Crab bioturbation and herbivory reduce pre- and post-germination success of *Sarcocornia perennis* in bare patches of SW Atlantic salt marshes

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ABSTRACT: Colonization of bare patches is a key process during community development given that pioneers usually have positive and negative effects on the forthcoming species. A variety of biotic and abiotic factors influence the process of colonization of bare patches. In salt marshes, however, the emphasis has been on abiotic factors and plant–plant interactions, while comparatively little attention has been paid to the role of plant–animal interactions in the successful colonization by pioneer plants. Thus, the goal of the present study was to evaluate whether bioturbation and herbivory by the burrowing crab *Neohelice* (*Chasmagnathus*) *granulata* affected the number of seedlings of the pioneer plant *Sarcocornia perennis* in SW Atlantic salt marshes. To evaluate this, we conducted an experiment using exclosures deployed at different times (post-dispersal and post-germination). The results showed that post-germination exclosures had 62% fewer seedlings than post-dispersal exclosures but 8 times more than plots always accessible to crabs. We also used glass beads to experimentally evaluate the potential effect of crab bioturbation on seed availability, and we used 1 yr old transplants to evaluate whether herbivory could explain post-germination mortality. Crab bioturbation reduced the number of glass beads on the surface by 56%, and transplants were highly consumed when crabs were present. These results suggest that seed burial by bioturbation exerts a pre-germination control while herbivory exerts a post-germination control. The results also highlight the importance of considering biotic factors when analyzing the success of marsh plants colonizing bare surfaces.

KEY WORDS: Bioturbation · Herbivory · Burrowing crabs · *Neohelice granulata* · *Sarcocornia perennis* · Salt marsh

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INTRODUCTION

One of the key processes during community development (in both primary and secondary successions) is the colonization of empty spaces, as pioneer species usually have profound positive or negative effects on forthcoming species (e.g. Connell & Slatyer 1977). Among the more common negative effects is competition for space between early and late successional species (Huston & Smith 1987). The positive effects that colonizers of bare surfaces can have on the late successional species generally include reducing otherwise harsh abiotic or biotic conditions (e.g. salinity: Bertness 1991; desiccation: Bortolus et al. 2002; low-nutrient conditions: Walker et al. 2003; herbivory: Alberti et al. 2008). However, a variety of biotic and abiotic factors can affect these pioneer species and thus retard community development (e.g. Connell & Slatyer 1977, Farrell 1991). For example, herbivory upon colonizer plants (that facilitate the establishment of other spe-

cies) ended up reducing a primary succession after a volcanic eruption (Fagan & Bishop 2000). Also, ecosystem engineering processes (sensu Jones et al. 1994), such as bioturbation caused by shrimp, can reduce the colonization of bare patches by invasive seagrasses (Dumbauld & Wyllie-Echeverría 2003).

In salt marshes, pioneer plant species that colonize bare areas (generally by seeds) (Bertness & Ellison 1987, Bertness et al. 1992, Pennings & Bertness 2001) play a key role in the dynamic of these areas, facilitating the establishment of competitively dominant species, ultimately leading to the final closure of these patches (Bertness 1991, Pennings & Bertness 2001). Bioturbation can also exert strong influences on the dynamic of bare areas. For example, burrowing crabs can promote erosion in some marshes (Escapa et al. 2007), and polychaetes can dramatically reduce the colonization of tidal flats (Paramor & Hughes 2005). Recent evidence also shows the relevance of herbivory in marshes, being particularly important in the maintenance and expansion of bare areas (e.g. Silliman et al. 2005, Jefferies et al. 2006). However, when studying the process of colonization of bare areas, the emphasis has been on abiotic factors and plant–plant interactions, while comparatively less attention has been paid to the role of herbivores and bioturbators.

The SW Atlantic (from southern Brazil to northern Argentinean Patagonia) salt marshes are mainly vegetated by *Spartina densiflora*, *Spartina alterniflora*, and *Sarcocornia perennis* (e.g. Isacch et al. 2006). In some of these marshes, the presence of *Sarcocornia perennis* is essential to the successful establishment of *Spartina densiflora* (Alberti et al. 2008). The burrowing crab *Neohelice (Chasmagnathus) granulata* is the dominant herbivore in the lowest reaches of these marshes (Bortolus & Iribarne 1999, Alberti et al. 2007a). Simultaneously, this crab is an important bioturbator capable of removing up to 2.4 kg m^{-2} d^{-1} of marsh sediment to create and maintain burrows (Iribarne et al. 1997). Its burrowing activity can have positive or negative effects on marsh plants depending on the environmental context (Daleo & Iribarne 2009). Crabs oxygenate the fine-grain sediments, facilitating the colonization of *Spartina densiflora* roots by arbuscular mycorrhizal fungi leading to increased plant productivity (e.g. Daleo et al. 2007). However, in certain coastal areas, they accelerate the expansion rate of tidal channels, increasing erosion in a *Sarcocornia perennis* salt marsh (Escapa et al. 2007).

In this context, the general goal of the present study was to evaluate the impact of herbivory and bioturbation by *Neohelice granulata* on the recruitment and survival of *Sarcocornia perennis* seedlings. In particular we evaluated whether: (1) crab presence reduced the number of *S. perennis* seedlings; (2) this effect was

pre- and/or post-germination; (3) seed burial could explain the pre-germination effect; and (4) herbivory was capable of increasing post-germination mortality of up to 1 yr old seedlings.

MATERIALS AND METHODS

Study sites. This study was conducted at 2 coastal lagoon salt marshes at Mar Chiquita, Argentina, (37° 44′ 20″ S, 57° 25′ 20″ W; 37° 44′ 57″ S, 57° 26′ 09″ W), and one at Bahía Blanca, Argentina, (38° 44′ 02″ S, 62° 19′ 07″ W) between April 2004 and August 2008. These marshes are irregularly flooded (10 to 15 times per month), and they are mainly vegetated by *Spartina densiflora*, *Spartina alterniflora*, and *Sarcocornia perennis* (Isacch et al. 2006), and densely populated by the burrowing crab *Neohelice granulata* (Bortolus & Iribarne 1999, Alberti et al. 2007a). At these sites, the first to colonize the mudflat is *Sarcocornia Perennis*, which grows in circular patches and facilitates the establishment of seedlings of the competitively dominant *Spartina densiflora* by reducing the impact of crab herbivory (Alberti et al. 2008). Each of the areas occupied by these 2 species extends for >600 m parallel to the shore, and is located on the edge between the *Spartina densiflora* marsh and the tidal flat. In these areas, there are up to 60 crabs m^{-2} (Botto et al. 2005), and >75% of the surface remains unvegetated.

Role of crabs in control of *Sarcocornia perennis* seedling abundance. To evaluate whether crab presence reduced the number of *Sarcocornia perennis* seedlings, we established 10 plots at unvegetated areas (50 × 50 cm) at each of the 2 Mar Chiquita marshes and 20 plots at the Bahía Blanca marsh, directly following seed dispersal (during April 2004). Half of the units per site were assigned to control (unmanipulated) treatments, while the other half were assigned to crab exclosures (n = 5 per treatment at both Mar Chiquita marshes, and n = 10 at Bahía Blanca). Crab exclusion plots were surrounded by a 1 cm plastic mesh fence 40 cm high. Gastropods (Canepuccia et al. 2007) and all other invertebrates in the marsh easily passed through the mesh (A. Canepuccia & O. Iribarne unpubl. data). Even though vertebrate herbivores could be excluded by the cages, rodents forage at higher intertidal levels (A. Canepuccia & J. Alberti unpubl. data). Fish could also be excluded, but there are no herbivorous fish in this system (Cousseau et al. 2001). And although *Micropogonias furnieri* and *Pogonias cromis* can sometimes bioturbate the intertidal sediment when looking for prey, it occurs at much lower intertidal elevations (P. Martinetto pers. comm.). After 4 mo (August 2004) we counted the number of *S. perennis* seedlings per plot and compared the number

of seedlings between treatments using a *t*-test for unequal variances (Welch approximation t_c) for each site. The t_c is equal to the *t* value when sample sizes are the same, but degrees of freedom decrease as the difference between variances of the 2 groups increases (Zar 1999).

Pre- and post-germination effects. The negative impact of crabs on seedlings could be due to pre- and/or post-germination effects. To investigate these possibilities, we conducted another experiment at one Mar Chiquita marsh during 2005. We identified 20 plots at unvegetated areas (50 × 50 cm) directly following seed dispersal that were randomly assigned to the following treatments (n = 5): (1) post-dispersal exclosures (fences as described above, deployed directly following seed dispersal); (2) post-germination exclosures (deployed right after early seed germination); (3) cage controls (3 sided fences deployed right after seed dispersal); and (4) controls (unmanipulated plots). In August we counted the number of *Sarcocornia perennis* seedlings per plot, and finally we compared the number of seedlings between treatments using an ANOVA on log-transformed data (Zar 1999). Here and henceforth we used Tukey's test after significant ANOVA for *a posteriori* contrasts (Zar 1999).

Role of seed burial in pre-germination control. Bioturbators can affect seedling densities by burying seeds (Paramor & Hughes 2005). To evaluate whether this could be occurring in our system, we conducted an experiment using glass beads at one Mar Chiquita marsh. We established 15 unvegetated plots (50 × 50 cm) after seed dispersal that were randomly assigned to Treatments (1), (3) and (4), described in the subsection above (n = 5). On the surface of each plot we evenly distributed 65 g of glass beads, the most similar to seeds in size and weight that we could find (mean ± SD glass bead size: 0.575 ± 0.076 mm diam.; glass bead weight: 2.281 ± 0.269 mg; seed size: 0.988 ± 0.052 mm; seed weight: 0.969 ± 0.043 mg). In August we collected samples from the sediment surface of each plot (5 cm diam. × 0.5 cm deep), then we sieved the samples and counted the number of glass beads per sample under 10× magnification. Finally we compared the number of glass beads between treatments using an ANOVA (Zar 1999). Given the differences in size and weight between beads and seeds, the results will only be used to show whether seed burial is a plausible mechanism.

Role of herbivory in post-germination control. To evaluate whether crab herbivory can reduce the survival of *Sarcocornia perennis* seedlings, we performed an experiment using transplants and exclosures at one Mar Chiquita salt marsh. We selected 40 *S. perennis* plants (approx. 1 yr old) from an adjacent and higher zone (without crabs), and we ran-

domly assigned them to the following treatments (n = 10 per treatment): (1) control (unmanipulated plants); (2) transplant control (plants extracted and put back in); (3) with crabs (transplants moved to the experimental site described above, this paragraph); and (4) crab exclosures (transplants moved to the experimental site and surrounded by fences as explained in the above subsections). Transplants and the surrounding sediment (10 × 10 × 10 cm) were carefully extracted using a shovel. The experiment started in September and lasted 2 wk, including the spring tides (because crabs consume plants mostly when under water) (Alberti et al. 2007b). At the end of this experiment we measured the maximum height and the number of branches of each transplant, and finally we compared both dependent variables between treatments using ANOVAs (one for each dependent variable) (Zar 1999).

RESULTS

Role of crabs in control of *Sarcocornia perennis* seedling abundance

Crab presence reduced the number of *Sarcocornia perennis* seedlings by around 60% at Bahía Blanca (t_c = 2.8, df = 16, p < 0.05), and between 90% (t_c = 4.2, df = 4, p < 0.05) and 95% at Mar Chiquita (t_c = 5.66, df = 4, p < 0.01; Fig. 1).

Pre- and post-germination effects

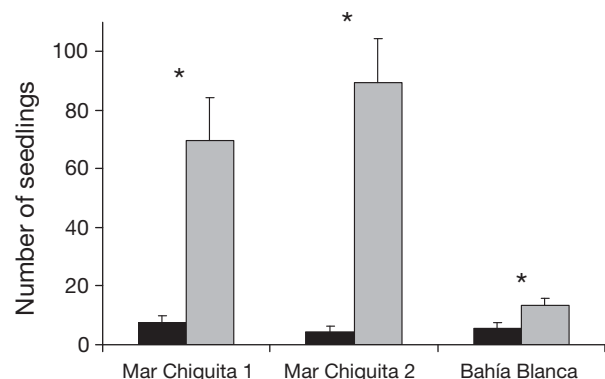Post-dispersal and post-germination exclosures revealed that crabs reduced the number of seedlings at

Fig. 1. *Sarcocornia perennis.* Number of seedlings per experimental plot (0.25 m²) in controls (black) and crab exclosures (gray) at 2 marshes at Mar Chiquita and 1 at Bahía Blanca. *Significant differences (p < 0.05) between treatments for a given study site. Data are mean + SE; data is shown prior to transformations

both instances. Post-germination exclosures showed 62% fewer seedlings than post-dispersal exclosures, while control and cage control plots showed 88% fewer than post-germination and 95% fewer than post-dispersal exclosures ($F_{3,16}$ = 21.72, p < 0.001; Fig. 2).

Role of seed burial in pre-germination control

Crab presence and bioturbation activity strongly reduced the number of glass beads on the top 0.5 cm of the sediment. On average, controls and cage controls showed 56% fewer glass beads than exclosures ($F_{2,12}$ = 5.95, p < 0.05; Fig. 3). There were no differences in the number of glass beads between control and cage control treatments (Tukey's test: p = 0.89; Fig. 3).
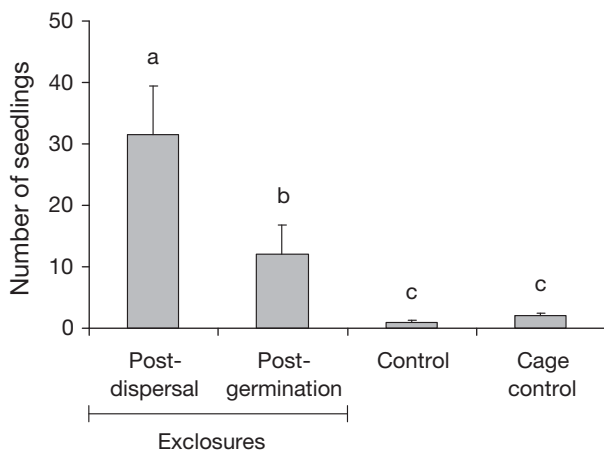

Fig. 2. *Sarcocornia perennis.* Number of seedlings per experimental plot (0.25 m²) with and without exclosures deployed after seed dispersal and after seed germination. Different letters denote significant differences between treatments. Control: unmanipulated plot; cage control: 3-sided fences deployed
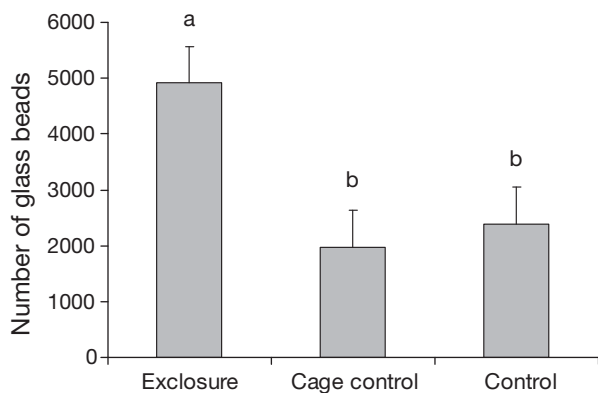

Fig. 3. *Sarcocornia perennis.* Number of glass beads in the top layer (0.5 cm) of the sediment in plots with exclosures, without (control), or cage controls (3 sided fences).

Role of herbivory in post-germination control

The experiment using transplants showed that crab herbivory can strongly affect the survival of seedlings up to 1 yr old. After only 15 d, crab herbivory reduced the maximum height of transplants by approx. 63% and the number of branches by approx. 83% (respectively, $F_{3,36}$ = 4.16, p < 0.05; $F_{3,36}$ = 14.89, p < 0.001; Fig. 4). There were no differences between control and transplant control treatments either in height (Tukey's test: p = 0.94; Fig. 4) or in the number of branches (Tukey's test: p = 0.98; Fig. 4). In fact, only 3 out of 10 transplants without exclosures were alive after those 2 wk, while 9 out of 10 survived inside exclosures.

DISCUSSION

Our results show that the crab *Neohelice granulata* can dramatically reduce the number of *Sarcocornia perennis* seeds that germinate, as well as their subsequent survival, by both bioturbation and herbivory. Results suggest that the mechanism involved in the control of seedlings after seed dispersal and before germination is seed burial by bioturbation, and that post-germination control involves herbivory. The study of these processes is of crucial importance to understand marsh functioning given that (1) many marshes are inhabited by bioturbators (e.g. Bertness 1985, Iribarne et al. 1997, Paramor & Hughes 2004, Jefferies et al. 2006); and (2) pioneer plants (such as *S. perennis*) play a key role in the dynamics of disturbance-generated patches (Bertness & Ellison 1987) usually by
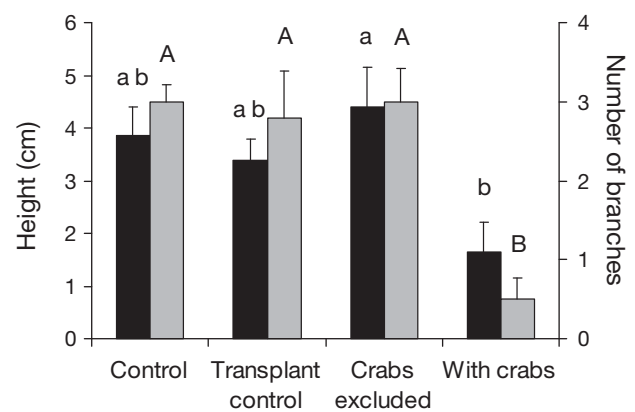

Fig. 4. *Sarcocornia perennis.* Maximum height (black) and number of live branches per plant (gray) in control (unmanipulated; high zone without crabs), transplant control (extracted and put back in; high zone without crabs), with crabs (transplanted to the experimental site), and crabs excluded (transplanted to the experimental site but with crabs excluded using a plastic fence) treatments. Letters denote significant differences between treatments comparing transplant height (lowercase letters) and number of branches (capital letters)

reducing physical stress and thus permitting the course of successions and closure of these patches (Bertness 1991, Pennings & Bertness 2001).

Potential effects of bioturbators on the germination and seedling survival of marsh plants

Many marshes throughout the world are inhabited by bioturbators. The polychaete *Nereis diversicolor* is found in Northern Europe and is an important source of mortality and erosion of *Salicornia* spp. salt marshes (Paramor & Hughes 2004, but see Morris et al. 2004). And it has been suggested that they can delay the colonization of bare surfaces through seed burial (Paramor & Hughes 2005). In Canada, when grubbing for roots and rhizomes, the lesser snow geese *Chen caerulescens caerulescens* destroy all vegetation cover and heavily disturb the sediment, producing extensive bare grounds that remain unvegetated for several decades (Jefferies et al. 2006). But bioturbators can also positively affect marsh plants: along the East Coast of United States, the fiddler crab *Uca pugnax* increases the productivity of *Spartina alterniflora* by oxygenating the sediment with their burrows (Bertness 1985). Similarly, the increased oxygenation caused by *Neohelice granulata* burrows is a possible cause of increased production of seeds by *Spartina densiflora* (Bortolus et al. 2004), and also facilitates the colonization of *Spartina densiflora* roots by mycorrhizal fungi, leading to higher plant productivity in southwestern Atlantic marshes (Daleo et al. 2007).

Sexual reproduction of marsh plants is considered to be unimportant for system functioning (Pennings & Bertness 2001). However, in certain contexts, such as the revegetation of large bare patches (Bertness 1991, Pennings & Bertness 2001) or the invasion of new habitats (suggested by Castillo et al. 2000), sexual reproduction can play an essential role. So much so that some marshes seem to be limited by the number of seeds, given that the artificial addition of seeds led to increased plant cover (Rand 2000). However, harsh abiotic conditions such as salinity or desiccation can dramatically reduce seedlings' success (Bertness et al. 1992, Bertness & Yeh 1994), and that is why positive interactions are so important during these early stages of development (Bertness & Yeh 1994, Callaway & Walker 1997). The present study highlights the importance of considering biological stress factors when analyzing the success of the sexual reproduction of marsh plants, especially if we take into account that many marshes throughout the world are inhabited by bioturbators that can have profound impacts on the dynamics of these systems.

Our results do not allow us to disentangle whether the pre-germination effect is due to bioturbation and/or seed predation. However, the mounds produced by crabs, when they create and maintain burrows, contain a larger amount of *Spartina densiflora* seeds than the surrounding area (Canepuccia et al. 2008), suggesting that seed predation may not be very intense. This evidence, coupled with our experimental results showing that burial can be very important, makes us believe that most of the pre-germination effect is due to bioturbation and not due to seed predation. However, further experiments are needed to confirm this process.

Bioturbation, herbivory, and succession dynamics in bare areas

Connell & Slatyer (1977) identified 3 models of succession during community development where early successional species can have either a positive (facilitation), neutral (tolerance), or negative (inhibition) effect on the establishment of later species. Regardless of the model, the current conception of plant secondary succession explains successional patterns as an effect of competitive replacement of colonizing species (i.e. fast-growing, high dispersers are the first to colonize disturbed zones but, after some time, they are replaced by slow-growing, competitively superior species that do not disperse so effectively; see Huston & Smith 1987, Tilman 1988). This bottom-up conception of secondary succession is based on the trade-offs between dispersion capacity and competitive capacity (Tilman 1988). Nevertheless, there is growing evidence that consumers can have great effects on plant successions (Schmitz et al. 2006), thus affecting plant community structure and species diversity (Buschmann et al. 2005). The impact of herbivores on the succession rates and community development varies depending on herbivore preferences and the succession model (Farrell 1991). Selective foraging can greatly decrease the biomass of target species and, when competitively superior species are preferred, herbivory is expected to slow down the succession (Farrell 1991) and to increase plant diversity by creating temporal gaps or decreasing dominant plant growth, preventing less competitive species from being overgrown (Olff & Ritchie 1998).

In related systems such as rocky shores, mangroves, and marshes, for example, herbivores can determine the final composition of species in those formerly bare areas (Farrell 1991, Clarke & Kerrigan 2002, Bromberg Gedan et al. 2009). In addition to herbivory, bioturbation can also have profound impacts during the course of successions that start in bare areas. In seagrass beds and marshes, bioturbation can prevent plant colonization of bare areas, acting mostly during the seedling phase (Dumbauld & Wyllie-Echeverría 2003, Paramor & Hughes 2005). Similarly, in our study system, *Sarco-*

cornia perennis colonizes the mudflat and facilitates the establishment (through seedlings) of the competitively dominant *Spartina densiflora* by reducing the impact of crab herbivory (Alberti et al. 2008). This facilitative succession is essential for the expansion of the *Spartina densiflora* marsh onto the mudflat, as the asexual expansion is extremely slow due to a combination of both physical stress and crab herbivory (Alberti et al. in press). However, these results are not universal, as similar species in different environmental scenarios may not have the same impacts. For example, grazing has long been recognized as a key factor in the dynamic of bare areas along rocky shores (Farrell 1991); however, extremely harsh abiotic conditions can preclude grazing (Bertness et al. 2006). Similarly, in salt marshes, herbivory can prevent the colonization of bare areas by *Spartina densiflora* only when physical stress is not very intense (Alberti et al. in press).

Consequences of limiting pioneer plants

In environments of high biological or physical stress, pioneer plants usually play a key role for the rest of the community, facilitating the establishment of late-successional species (Connell & Slatyer 1977, Fagan & Bishop 2000, Pennings & Bertness 2001). For example, wrack deposition frequently occurs in marshes, killing the underlying vegetation and thus forming large bare patches (Brewer et al. 1998) that sometimes become hypersaline (Bertness 1991, Pennings & Bertness 2001). Asexual colonization of these bare patches is extremely slow (Bertness 1991), and then a fast closure can only occur when pioneer plants (tolerant to harsh abiotic conditions) colonize these patches and facilitate the establishment of other species through changes in the physical environment (Bertness & Ellison 1987, Bertness 1991). Northwestern Atlantic coastal marshes usually show these disturbance-generated patches that are completely recovered in a couple of years, largely due to the sexual reproduction of marsh plants (Bertness & Ellison 1987). However, at the middle marsh of the Mar Chiquita coastal lagoon, these patches can remain completely bare for more than 5 yr (J. Alberti unpubl. data). Even though the causes were not evaluated, it is possible that bioturbation combined with herbivory delays the recolonization of these bare patches. Analogous situations occur in many other stressful environments. For example, herbivore insects retard the expansion of a N-fixing pioneer plant at Mount St. Helens in the United States, delaying the recovery of the disturbed areas (Fagan & Bishop 2000). Along rocky shores, the consumption of colonizers affects the successional speed and can lead to completely different communities (Farrell 1991). Asexual

reproduction is not as efficient as sexual reproduction in the recovery of disturbed areas in physically stressful environments such as salt marshes (Pennings & Bertness 2001). Even though we did not evaluate it here, biological stress may reduce the efficiency of sexual reproduction, comparatively increasing the importance of not-so-efficient asexual reproduction, and thus delaying full recovery. Clearly, limiting the settlement of pioneer species has consequences than can go much further than the direct interaction between the bioturbator/ herbivore and the plant, given that it will probably affect the dynamic of the system.

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