Crab herbivory regulates re-colonization of disturbed patches in a southwestern Atlantic salt marsh

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Recent work exploring the effects of physical stress and herbivory on secondary succession in estuarine plant communities agrees with basic stress models and reveal that herbivory is an important force in brackish and oligohaline marshes but negligible in physically stressful salt marshes. In these systems, herbivores are terrestrial, and thus negatively affected by the same stressful factors that affect marsh plants (i.e. frequent flooding or high salinities). We evaluated the effects of a marine herbivore (i.e. the crab *Neohelice granulata*) on plant secondary succession in a southwestern Atlantic salt marsh. Field surveys revealed that disturbance-generated bare patches have harsh physical conditions and that their edges suffer higher herbivore pressure compared to the marsh matrix. A factorial experiment demonstrated that asexual expansion of the surrounding plants is the only possible mechanism to re-colonize disturbed patches and that crab exclusion can increase this colonization rate by more than 30 times. Our results show that even in highly stressful environments, herbivores strongly impact marsh structure by regulating patch recovery. The synergism of physical stress and herbivory may make plant succession an extremely slow process and lead to the prevalence of bare areas.

In natural systems, disturbance is a common phenomenon that can create mosaics of patches of different successional stages (Paine and Levin 1981). The recovery of communities from disturbance (i.e. secondary succession) can play a major role in ecosystem structure and function, especially in densely packed systems, where free space is a primary limiting resource (Connell and Slatyer 1977, Sousa 1979). After disturbance, some communities can rapidly return to the original state, usually following the tolerance (i.e. fast growing and high dispersers are the first to colonize the disturbed zones but are replaced by slow growing competitively superior species over time; Tilman 1988) or the facilitative pathway (i.e. early arriving species change the environment, making it suitable for late successional, competitively superior species; Connell and Slatyer 1977, Harris et al. 1984, Bertness 1991). In other cases, the process can be more complex, and lead to multiple persistent community stages influenced by biotic and abiotic factors (Bertness et al. 2002, Jefferies et al. 2006, Crain et al. 2008). Consumers, for instance, can govern succession through top–down effects (Schmitz et al. 2006), not only determining the rate of species replacement (Farrell 1991) but also the succession model (Rousset and Lepart 2000, Alberti et al. 2008). Thus, understanding the mechanisms behind succession dynamics is fundamental not only for the comprehension of community assemblages, but also for conservation and restoration.

In salt marshes, disturbance by ice, fire, herbivory, sedimentation or accumulation of plant debris can generate bare patches and profoundly influence plant community structure, function and diversity (Bertness and Ellison 1987, Pennings and Bertness 2001, Silliman et al. 2005, Jefferies et al. 2006). The most common and well documented disturbance factor occurs when spring high tides transport and accumulate floating plant debris to the high marsh (named 'wracks'). Wracks often stays stationary long enough to cause plant mortality, generating patches of secondary succession (Bertness and Ellison 1987, Brewer et al. 1998). In south New England (US) salt marshes, bare patches created by wrack provide temporal competitive refuges from dominant plants (Bertness et al. 1992, Pennings and Richards 1998) and are rapidly invaded by seedlings of species like *Salicornia europea* and *Distichlis spicata* or by annual forbs (Bertness 1991). These colonizing species ameliorate soil salinity stress previously generated by high evaporation after plant cover loss, allowing matrix species like *Spartina pattens* or *Juncus gerardi* to re-colonize and close the gaps (Bertness and Ellison 1987, Ewanchuk and Bertness 2004). Nevertheless, in low-marsh habitats, harsh physical conditions prevent the occurrence of many marsh plants and thus, secondary succession usually involves the clonal re-colonization of bare patches by the matrix species, the only ones capable of living on such stressful conditions (usually *Spartina alterniflora*, Hartman 1988, Pennings and Bertness 2001). Recent evidence (Crain 2008, Bromberg Gedan et al. 2009), revealed that herbivory can also influence marsh secondary succession, following the predictions of basic stress models: in physically stressful salt

marshes, secondary succession is slow and mediated largely by physical processes, whereas in less stressful, brackish and oligohaline marshes, herbivory slows the relatively high rate of succession and, most important, radically alters plant species composition.

Salt marshes occurring between southern Brazil (32°S) and northern Argentinean Patagonia (42°S) are dominated by the cordgrass *Spartina densiflora* (Isacch et al. 2006). *Spartina densiflora* is a perennial salt tolerant grass from South America (Bortolus 2006) that grows year-round and forms monospecific stands interspersed with extensive bare patches across the entire intertidal (Isacch et al. 2006). This halophyte tolerates a broad range of edaphic and hydrological conditions due to high interspecific and interpopulation morphological variations (Nieva et al. 2001). In Europe and North America, *S. densiflora* is an aggressive invader that can rapidly colonize empty zones through high rates of both sexual and clonal reproduction (Nieva et al. 2001, 2005). However, along its native range, *S. densiflora* sexual reproduction may be less important not only because granivory is intense (Canepuccia et al. 2008) but also because seed viability is extremely low (Bortolus et al. 2004).

The burrowing crab *Neohelice granulata* inhabits almost the entire intertidal zone of these southwestern Atlantic salt marshes (Iribarne et al. 1997, Bortolus and Iribarne 1999). This crab is a herbivore–detritivore (Iribarne et al. 1997, Bortolus and Iribarne 1999) and stable isotope analyses show that plants of the genus *Spartina* are its primary food source (Botto et al. 2005). Through grazing activities, crabs can exert strong control over marsh plant production (Bortolus and Iribarne 1999, Alberti et al. 2007a), affect *Sarcocornia perennis* seedling colonization of bare areas (Alberti et al. 2010a) and influence subsequent succession in tidal flats (Alberti et al. 2008), potentially affecting marsh secondary succession. The presence of this herbivorous crab confers to southwestern Atlantic salt marshes a fundamental difference with other previously studied systems (Crain 2008, Bromberg Gedan et al. 2009) where herbivores had no effect on secondary succession in stressful zones. In those systems, herbivores are terrestrial, and thus negatively affected by the same stressful factors that affect marsh plants (i.e. frequent flooding or high salinities). However, in our system, physical conditions associated with marine water are stressful for plants but not for herbivorous crabs, that are instead affected by desiccation (Bortolus et al. 2002). Thus, a stressor for a given trophic level is not necessarily a stressor for other trophic levels. In fact, we recently showed that, in contrast to the general pattern emerging from other salt marshes where lower limits of plant species are set by physiological tolerance of inundation-related physical conditions (Castillo et al. 2000), in our system, crab herbivory is positively correlated with flooding periods (Alberti et al. 2007b), and can control the lower limit of *S. densiflora*, showing fundamental differences with other systems in the importance of herbivory on stressful zones (Alberti et al. 2010b). In this context, the objective of this work was to evaluate the separate and interactive importance of crab herbivory and vegetative recruitment on the re-colonization of disturbance patches on a southwestern Atlantic salt marsh.

Methods

This study was performed in an extensive salt marsh located near a creek at the mouth of the Mar Chiquita coastal lagoon (Argentina, 37°32`S, 57°19´E). This lagoon is affected by semidiurnal microtides (<1 m) and is characterized by mudflats and a large *Spartina densiflora* marsh (Isacch et al. 2006). The burrowing crab *Neohelice granulata* is a dominant macro-invertebrate often found at densities of more than 60 crabs m^{-2} (Iribarne et al. 1997).

To evaluate the natural re-colonization patterns of bare patches, on October 2002 (spring) we marked and followed bare patches created by wrack accumulation during autumn 2002. We randomly selected 11 bare patches (patch size ranging from 3 to 12 m^2) and marked eight different fixed points on the edges of each patch with plastic flags to detect edge movement. After more than four years (i.e. November 2006), we quantified the average distance between the new position of the edge and the flags marking the previous edge. The null hypothesis of no movement of the edge position was evaluated with a t-test analysis. Monthly searches were also performed for seedlings of *S. densiflora*, *S. perennis*, or any other marsh species, to quantify sexual colonization of patches.

To evaluate if soil abiotic conditions are different between the marsh matrix and disturbed patches, we measured soil salinity, soil water content and redox potential (Eh) of both habitats during low tide on 3 November 2002. Sediment salinity and water content was obtained by collecting sediment samples (5 cm ø, 8 cm deep) and concentration of salt was measured with refractometry (see Alberti et al. 2010b for a complete description of the technique). In situ sediment redox potential was measured at a depth of 5 cm, with a combined platinum electrode with silver/silver chloride internal reference. We corrected values with respect to a reference hydrogen electrode. To evaluate the null hypotheses of no difference in sediment salinity, water content and redox potential between habitats, we used t-test analyses. To evaluate if crab grazing intensity changed between the marsh matrix and bare patch edges, we scored percent leaves damaged per stem following Alberti et al. (2007a) and Daleo et al. (2009). We performed the surveys on 120 stems on the edge of bare patches and 120 stems in the dense marsh matrix during fall 2006 (the time of the year with greatest herbivory; Alberti et al. 2007a). We evaluated the null hypothesis of no difference in percent damaged leaves between marsh matrix and patch edges with a t-test analysis.

To experimentally evaluate the importance of asexual colonization and herbivory on patch recovery dynamics, we conducted a field factorial experiment by creating experimental bare patches that mimic natural disturbed areas created by wrack. We removed *S. densiflora* aboveground and rhizomes on 20 plots (0.7 × 0.7 m) separated at least by 3 m. We carefully removed aboveground plant material and rhizomes, trying to have the least impact on sediment structure. When necessary, we added sediment from the surroundings to equal sediment level. The experiment was a 2 × 2 factorial design with five replicates of each of the following treatments: (1) crab exclosures (0.7 × 0.7 × 0.6 m plastic mesh fences, with 1 cm openings and buried 0.3 m), (2) rhizome exclosures (along the perimeter of the plot we

buried 10 cm tall plastic walls), (3) crab and rhizome exclosures, and (4) unmanipulated controls. Crab exclosures have been widely used in this system and the use of cage controls which allowed crabs to move in and out consistently revealed that there are no associated cage artefacts (Alberti et al. 2007a, 2010a, b, Daleo et al. 2007, 2009, Daleo and Iribarne 2009). The experiment began on November 2006 and ran until March 2010. At the end of the experiment, we counted the number of stems inside each plot, measured if the vegetation edge moved from the plot edge (maximum distance), and measured plant biomass by removing above ground material and drying to a constant weight (60°C). Given that there was no colonization in plots where rhizomes were excluded, and only one plot where rhizomes and crabs were excluded was colonized (by two stems), we were not able to perform a two-way ANOVA to evaluate the null hypothesis of no effect of crabs and rhizomes on the measured variables (as those treatments had only 0 values and the assumptions were impossible to meet). Instead, we evaluated the null hypothesis of no effect of crab exclusion by t-tests comparing crab exclusion treatments with control treatments.

Results

We found no seedlings of *Spartina densiflora, S. perennis* or other plant species inside the bare patches. Movement of the plant edge around natural bare patches ranged from –60 mm (the bare patch increased its size) to 171 mm (the bare patch decreased) with a mean value of 6 mm, but t-test revealed that there were no significant net movement (the mean movement was not significantly different from 0; t = 0.27, DF = 10, p = 0.79). Sediment water content in the marsh matrix was almost twice as high as in the sediments of bare patches (Table 1) and salinity was almost four times lower (Table 1). In addition, sediment redox potential was higher in the vegetated marsh matrix compared with bare patches (Table 1). Finally, herbivory was higher on the edge of bare patches compared with the interior of marsh matrix (Table 1).

As in natural bare patches, there was no sexual colonization on experimentally created bare patches. Additionally, there was no asexual colonization in plots where rhizomes were excluded except in one plot of rhizomes and crab exclusion. Crab exclusion positively affected colonization of bare patches and increased more than five times the expansion

of *S. densiflora* into the experimentally created bare patches (movement from the edge, control vs crab exclusion, t = 5.37, DF = 8, p = 0.0007; Fig. 1A). The number of tillers growing inside experimentally created bare patches was also higher in crab exclusion treatments (log transformed data, t = 6.92, DF = 8, p = 0.0001; Fig. 1B). Additionally, plant biomass was more than 30 times higher in crab exclusion plots compared to control plots (log transformed data, t = 8.79, DF = 8, p = 0.00002; Fig. 1C).

Discussion

Our results show that recovery of disturbed patches, in a southwestern Atlantic salt marsh, can be extremely slow. This is likely due to the interaction of two classically recognized opposing forces: herbivory and physical stress. Stressful conditions of disturbed patches may preclude the establishment of seedlings, restricting patch closure to asexual reproduction (Pennings and Bertness 2001). However, crab herbivory appears to also play an important role in patch closure dynamics, demonstrated by the drastically

Table 1. Results of the comparisons of sediment characteristics and grazing intensity between bare patches and vegetated marsh matrix. ([t]) Redox potential and salinity data were log transformed to achieve homocedasticity; (*) Herbivory was measured in the edges of bare patches. Reported values are statistical means (standard errors).

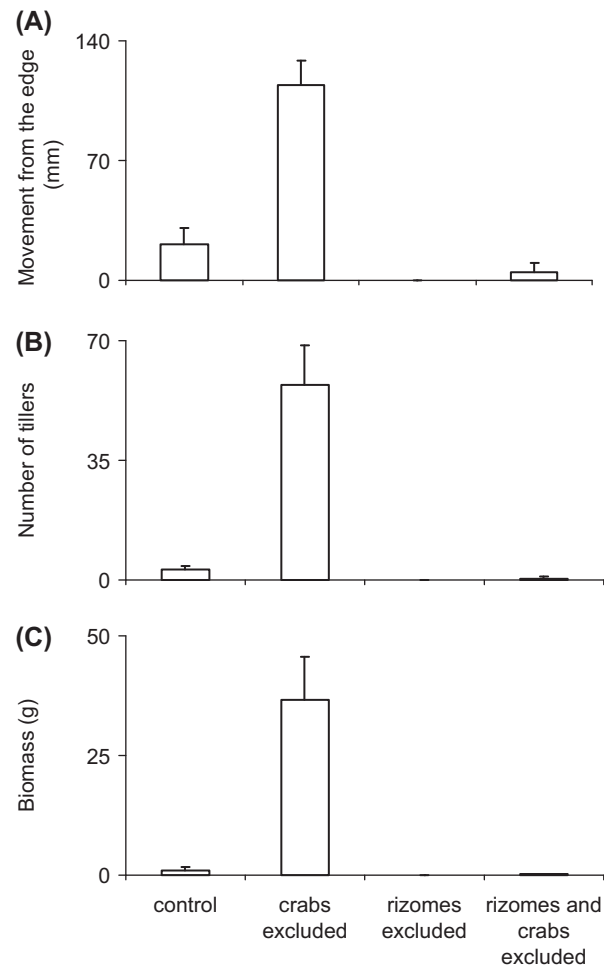|	Bare patches	Marsh matrix	t	DF	p
Redox potential (Eh (mV))	106 (5)	276 (73)	10.9[t]	10	10^{-6}
Salinity (PPT)	120 (28)	34 (4)	10.97[t]	8	4×10^{-6}
Water content (%)	26 (1.5)	54.9 (2.4)	22.4	8	~0
Hervibory (% damaged leaves)	37 (34)*	26 (31.3)	2.62	238	0.009

Figure 1. The effect of prevention of asexual colonization and exclusion of crabs on *Spartina densiflora* re-colonization of experimentally created bare patches. (A) Movement of the vegetation edge inside bare areas; (B) number of tillers and, (C) biomass of plants growing inside bare areas. Bars show means + SE.

reduced asexual expansion of *S. densiflora* into bare zones when crabs were present.

Asexual reproduction and clonal integration allow plants to share resources (Alpert and Mooney 1986, Alpert 1996) and redistribute water, nutrients and fixed carbon among stems in patchy environments (Pennings and Callaway 2000). These advantages permit clonal plants to support individual stems experiencing physical stress, competition, and even herbivory (Hartnett and Bazzaz 1985, Shumway 1995, Brewer and Bertness 1996). Thus, in very stressful conditions, the re-vegetation process of bare areas is thought to be governed by asexual reproduction (Hartman 1988, Pennings and Bertness 2001). Although *S. densiflora* can germinate on relatively high stressful conditions (as high salinity; Mateos-Naranjo et al. 2008), our results showed almost no plant colonization in artificial bare patches when asexual reproduction was prevented. This is probably the result of low seedling viability (Bortolus et al. 2004) as well as harsh environmental conditions (Kittelson and Boyd 1997). However, asexual colonization per se was not enough to explain the re-vegetation process of disturbance-generated patches, as sampling revealed that these patches remain bare and almost unchanged for more than four years. These results contrast with others from US salt marshes where the closure of similar wrack-generated patches occurs in almost a year, returning to the original state in around three years (Bertness and Ellison 1987, Pennings and Bertness 2001). According to previous results (Alberti et al. 2007a), we found that crab herbivory was concentrated on the edge of vegetated areas. In addition, our experimental results also showed that most stems colonizing bare patches were removed by crab herbivory, dramatically slowing down patch closure. Thus, even though *S. densiflora* asexual reproduction seems to play a key role in the recovery of disturbed patches, its importance might be obscured by the high rates of crab herbivory.

Clements (1916) proposed a model of succession focused on the interactions between plants and the environment. After including biological interactions as forces that affect successions, Connel and Slatyer (1977) improved the Clements (1916) model and proposed three models: inhibition, tolerance and facilitation (depending on the effects of early on late successional species). Later, Farrell (1991) modified these models to include the role of herbivores on the rates of succession. In salt marshes the prevailing concept of plant secondary succession is the facilitation model, the progression of disturbed patches as the result of stress amelioration by early successional species, which are then replaced by competition (Bertness 1991, Pennings and Bertness 2001). In dryer salt marshes, where salinity in bare patches is as high as in our study system, harsh abiotic conditions as well as facilitative interactions coupled with sexual and asexual reproduction may play key roles in governing plant successions (Castellanos et al. 1994, 1998, Nieva et al. 2005). For example, the primary colonizer of salt pans in Mediterranean marshes, glaucous glasswort *Arthrocnemum macrostachyum*, plays an essential role in their succession reducing abiotic stress, and thus facilitating the establishment of other plant species (Rubio-Casal et al. 2001). In California salt marshes, high salinity also prevents seedling growth, and the recovery of disturbed patches depends on vegetative runners, clonally integrated to plants in less harsh environments (Allison

1995). It was not until the last two decades that herbivory was considered as a force strong enough to influence marsh functioning (Silliman and Zieman 2001, Silliman et al. 2005, Jefferies et al. 2006), and it was recently noted that herbivores might heavily affect disturbance-generated patch dynamics (Silliman et al. 2005, Bromberg Gedan et al. 2009). Most marsh studies show that the impact of herbivory on plant dynamics generally diminishes with increasing environmental stress, being negligible in stressful salt marshes (Crain et al. 2008, Bromberg Gedan et al. 2009). However, given that in our system herbivores are not terrestrial, they are not negatively affected by the same stressful factors that affect marsh plants (i.e. frequent flooding or high salinities; see Alberti et al. 2010b for more details), our results show that herbivores might strongly impact marsh re-colonization of disturbed areas even in highly stressful environments. The synergism of physical stress and herbivory may make plant colonization an extremely slow process thus driving to the prevalence of bare areas.

Basic stress models predict that herbivory will be a negligible force in physically stressful conditions because high trophic-level species are expected to be more susceptible to environmental stress than basal-level species (Menge and Sutherland 1987). However, those models assume a unique stress factor that similarly affects different trophic levels. Opposing stress gradients, or single stress gradients that differentially affect different trophic levels, nevertheless, are not uncommon in natural systems (Kawai and Tokeshi 2007, Sanderson et al. 2008). In salt pans of many southern Atlantic US salt marshes, for example, salt stress negatively affects *S. alterniflora* but has no effect on the herbivorous snail *Littoraria irrorata*, leading to large-scale die-off areas (Silliman et al. 2005). These significant effects of consumers when the stress is decoupled among trophic levels are not exclusive of salt marshes. For example, on the rocky shores of Oregon (US), desiccation stress during the summer strongly affects fast-growing algal species but not limpets that consume those algae, and then, the strongest impact of herbivores on algae abundance are observed during the months with harshest abiotic conditions (Cubit 1984; see also Underwood 1980). Moreover, in mangrove systems, and analogously to our study, crab consumption of tree seedlings is higher at low and anoxic tidal levels because crabs avoid desiccation stress related to higher tidal levels (Sousa and Mitchell 1999). Thus, if the different members of the trophic web are not affected by the same stress factors, or are not affected similarly, it might not be accurate to assume reduced importance of negative biological interactions under stressful conditions.

Our study system shares many patterns and processes with other marshes throughout the world (e.g. competition governing zonation: Bertness and Leonard 1997, Daleo et al. 2008; nitrogen limitation: Valiela et al. 1976, Alberti et al. 2010b; strong herbivory: Jefferies et al. 2006, Alberti et al. 2007a). However, the presence of an herbivore whose effects increase towards the flooding-stress extreme makes herbivory pressure so intense at low tidal heights that herbivory became the most important process setting plant lower distribution (Alberti et al. 2010b) and, as shown here, also profoundly affects the dynamics of disturbance-generated areas. Hence, our results highlight the necessity of cautious extrapolations

when generalizing experimental results obtained in restricted locations. The combination of this study with previous results, nevertheless, indicate that, in the long term, bare areas are eventually colonized by *Sarcocornia perennis* that, once established, facilitates *S. densiflora* colonization by protecting young susceptible stems from crab herbivory until they reach a threshold size for escaping herbivory, turning into a competitive interaction (Alberti et al. 2008). Thus, the general model of facilitation for salt marsh plant secondary succession still holds but, in this case, driven by biological stress (herbivory) instead of physical stress.

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