

Biological and physical factors affecting the colonization of vegetation-free patches in a SW Atlantic salt marsh

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ABSTRACT: In many Northern Hemisphere salt marshes, recovery of disturbance-generated bare areas usually occurs within a few years. However, in some southwestern Atlantic marshes, bare patches may remain unchanged for several years. Here we investigated biological and physical factors that might affect bare patch colonization in a Mar Chiquita coastal lagoon salt marsh (Argentina). We evaluated natural seedling emergence of the pioneer pickleweed plant *Sarcocornia perennis*, considering distance to mature plants and the herbivory/bioturbation exerted by the crab *Neohelice granulata* (using exclosures). Almost no seedling emergence was observed in patches distant from mature plants, while higher emergence resulted in close patches. Crab exclusion did not affect seedling counts. Nevertheless, most of these seedlings did not survive high-temperature months. We analyzed if colonization was favored by increasing the availability of *S. perennis* seeds, and we found similar seedling emergence in patches both close and distant to mature plants. As in the previous experiment, most of them did not survive the high-temperature months, but some seedlings could establish within crab exclosures. Finally, we used a shade cloth to reduce solar radiation, but this did not increase seedling survival, which was only favored in crab exclosures. In summary, our results suggest that seed availability, followed by the presence of crabs (but not solar radiation), affect the rate of patch recovery. Additionally, our results show that life-history traits (seed ecology) of the colonizer can be a key and are a usually overlooked driver of salt marsh secondary succession.

KEY WORDS: Patch dynamics · Seedling emergence · Colonization · *Sarcocornia perennis* · *Neohelice (Chasmagnathus) granulata* · Seed dispersal · Bioturbation · Salt patches

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INTRODUCTION

The colonization of vegetation-free zones is considered one of the key processes in the development of communities where natural or anthropogenic disturbance has initiated a secondary succession (e.g. Odum 1969, Grubb 1977, Pickett & White 1985). A set of environmental filters that interact within differ-

ent temporal scales will determine successional dynamics in each system (Morin 1999). In this respect, a variety of biotic and abiotic factors may affect pioneer species development and therefore delay or accelerate the covering of bare areas (Connell & Slatyer 1977, Farrell 1991). The occurrence of natural disturbances which generate bare areas where a secondary succession starts is common in intertidal envi-

ronments (e.g. Pennings & Bertness 2001, Clarke 2004). Among the different factors involved in patch dynamics within intertidal communities, direct and indirect effects have been described for these systems, including positive (e.g. Bertness & Leonard 1997) and competitive interactions (e.g. Levine et al. 1998), influence of consumers (e.g. Lubchenco & Menge 1978), nutrient availability (e.g. Levine et al. 1998) and physical stress (e.g. Shumway & Bertness 1992).

Understanding the relative importance of the factors that regulate successional dynamics is essential for conservation and management purposes. Particularly in salt marsh communities, the deposition of dead plants transported by tides (i.e. wrack) promotes the mortality of the vegetation (Brewer et al. 1998), changing relative abundances and generating bare patches when the disturbance persists in the long term (Bertness & Ellison 1987). The colonization of these vegetation-free patches is strongly conditioned by the spatial variation in biotic and abiotic stressors characteristic of these systems, which generate spatial patterns that determine the structure of communities dominated by a small number of species (Chapman 1974, Shumway & Bertness 1992, Bertness & Hacker 1994). It has been observed that successional dynamics in post-disturbed areas in New England (USA) salt marshes involve a series of species that depend on these openings and that after colonizing those areas, they promote its closure in a period of about 3 yr (Bertness & Ellison 1987). The establishment possibilities of different species strongly depends on their location within the intertidal, which in turn determines the relative importance of the factors involved: salinity and flooding frequency (Shumway & Bertness 1992), propagule availability (Rand 2000), competition (Bertness & Hacker 1994), presence of consumers and bioturbators (Pennings & Bertness 2001). Commonly, after pioneer species colonize, they shade the surface and reduce the salinity stress, facilitating the invasion of less tolerant but competitively dominant species over relatively short periods of time (Bertness & Leonard 1997).

The biotic factors that may have significant effects on germination and seedling establishment of pioneer species include certain characteristics of these species as well as interactions with other species and the abiotic environment (Friess et al. 2012). The establishment of marsh plants through seedlings can be strongly reduced by the presence of herbivores and/or ecosystem engineers (Crain 2008, Gedan et al. 2009, Alberti et al. 2010a). For example, poly-

chaetes are known for their negative impact on seed availability and seedling survival of marsh pioneer species through herbivory and bioturbation (Paramor & Hughes 2004). In addition, crabs can bury seeds through their burrowing activities and at the same time maintain and expand bare patches by grazing on seedlings and new shoots (Alberti et al. 2010a, Daleo et al. 2011). Regarding characteristics of the pioneer species, the number of available seeds may play an important role in the colonization of bare areas. Indeed, experimental seed additions in southern New England salt marshes resulted in an increase in plant cover (Rand 2000). Different factors may limit the availability of seeds, including herbivory, sediment entrapment or tidal export (Shumway & Bertness 1992).

Among the abiotic factors that impose strong control on germination and seedling establishment of pioneer species, salinity plays a key role in delaying the time to germination or reducing the seedling fitness (Shumway & Bertness 1992). Commonly, bare patches tend to become hypersaline because of increased porewater evaporation (caused by the lack of shading by the vegetation), which in turn limits their colonization by pioneer species (Bertness et al. 1992). Seeds of halophytic plants have the capacity to sustain their viability and recover after being exposed to high salinities, allowing germination when the stress is relaxed (Freitas & Costa 2014). However, high variability exists between marsh plant species in their ability to germinate in high salt conditions (Khan et al. 2000). Moreover, as temperature and solar radiation increase in summer, desiccation and sediment salinity increase as well, contributing to the persistence of bare patches (Bertness 1991).

Succession models have been proposed for many salt marshes from the Northern Hemisphere, where the recovery of disturbance-generated bare areas occurs within 3 yr (Pennings & Bertness 2001). In the Southern Hemisphere, however, previous observations revealed that bare patches found on the southwestern (SW) Atlantic Mar Chiquita coastal lagoon (37° 44' S, 57° 26' W, Argentina) remain almost unchanged for more than 4 yr (Daleo et al. 2011). Thus, the aim of our study was to determine which biological and physical factors condition the colonization of bare patches in a SW Atlantic salt marsh. For this purpose, we evaluated the following hypotheses: (1) the number of seeds of the pioneer plant (*Sarcocornia perennis*) available on bare patches is not enough to overcome the environmental (i.e. abiotic and biotic) filters, (2) the herbivory and/or bioturbation pressure exerted by the intertidal crab *Neohelice granulata*

plays a key role in germination and seedling survival of the pioneer plant and (3) the physical stress imposed by desiccation is an important control in seedling survival.

MATERIALS AND METHODS

Study site

This study was conducted at the Mar Chiquita coastal lagoon, a UNESCO Man and the Biosphere reserve. Salt marshes within this area can be classified as SW Atlantic temperate marshes, which extend from southern Brazil (31° S) to northern Argentinean Patagonia (43° S; Isacch et al. 2011). The strong freshwater input from the basin in Mar Chiquita leads to the dominance of *Spartina densiflora*, relegating *Sarcocornia perennis* to isolated areas (Isacch et al. 2006). The Mar Chiquita lagoon presents semi-diurnal microtides with 0.79 m of tidal amplitude (Isacch et al. 2011). Lagoon salinity shows strong spatial variations, with a range of 0 to 35‰, depending on the considered area (Reta et al. 2001). Considering precipitation and temperature patterns, this area corresponds to a temperate subwet–wet system (Isla & Gaido 2001, Canepuccia et al. 2013). During the study period, the average monthly temperature was similar to the historical range, while precipitation was ~40% lower during the first 3 mo after *Sarcocornia perennis* germination (August to October) followed by months with higher than average precipitation (data from the Servicio Meteorológico Nacional Argentino for the Mar del Plata airport station, 37° 56' S, 57° 35' W, located 25 km south of our study site with similar geographic characteristics; Table S1 in the Supplement at www.int-res.com/articles/suppl/m531p033_supp.pdf).

The halophytic perennial shrub *Sarcocornia perennis* is distributed over different salt marshes around the world, including the southern and western coasts of Europe, the southern coasts of Africa, and Brazil, Uruguay and Argentina in the western Atlantic (Davy et al. 2006). This species is commonly found in SW Atlantic marshes colonizing vegetation-free patches and promoting the establishment of the competitively dominant species *Spartina densiflora* through reduced crab herbivory rates (*S. perennis* structure impedes crab access to *S. densiflora* leaves) at low intertidal elevations (Alberti et al. 2008). *Sarcocornia perennis* is able to preserve viability and germinate under high salinity conditions, even though germination is reduced with increasing salinity (Davy et al. 2006).

The burrowing crab *Neohelice (Chasmagnathus) granulata* is a herbivore–detritivore macroinvertebrate that dominates SW Atlantic salt marshes (e.g. Bortolus & Iribarne 1999). Its wide distribution along tidal flats and marshes, in addition to its role as a herbivore and ecosystem engineer, place this species among the most important biological factors in the structuring of SW Atlantic marshes (e.g. Iribarne et al. 1997, Alberti et al. 2015). Although *N. granulata* feeds mainly on *Spartina* spp. (e.g. Botto et al. 2005), it also negatively affects the distribution of *Sarcocornia perennis* through bioturbation and herbivory (Alberti et al. 2010a), and therefore it may determine the possibilities of colonization of vegetation-free patches.

Effects of seed source distance and crabs on natural seedling emergence

To evaluate whether the distance to mature *S. perennis* (i.e. those producing seeds) results in differences in seedling emergence, bare patches were randomly chosen at an intermediate intertidal elevation within the following 2 categories: bare patches close to and bare patches distant from mature *S. perennis* (i.e. 0.75 and 11 m, respectively, with an average area of 6 m²; hereafter 'close' and 'distant' patches, respectively). In addition, to determine the joint effect of herbivory and bioturbation exerted by *N. granulata* on *S. perennis* seedlings, 3 treatments were defined in each of those 2 categories (50 × 50 cm, 8 replicates) during February 2011: crab exclosures, cage controls and undisturbed controls. Crab exclosure plots were surrounded by a 40 cm high, 1 cm mesh size plastic fence. Cage controls were like exclosures but with 3 sides instead of 4, allowing free movement of crabs. Seedlings within plots were counted on a monthly basis in each plot (2 bare patch categories × 3 treatments × 8 replicates = 48 plots) from August (right after the first seedlings emerged) until November, when seedlings reached the vegetative stage (following Davy et al. 2006). These vegetative plants were counted again when flowering, in March 2012.

Effects of seed availability on bare patch colonization

To determine whether the number of seeds is a limiting factor in the colonization of bare patches, approximately 50 *S. perennis* seeds were added in each

of the plots described above within small baskets, to avoid confusion with the natural seedling emergence. Small baskets were made using a 1 mm² plastic mesh (2.5 × 7 cm × 4.5 cm). They were filled with sediment from the bare patch, and then seeds were added on the surface. These seeds were collected from neighboring *S. perennis* plants during April 2011, at the peak of seed availability. Given that many of the seeds that we collected were empty, a regression was estimated to add 50 filled seeds in each small basket using weight as a proxy of seed number. Seed samples of different weights were prepared, and then filled seeds were counted within each sample using a magnifying glass. Finally, a regression analysis was performed between sample weight and the number of filled seeds (linear regression model: $y = 1308x + 6.7056$; $r^2 = 0.76$; $F = 33.82$, $df = 1, 11$, $p = 0.0001$). Seeds were added just before the start of their natural emergence in July to avoid processes that might act before germination, like bioturbation (Alberti et al. 2010a). Seedlings within the small baskets were counted biweekly until they reached the vegetative stage (November 2011) and then again when flowering (March 2012).

Sediment salinity and water content

To evaluate if the seedling emergence and survival observed was associated with changes in sediment salinity or water content, sediment samples were taken bimonthly from each plot between March 2011 and January 2012 and processed in the lab following Alberti et al. (2010b).

Effect of reduced sunlight on bare patch colonization

To analyze whether the presence of post-germination environmental filters, particularly desiccation, might limit colonization, a third experiment was performed in a 400 m² area with similar environmental conditions but with higher *S. perennis* abundance. In June 2011, and coinciding with natural seedling emergence, 40 plots (25 × 25 × 30 cm high, 8 replicates) close to mature *S. perennis* plants were established. Eight of those plots were randomly assigned to each of the following treatments: (1) crab exclosures, (2) cage controls and (3) undisturbed controls without shade, in addition to (4) crab exclosures and (5) undisturbed controls with shade. Crab exclosures and cage controls were fenced as described above.

Shade treatments consisted of the addition of a shade cloth at the top and the highest half of each side (i.e. 15 to 30 cm high in each of the 4 sides of each replicate) in early September, coinciding with temperature increases, and right after the peak in seedling counts observed in the results of previous sections. Incident solar radiation was measured in 4 replicates from each treatment with a LI-COR LI-1000 radiometer at around noon in the early fall (April 2012). The shade cloth addition as well as the plastic mesh fence used in exclosures caused a reduction in incident radiation. The incident radiation measured in controls was (mean ± SD) $1390 \pm 12.49 \mu\text{mol s}^{-1} \text{m}^{-2}$. The addition of shade caused an 87 % reduction, on average $227 \pm 262.4 \mu\text{mol s}^{-1} \text{m}^{-2}$; inside exclosures was 57 % less, on average $596 \pm 203.53 \mu\text{mol s}^{-1} \text{m}^{-2}$; and inside exclosures with shade was 77 % less, on average $317 \pm 114.04 \mu\text{mol s}^{-1} \text{m}^{-2}$. Seedlings were counted just before shade cloth addition and 1 mo later (October 2011). From then on (November 2011), seedlings reached the vegetative stage, and we measured them again at the end of the summer (March 2012). None of the surviving vegetative plants produced flowers.

Statistical analysis

All analyses were performed using R statistical software (3.1.2). ANOVAs were performed following the recommendations of Zar (2010); generalized linear models (GLMs) and zero-inflated negative binomial (ZINB) models were performed following the recommendations of Zuur et al. (2009). Below we present the analysis details for each experiment.

Effects of seed source distance and crabs on natural seedling emergence. To evaluate the separate and interactive effect of crab exclusion treatments and bare patch location (close to and distant from mature *S. perennis*) on the number of seedlings, we did a Poisson GLM (for the first 2 sampling dates), detected overdispersion and corrected the standard errors using a quasi-GLM model, where the variance is given by $\phi \times \mu$, where μ is the mean, and ϕ is the dispersion parameter (see Zuur et al. 2009). Given that for the last sampling date for seedlings as well as vegetative and flowering plants we found an excessive number of zeros, we did a ZINB (see Zuur et al. 2009).

Effects of seed availability on bare patch colonization. To evaluate the separate and interactive effect of crab treatments and bare patch location on the number of seedlings, we did a Poisson GLM as described above. Given that for vegetative and flow-

ering plants we found an excessive number of zeros, we did a ZINB.

Sediment salinity and water content. Sediment salinity (March and August 2011 log-transformed) and water content (August 2011 square root-transformed, January 2012 reciprocal square root-transformed) were compared between bare patch condition and crab treatment using a 2-way ANOVA for each sampling date.

Effect of reduced sunlight on bare patch colonization. To evaluate the separate and interactive effect of crab treatments and shade on the number of seedlings, we did a Poisson GLM as described above. Given that for vegetative and flowering plants we found an excessive number of zeros, we did a ZINB. For each dependent variable and sampling date, controls were compared against cage controls and no cage effects were found.

RESULTS

Effects of seed source distance and crabs on natural seedling emergence

Almost no natural emergence of *Sarcocornia perennis* was found in distant patches. In contrast, many more seedlings, that gradually decreased in number over time, were found in close patches: 21 times more in August, 18 times more in September and 5 times more in October (Fig. 1; August, Poisson GLM: $F = 59.94$, $df = 1, 46$, $p < 0.001$; September, Poisson GLM: $F = 48.74$, $df = 1, 46$, $p < 0.001$; October, final ZINB model = seedlings ~ distance | 1: $\chi^2 = 10.75$, $df = 1$, $p = 0.001$). However, crab exclusion treatments did not affect the number of seedlings at any given sampling date, and this variable was never retained in the final model. Even though some seedlings were able to survive and reach the vegetative and flowering stages only within crab exclusions, neither distance to mature *S. perennis* nor exclusion treatments played a significant role in vegetative or flowering plant counts.

Effects of seed availability on bare patch colonization

The observed differences in naturally emerged seedlings between close and distant patches disappeared after seed addition (distance to mature *S. perennis* was never retained in the final model, except for late September, when there were more

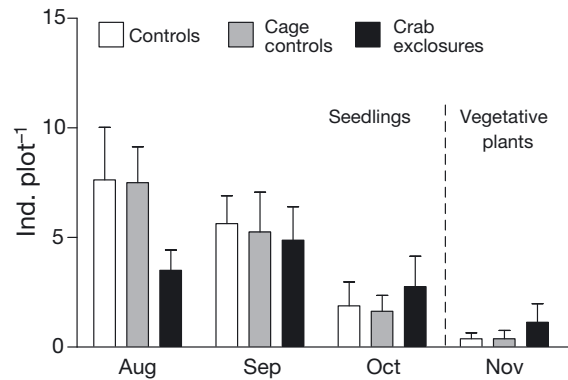


Fig. 1. Seedling emergence (mean + SE) of *Sarcocornia perennis* in the different treatments deployed on bare patches close to mature *S. perennis* (seed sources). November (spring) measurements correspond to vegetative plants. Natural seedling emergence from distant patches is not presented because almost no emergence was found

seedlings close to than distant from mature *S. perennis*; Poisson GLM, distance \times treatment interaction: $F = 5.63$, $df = 2, 42$, $p = 0.007$) but followed the same temporal pattern (Fig. 2). Exclusion of crabs did not affect seedling or flowering plant counts, but more vegetative plants were found inside the exclusions than in the control plots (final ZINB model = vegetative ~ treatment | 1: $\chi^2 = 8.06$, $df = 2$, $p = 0.018$).

Sediment salinity and water content

There were no differences in sediment salinity or in water content, either between close and distant patches or between crab exclusion treatments (except for higher salinities in control plots during March 2011), but as in the previous section, a temporal pattern was found (Tables S2–S4 in the Supplement at www.int-res-com/articles/suppl/m531p033.supp.pdf). During winter, salinity showed minimum values, while during spring and summer months it was more than 3 times higher. Sediment water content followed the opposite pattern: values were highest during autumn and winter but were 50% reduced during higher temperature months.

Effect of reduced sunlight on bare patch colonization

After addition of shade cloth, there were more seedlings and vegetative plants in crab exclusions than on control plots (Fig. 3; October, Poisson GLM: $F = 6.12$, $df = 1, 30$, $p = 0.019$; November, final ZINB model = vegetative ~ treatment | 1: $\chi^2 = 10.28$, $df = 1$,

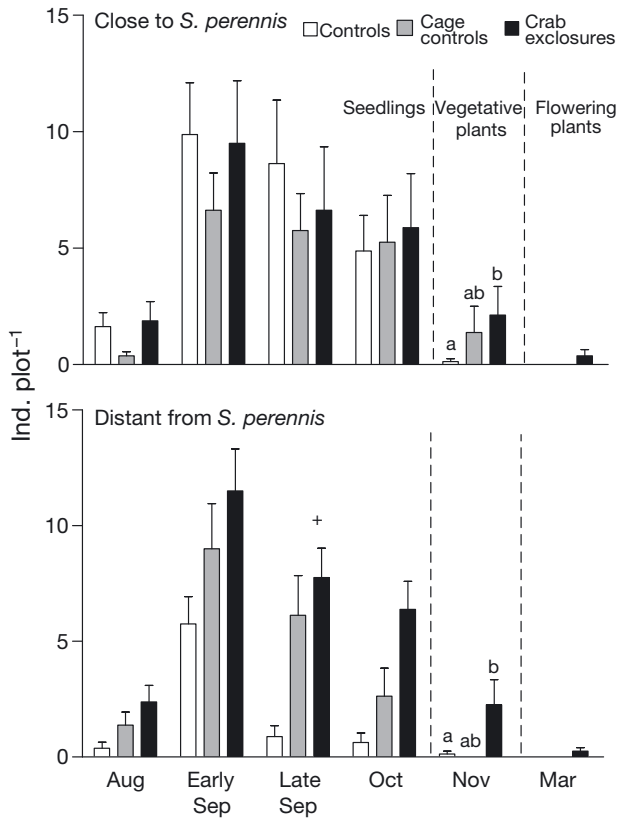


Fig. 2. Seedling emergence (mean + SD) of *Sarcocornia perennis* in undisturbed controls and crab exclosures from shaded and unshaded plots. November (spring) and March (late summer) measurements correspond to vegetative plants, and March (late summer) measurements correspond to flowering plants. Significant differences between close and distant patches in late September are indicated with '+', while letters denote significant differences between treatments

$p = 0.001$; March, final ZINB model = vegetative ~ treatment | 1: $\chi^2 = 10.39$, $df = 1$, $p = 0.001$). Shading did not show a significant effect on the number of individuals on any of the sampling dates, though exclosures with shading exhibited 25% more vegetative plants in total than exclosures without shading (i.e. 15 vs. 12) as well as more replicates with vegetative plants (6 vs. 4) during our last sampling date.

DISCUSSION

Our results show that in Mar Chiquita salt marshes, successful colonization of vegetation-free patches by *Sarcocornia perennis* is determined by the combination of biotic and abiotic forces that act on stages prior to and after seed germination. The availability of *S. perennis* seems to be the most important filter given that differences in natural emergence between

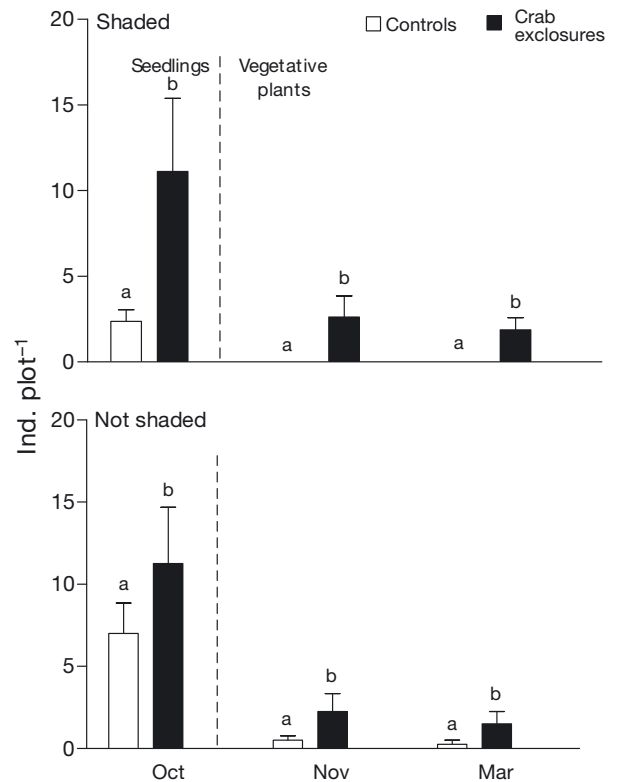


Fig. 3. Seedling emergence (mean + SD) of *Sarcocornia perennis* in undisturbed controls and crab exclosures from shaded and unshaded plots. November (spring) and March (late summer) measurements correspond to vegetative plants. Letters denote significant differences between crab treatments for a given date

close and distant patches disappeared with the addition of seeds. The exclusion of crabs did not have a consistent effect over time, with no effect on seedling survival but a positive effect on vegetative plants. However, among the 660 seedlings we counted during the whole experiment, only 11 became vegetative and flowering plants, and all of them were found growing within exclosures. In addition, we also observed a strong decrease in survival coincident with increases in sediment salinity and decreases in water content, but the addition of shade did not affect seedling survival. Most importantly, our results reveal that seed ecology (i.e. production, dispersal, survival and establishment) of the pioneer species can be a key and this is a usually overlooked driver of salt marsh patch dynamics.

Seed availability

There are some studies showing that seed availability plays a key role in the recovery and species

assemblages of salt marshes. For example, seed availability was considered the most important factor determining the sequence of species establishment during a salt marsh restoration in Belgium (Erfanzadeh et al. 2010). Seed availability on a particular salt marsh area is strongly dependent on seed dispersal, which could occur by abiotic and biotic drivers. Among these drivers, tidal waters seem to play a prominent role (Bakker et al. 1985). However, dispersal is not necessarily always high. Rand (2000) showed that seed availability in New England (USA) salt marshes was likely the result of localized dispersal (i.e. seed distributions resembled adult plant distributions). However, subsequent seedling survival was also limited by post-dispersal factors such as competition and abiotic stress.

Our results mostly coincide with this evidence, particularly with those of Rand (2000). The distance to seed sources appears to strongly condition the arrival of seeds to the vegetation-free patches. As was proposed in our first hypothesis, the dispersal of *S. perennis* seeds from adult individuals could be a strong environmental filter that limits colonization in these marshes and thereby delays secondary succession. In this context, the existence of a *Spartina densiflora* matrix might be acting as a natural barrier for seed dispersal, given that bare patches and *Sarcocornia perennis* plants occur sparsely within this matrix (Daleo et al. 2011).

Plant–animal interactions

The dynamics of salt marsh successions are also known to be influenced by plant–animal interactions. For example, bioturbation and herbivory by polychaetes or crabs can reduce the availability of seeds and seedlings of pioneer salt marsh plants (Paramor & Hughes 2004, Alberti et al. 2010a). In addition, seed consumption by hares and geese does not have a strong impact on seed dispersal, and seed viability is reduced after digestion (Chang et al. 2005). Furthermore, the consumption of seedlings of the dominant plant species by rodents has been shown to slow down bare patch recovery (Gedan et al. 2009, Daleo et al. 2014). Herbivory on established plants can also slow down primary and secondary succession (Kuijper et al. 2004, Alberti et al. 2008).

Based on this information and according to previous studies in Mar Chiquita salt marshes (Alberti et al. 2010a), we were expecting to observe more emergence and seedling survival within crab exclusions. However, we found that crabs only reduced the

abundance of vegetative plants, while they did not reduce the number of seedlings and flowering plants. This might have occurred because crabs are more active at lower elevations (Alberti et al. 2007), but wrack-generated bare patches are usually found at higher elevations (Brewer et al. 1998). In addition, the extremely low numbers of plants that reached the flowering stage (only 11 plants produced flowers, and all of them were growing within exclusions) might also reduce the chances of detecting differences between treatments. Whatever the case, it is clear that compared to seed availability, herbivory and bioturbation played a comparatively minor role in patch dynamics, and therefore our second hypothesis was not supported.

Abiotic stress

Desiccation and the associated increases in salinity have been described as other strong forces regulating bare patch dynamics in salt marshes. For example, Shumway & Bertness (1992) explored the role of seed addition and sediment salinity on the bare patch dynamics of New England (USA) salt marshes and found that emergence and survival was favored when the salinity was decreased. Indeed, positive interactions are essential for the full recovery of these bare patches, with the pioneer species ameliorating the otherwise too high salinities (due to the increased solar radiation that takes place after the loss of the vegetation cover) for the late successional species (Bertness & Leonard 1997, Pennings & Bertness 2001). However, pioneer species might also suffer from abiotic forces during their establishment, such as current velocities (Bouma et al. 2009a), and their establishment might not be possible below a threshold shoot density (enough to reduce current velocity; Bouma et al. 2009b). In these scenarios, a momentary relaxation of the stressful abiotic conditions (window of opportunity sensu Balke et al. 2014) will be necessary to allow the successful establishment of these pioneer species.

Even though we found a high mortality of seedlings that occurred simultaneously with higher sediment salinities and lower sediment water content, we did not find a significant effect of shading on seedling survival. These results suggest that solar radiation does not play a very important role in our study system. Alternatively, this lack of effect might have been an artifact. Lack of enough shading to prevent desiccation, too late or short shading addition or too few surviving vegetative plants could all

explain why we found results that were contrary to our expectations. Regarding our third hypothesis, we propose that regardless of whether the effect of shading could have been significant or not, the role played by solar radiation is subordinate to the role played by seed availability and probably to crab presence as well.

Secondary succession in SW Atlantic salt marshes

The secondary succession and patch dynamics in SW Atlantic salt marshes has been previously studied with a focus placed on the interactions between plant species that dominate these marshes, *Spartina densiflora* and *Sarcocornia perennis* (Alberti et al. 2008), and between these species and the crab *Neohelice granulata* (Alberti et al. 2010a, Daleo et al. 2011). These studies showed that after colonizing, *Sarcocornia perennis* facilitates the establishment of *Spartina densiflora* through reduced herbivory rates and is finally displaced by the higher competitive ability of *S. densiflora*. Overall, *N. granulata* retards succession dynamics through bioturbation prior to the germination of *Sarcocornia perennis* and through herbivory and bioturbation on *S. perennis* seedlings (Alberti et al. 2010a). Herbivory also retards later stages of succession, negatively affecting *Spartina densiflora* once this species colonizes *Sarcocornia perennis* patches (Alberti et al. 2008). Finally, crab herbivory also prevents the asexual closure of disturbance-generated bare areas (Daleo et al. 2011).

However, our results reveal that the secondary successions in these marshes are not entirely driven by biological interactions (i.e. facilitation, competition, herbivory or bioturbation). Our experimental approach allows us to include seed availability to the factors that would be promoting the persistence of vegetation-free patches in these salt marshes. Moreover, our results suggest windows of opportunity (see Balke et al. 2014), in which seed availability is increased and probably crab activities and salinity are decreased to reach the threshold of *Sarcocornia perennis* abundance needed to guarantee bare patch closure. Future studies could focus on dispersal dynamics inside the matrix (following Nathan & Muller-Landau 2000), and how salinity and crabs influence seed viability, to evaluate potential thresholds in this apparent bottleneck of seed availability. Finally, our results show that life-history traits (seed ecology) of the colonizer can be a key and are a usually overlooked driver of salt marsh secondary succession.

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