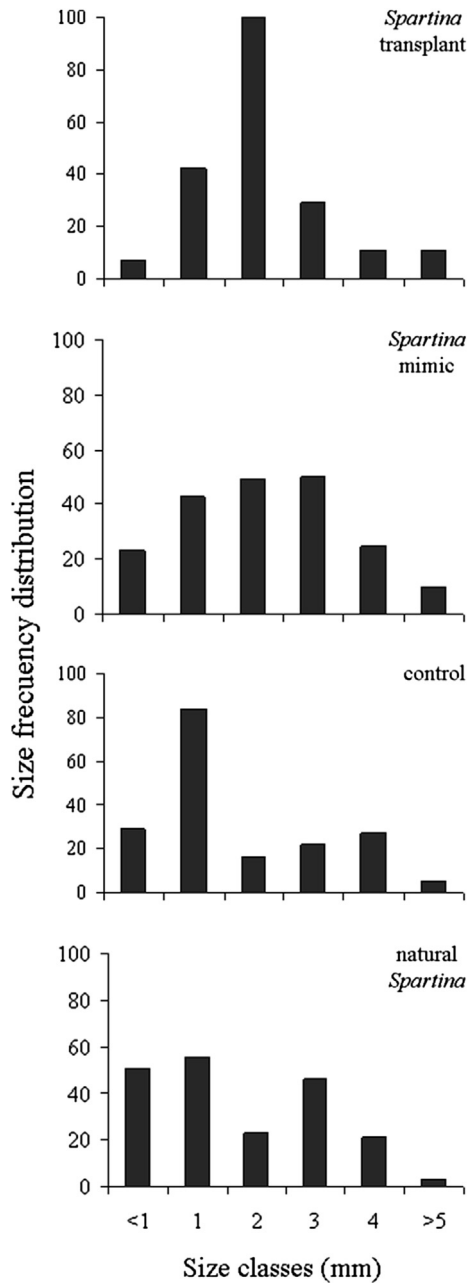
Fig. 3. Size frequency distributions of barnacles per class size (in mm) found in *Spartina* transplant, *Spartina* mimic, natural *Spartina* and control treatments.

Fig. 4. Percentage of *Balanus glandula* attached on different types of substrate in natural *Spartina* ($n = 2694$), *Spartina* mimic ($n = 1911$), *Spartina* transplant ($n = 780$) and control ($n = 169$) plots.

effect of *S. densiflora* on the barnacles is largely physical, and it appears to be independent of *Spartina*'s biological properties.

The mechanisms by which this facilitation occurs on *B. glandula* might be related to the mitigation of physical stressors exerted by the physical structure provided by *Spartina*. In this sense, heat and dehydration stress are among the most critical forces that affect the larval settlement and adult survival of *B. glandula* (Lohse, 1993; Menge and Branch, 2001; Gedan et al., 2011). Thus, the shelter supplied by plant structure can attenuate these stressful conditions (Bortolus et al., 2002; Canepuccia et al., 2007) creating a favorable micro-habitat for the establishment of this nonnative barnacle. The recruitment of *B. glandula* could be on *Spartina* surface (Schwindt et al., 2009) as well as on any suitable substrate trapped by the plant structures (Mendez, 2013). In fact, it has been proposed that ecosystem engineers inha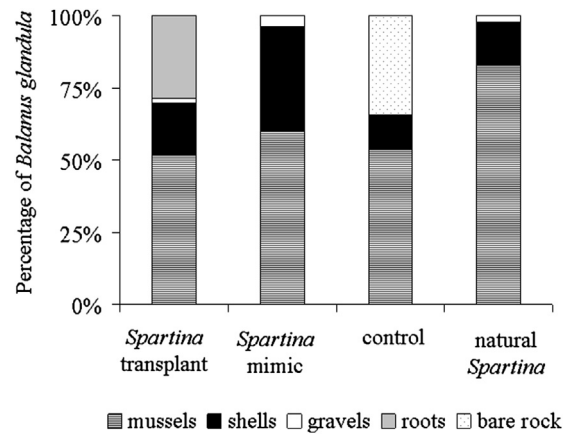biting stressful environments can facilitate the colonization, persistence or survivorship of invaders, and may generate a hot spot for successful invasive species (Badano et al., 2007; Bulleri et al., 2008).

In addition, standing structures like *Spartina* trap, retain, and stabilizes inert particles (organic and inorganic), as well as living organisms, providing substrates for invertebrate attachment (Netto and Lana, 1999; Bos et al., 2007; Sueiro et al., 2011). After one year, our experimental plots containing plant structures (living and mimic) became visually (and statistically) identical to the surrounding vegetated areas (natural *Spartina*), characterized by a thick carpet of mussels covering the bottom, many of which in turn were covered with barnacle aggregations. This result was likely due to the trapping and stabilization effect exerted by plant structure, especially on those mussels that were dislodged by waves from surrounding areas. Thus, plant structures may facilitate the invasion of this barnacle via a facilitation cascade (*sensu* Altieri et al., 2007). In this cascade, *Spartina* facilitates mussels which, once within the cordgrass bed, enhance physical conditions and provide crevices and hard substrate for barnacles to attach on. However, taking into account the duration of the experiment, the fact that some of the barnacles actually attached to mussel were more than 1 year old (following Savoya, 2006; Savoya and Schwindt, 2010) suggests that the individuals were not recruited (i.e., larval settlement) within experimental plots. This result also would explains why *B. glandula* was so scarce on scraped control plots. Therefore, *Spartina* structure is likely to be facilitating the introduced *B. glandula* by reducing the death or loss of mature individuals that were dislodged together with the substrata where they originally recruited.

The invasive acorn barnacle *B. glandula* is currently expanding its distributional range worldwide. First, it was reported in the Argentinean coast (Spivak and L'Hoste, 1976; Schwindt, 2007) and few years later on rocky shores along the west coast of Japan (Kado, 2003) and later in South Africa (Simon-Blecher et al., 2008). After its introduction in the Argentinean coast, this species has shown a remarkable high ecological plasticity, being capable of colonizing not only the typical rocky shores but also exploiting a variety of hard substrata to persist on unusually environments, like salt marshes (Schwindt et al., 2009; Sueiro et al., 2011; Mendez et al., 2013). Our results highlight the idea that complex relationships between barnacles and the native community, such as facilitation cascade processes, are taking place in this invaded region. Considering that this species is a key ecosystem engineer along its native distribution range (Farrell, 1991; Schubart et al., 1995;

Barnes, 2000; Harley, 2006), we predict that the facilitation of *B. glandula* may in turn affect the distribution and abundance of several native species as recently reported for the invertebrate assemblages of the Patagonian salt marshes (Mendez, 2013).

In this study we found that a native ecosystem engineer, the austral cordgrass *Spartina densiflora*, might facilitate the invasion, and/or the local spread of the nonnative acorn barnacle *B. glandula.* Although we can speculate about potential pathways by which this interaction takes place, it is necessary to perform experiments in order to accurately elucidate the exact mechanisms underlying this process of facilitation. Nevertheless, it could be thought that native intertidal vascular plants will favor local invasions elsewhere. Given that many emergent plants, including seagrasses, sea-palm algae, *Spartina* and *Phragmites* grasses, *Sarcocornia* and *Salicornia* bushes, and several mangrove trees are common in intertidal systems worldwide (Chapman, 1977; Ricketts et al., 1985; Seeliger, 1992; Adam, 1993; Mitsch and Gosselink, 2000; Bertness et al., 2001), more inter-regional integrated efforts should be directed to explicitly address this ecological problem at global scale.

Acknowledgments

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