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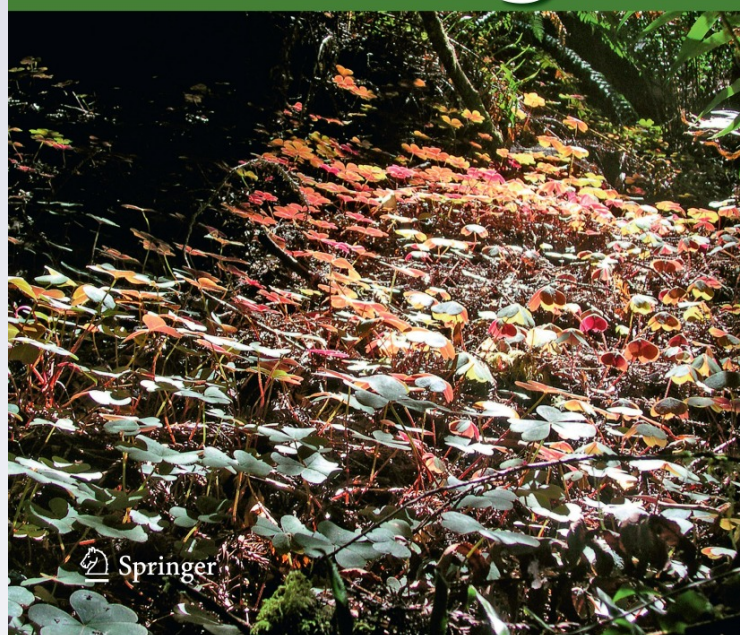
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Herbivory affects salt marsh succession dynamics by suppressing the recovery of dominant species

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Abstract Disturbance can generate heterogeneous environments and profoundly influence plant diversity by creating patches at different successional stages. Herbivores, in turn, can govern plant succession dynamics by determining the rate of species replacement, ultimately affecting plant community structure. In a south-western Atlantic salt marsh, we experimentally evaluated the role of herbivory in the recovery following disturbance of the plant community and assessed whether herbivory affects the relative importance of sexual and clonal reproduction on these dynamics. Our results show that herbivory strongly affects salt marsh secondary succession by suppressing seedlings and limiting clonal colonization of the dominant marsh grass, allowing subordinate species to dominate disturbed patches. These results demonstrate that herbivores can have an important role in salt marsh community structure and function, and can be a key force during succession dynamics.

Keywords Community structure · Secondary succession · Colonization · *Spartina*

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Introduction

Understanding the processes that drive species diversity is one of the major issues of community ecology (Levine and HilleRisLambers 2009). Given that disturbance is a widespread process that can increase species diversity by temporarily suppressing dominant species (Pierce et al. 2007), the study of community recovery after disturbance has been a seminal issue for decades (e.g., Dayton 1971; Horn 1974; Bazzaz 1979). The current conception of secondary succession explains patterns of species replacement as a consequence of the trade-off between competitive ability and dispersal capacity (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; see Tilman 1988; Foster and Tilman 2000) or as a trade-off between competition capacity and stress tolerance (i.e. early arriving species tolerate and ameliorate the otherwise stressful environment, making it suitable for late successional, competitively superior species; see Connell and Slatyer 1977; Harris et al. 1984; Bertness 1991). In addition to those models based on competitive or facilitative interactions, there is growing evidence that consumers can influence succession after disturbance (Bertness et al. 2002; Schmitz et al. 2006) thus affecting community structure and species diversity (Buschmann et al. 2005). Hence, consumers can govern succession through top-down effects (Schmitz et al. 2006), not only determining the rate of species replacement (Farrell 1991) but also by increasing the importance of facilitative interactions (see Bertness et al. 2002), potentially affecting the course of succession (Rousset and Lepart 2000; Alberti et al. 2008).

In herbaceous perennial communities, most of the early work evaluating the effect of different factors on successional dynamics has focused on the interactions between

plants and physical factors (e.g., Bazzaz 1979; Bertness and Ellison 1987), intraspecific competition for limiting resources (e.g., Al-Mufti et al. 1977; Tilman 1987), herbivory (Olf and Ritchie 1998) and, more recently, soil fauna (De Deyn et al. 2003). One characteristic that may profoundly influence the recovery dynamics of these communities is the existence of both clonal and sexual reproduction (Richards 1986), which confer alternative routes to gene transmission and provide both complementary and contrasting ecological and evolutionary advantages (Vallejo-Marín et al. 2010). Depending on environmental conditions, propagules generated by sexual and clonal reproduction can have dissimilar adaptive advantages due to differences in characteristics such as survival rates, dispersal potential, and genetic variability (Abrahamson 1980; Dorken and Eckert 2001). Sexual reproduction, for instance, may enhance rapid colonization of new or disturbed sites (Niu et al. 2012), being key to succession dynamics. But, in cases where well-established individuals share resources with propagules, clonal reproduction can increase colonization success in environments with high physical stress, strong competition, or high herbivory pressure (Gardner and Mangel 1999; Pennings and Callaway 2000). Thus, asexual reproduction and clonal integration can be fundamental in the colonization of disturbed zones, and their relative importance on succession dynamics is expected to change depending on environmental conditions such as physical stress or herbivory (see Fahrig et al. 1994). Although the importance of clonal integration in relation to physical stress has been widely studied (e.g., Shumway 1995; Brewer and Bertness 1996; Pennings and Callaway 2000), its importance in relation to herbivory pressure has so far received little attention.

Along with the inundation-related stress gradient, physical disturbance is one of the major abiotic forces generating community patterns in salt marshes (Bertness and Ellison 1987). A common disturbance factor occurs when spring high tides transport and accumulate floating plant debris to the middle and high marsh (named “wrack”), killing the underlying vegetation and generating transient gaps (see Bertness and Ellison 1987; Brewer et al. 1998). Models of succession dynamics after wrack disturbance come from the well-studied southern New England (US) saltmarshes, where bare patches are rapidly invaded by seedlings of salt-tolerant species like *Salicornia europaea*, clonal runners like *Distichlis spicata*, or by annual forbs (see Bertness and Ellison 1987; Bertness 1999). After colonizing bare patches, those opportunistic species ameliorate soil salinity stress (generated by high evaporation after plant cover loss), allowing perennial matrix species like *Spartina patens* or *Juncus gerardii* to clonally recolonize and close the gaps (see Bertness and Ellison 1987; Bertness 1999; Ewanchuk and Bertness 2004), following the

so-called facilitation model of succession (Connell and Slatyer 1977). Transient patches provide temporal niches for those fugitive and annual species and greatly contribute to salt marsh plant diversity (Brewer et al. 1998; Bertness 1999; Ewanchuk and Bertness 2004). Asexual reproduction and clonal integration are, thus, key features that influence patch recovery and control community structure (see Brewer et al. 1998; Bertness and Ellison 1987; Bertness 1999; Pennings and Callaway 2000; Angelini and Silliman 2012). Recent evidence (Crain 2008; Crain et al. 2008; Bromberg Gedan et al. 2009) suggests that herbivory can also influence marsh secondary succession, slowing down the relatively high rate of patch recovery and, most importantly, radically altering plant species composition. In this context, the objective of this work was to evaluate the separate and interactive effect of herbivory and clonal integration in governing succession dynamics.

Materials and 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'W). This lagoon is affected by semidiurnal microtides (<1 m; Isla 1997) and is characterized by mudflats in the low zone followed by a *Spartina densiflora* monoculture at intermediate elevations and an extended salt marsh community at high elevations dominated by *S. densiflora* and *Sarcocornia perennis*, occasionally intermixed with other halophyte species such as *Limonium brasiliense*, the saltgrass *Distichlis spicata*, and other herb species such as the alkaliweed *Cressa truxillensis* (Isacch et al. 2006; Alberti et al. 2011). The pickleweed *S. perennis* is among the first plant species to colonize bare areas (Alberti et al. 2010a), while *S. densiflora* generally arrives later, often facilitated by *S. perennis* (Alberti et al. 2008). The grass *D. spicata* and the herb *C. truxillensis* mostly exhibit a fugitive strategy, being most abundant on disturbed areas.

The dominant herbivores in this system are crabs (*Neohelice granulata*) and wild guinea pigs (*Cavia aperea*). In these salt marshes, herbivores can exert strong control over plant production (Alberti et al. 2010b). In marshes recovering after burning, for example, crabs can decrease aerial biomass of *S. densiflora* (primarily through consumption of young shoots) by up to 87 % (Bortolus and Iribarne 1999), and can prevent *S. densiflora* from colonizing large bare zones unless they grow within *S. perennis* patches that are less preferred by crabs (Alberti et al. 2008). In addition to the crab, recent evidence suggests that wild guinea pigs can also exert strong control over plant production and diversity (Alberti et al. 2011). The importance of crab herbivory decreases with increasing elevation (Alberti et al. 2010b).

Given that wild guinea pigs are terrestrial herbivores, their major impact on marsh plants occurs at intermediate and high marsh elevations (Alberti et al. 2011), where we performed our experiment.

To experimentally evaluate the importance of sexual or asexual colonization and herbivory on patch recovery dynamics, we conducted a field factorial experiment at intermediate elevations of the marsh by creating experimental bare patches that mimic natural disturbed areas produced by wrack. The experiment consisted of 20 plots (0.7 m × 0.7 m) separated by at least 2 m in which we removed aboveground plant material and rhizomes. This manipulation was done with scissors and knives to minimize the impact on sediment structure. Where necessary, we added sediment from the surroundings to reach equal sediment level. The experiment was a 2 × 2 factorial design with five replicates of each of the following treatments: (1) herbivore exclusion (0.7 m × 0.7 m × 0.6 m high plastic mesh fences, with 1-cm openings and buried 0.3 m), (2) prevention of clonal colonization (along the perimeter of the plot we buried 10-m rigid plastic strips as clonal walls), (3) herbivore exclusion and prevention of clonal colonization, and (4) unmanipulated controls. In addition, five cage controls similar to herbivore exclusions but with two open sides (allowing rodents and crabs to freely move in and out) were set up to test for caging artefacts.

The experiment ran from March 2006 until March 2012. Plant species biomass was indirectly measured during March 2008 and March 2010 and directly measured at the end of the experiment. To indirectly estimate plant biomass, we used a non-destructive method in which we measured plant species abundance and transformed those values to biomass. In each plot, we counted the number of tillers for grasses (i.e. *S. densiflora* and *D. spicata*), and the number of plant individuals, and classified them using a discrete size scale (i.e. very small, small, medium, large, and very large) for *S. perennis* and other herbaceous species. We then sampled the same number of tillers (for grasses) and number and sizes of plant individuals (for herbaceous species) in zones adjacent to the experimental plots. We dried and weighed all plant material. For each replicate, we thus obtained an estimation of aboveground biomass for each plant species. To evaluate the accuracy of the method, in March 2010 we double-sampled plant biomass in ten randomly selected 0.7 m × 0.7 m zones using the indirect method as well as directly removing, classifying by species, drying, and weighing all plant material. We performed simple linear regression between estimated and directly measured aboveground biomass for each plant species to evaluate the null hypothesis of no relationship between both variables. We used this indirect method because there is a strong variability in the height–weight relationship or even in the growth form of these marsh plant species, especially

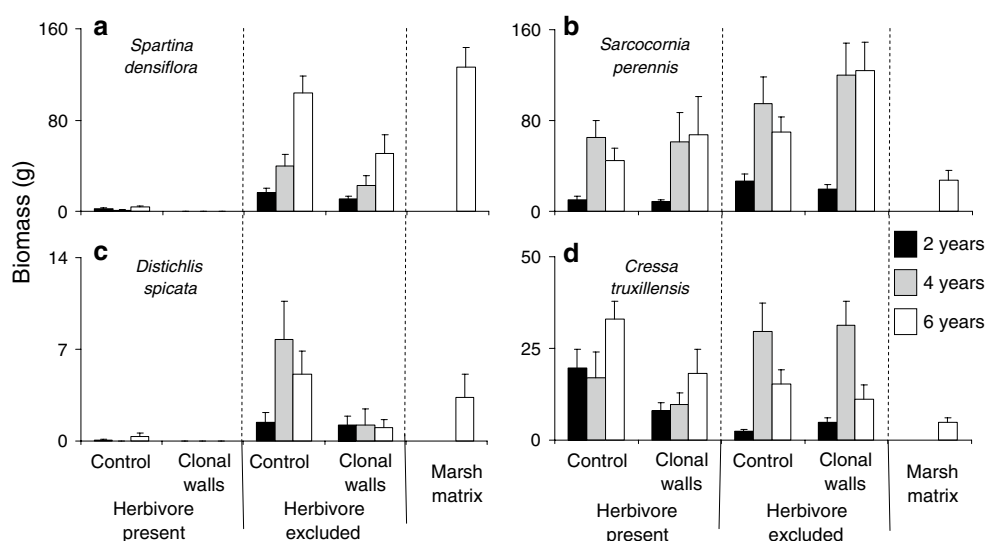
S. perennis and *C. truxillensis* that can have either erect or creeping forms, making classic cover–biomass or height–biomass regression methods of estimation less accurate.

To evaluate the effect of herbivory and clonal colonization on the biomass of the four more abundant species (*S. densiflora*, *D. spicata*, *S. perennis*, and *C. truxillensis*), we performed a repeated-measures ANOVA (see Zar 1999) with herbivory and clonal colonization as main factors, and time as a repeated measurement factor. To evaluate the separate and interactive effects of time, herbivory, and clonal colonization on plant community composition (including the four more abundant species named above and other less abundant species such as *Limonium brasiliense*, *Acmella decumbens*, *Conyza bonariensis*, *Apium sellowianum*, and *Picris echioides*), we performed the permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) based on the Bray–Curtis similarity index and with 9,999 permutations. The three main factors (i.e. herbivory, clonal colonization, and time) were considered as fixed factors and plot number was considered as a random factor nested in herbivory and clonal colonization, as an approximation to a repeated-measures design where time was the repeated-measures factor (following Anderson et al. 2008). To determine if, after 6 years (2006–2012), plant assemblage composition in the herbivore exclusion treatment was similar to that in the undisturbed marsh matrix, we performed a one-way PERMANOVA between both treatments. To achieve this, at the end of the experiment, we also collected all aboveground plant biomass from five undisturbed areas of 0.7 m × 0.7 m, and processed the samples as described above. Analyses were conducted using Primer (v.6.1.13) with the PERMANOVA+ extension (v.1.0.3) software. We also looked at the treatment effects on species assemblages using non-metric multi-dimensional scaling ordination (NMDS) based on the Bray–Curtis similarity index (Warwick and Clarke 1991). The NMDS ordination patterns were obtained using the *metaMDS* function of the *vegan* package (v.2.0-4; Oksanen et al. 2012) for the R statistical software (v.2.15.1).

Results

Validation of the indirect method used for biomass determination showed a strong linear fit between estimated and observed biomass for the four most abundant species (see Table S1 in Supporting Information). When herbivory was allowed, plots were rapidly colonized by the pickleweed *Sarcocornia perennis* and the alkaliweed *Cressa truxillensis*, which dominated the plots over the 6 years of the experiment, with nearly negligible recovery of the cordgrass *Spartina densiflora*. When herbivory was impeded, in contrast, plots progressed towards a pre-disturbance state of *S. densiflora* dominance, especially in

Fig. 1 Effects of prevention of clonal colonization (clonal walls) and herbivore exclusion on biomass of the salt marsh plants. **a** *Spartina densiflora*, **b** *Sarcocornia perennis*, **c** *Distichlis spicata* and **d** *Cressa truxillensis* during re-colonization of experimentally created bare patches. Bars means and standard errors. Biomass of salt marsh species on the undisturbed marsh matrix was only measured in the 6th year of the experiment



plots where clonal colonization was allowed (see Fig. 1a). In plots with herbivory, *S. densiflora* biomass was very low, especially where clonal colonization was impeded, and did not change for the 6 years of the experiment (see Fig. 1a). However, when herbivores were excluded, *S. densiflora* biomass was higher and increased with time (Herbivory \times Time effect; see Table 1). In plots without herbivory, prevention of clonal colonization also decreased *S. densiflora* biomass, but to a lesser amount than plots with herbivory (Herbivory \times Clonal colonization effect; see Table 1). For *S. perennis*, in contrast, there was relatively high biomass in all treatments, especially after the fourth year of experiment (Time effect; see Fig. 1b; Table 1). Biomass of *S. perennis*, in addition, was higher in plots without herbivory (Herbivory effect; see Fig. 1b; Table 1). In plots with herbivory, the saltgrass *Distichlis spicata* was only present where clonal colonization was allowed. Similar to *S. densiflora*, *D. spicata* biomass was higher in plots without herbivory (Herbivory \times Clonal colonization effect; see Table 1) but with no clear increase over time (see Fig. 1c; Table 1). For *C. truxillensis*, biomass was higher, and increases over time, in plots with herbivory. However, in plots without herbivory, biomass greatly increased by the fourth year of experiment but then decreased (Herbivory \times Time effect; see Fig. 1d; Table 1). There were no cage effects on the biomass of the four species (i.e. cage control vs. control; *S. densiflora*: $t = 1.17$, $df = 8$, $P = 0.28$; *S. perennis*: $t = 0.69$, $df = 8$, $P = 0.51$; *D. spicata*: $t = 0.41$, $df = 8$, $P = 0.69$; *C. truxillensis*: $t = 0.57$, $df = 8$, $P = 0.58$).

The results of the factorial PERMANOVA showed that preventing clonal colonization on disturbed areas affected species assemblage (pseudo- $F_{1,32} = 2.95$, $P = 0.033$, see Figs. 2, 3, and Fig. S1), while the effect of time varied with the presence of herbivores (Herbivore \times Time interaction:

pseudo- $F_{2,32} = 7.82$, $P < 0.001$; Fig. S1). For any given year, there were differences in species assemblage between treatments with and without herbivores. Herbivory, in addition, retarded community recovery, as there were no differences between the fourth and the sixth year following initial disturbance in treatments with herbivory, but there were differences between all sampling dates in those treatments in the absence of herbivory (see Fig. S1). Even more, there were no differences in community composition between the undisturbed marsh matrix and the herbivore exclusion treatment after 6 years (pseudo- $F_{1,8} = 2.82$, $P = 0.111$; see Figs. 2, 3).

Discussion

Our results indicate that herbivory strongly affects re-colonization of salt marsh disturbed patches, limiting the recovery of the dominant marsh grass *Spartina densiflora* and allowing subordinate species to maintain a relatively high abundance even 6 years after initial disturbance. Herbivory, in fact, nearly suppresses *S. densiflora* completely when clonal colonization was impeded. The pickleweed *Sarcocornia perennis* and the alkaliweed *Cressa truxillensis*, in contrast, were able to sexually colonize bare patches, even in the presence of herbivores. Our results also show that recovery of disturbed patches is very slow. Indeed, recovery from disturbance (in terms of community composition but not in terms of biomass), was only possible after 6 years without herbivory. When herbivores were not excluded (i.e. control plots), disturbed patches remained dominated by *S. perennis* and *C. truxillensis*, with negligible *S. densiflora* recovery over the length of the study. Overall, these findings show that the importance of clonal integration on salt marsh recovery increases with herbivory pressure and that, under high herbivory pressure, marshes may permanently be kept in a state of early succession.

Table 1 Repeated measures ANOVA on the effect of herbivory and clonal colonization on biomass of abundant plant species re-colonization of experimentally created bare patches

Source	df	MS	F	P
<i>Spartina densiflora</i>				
Herbivory (H)	1	23,413.2	77.62	<0.0001
Clonal colonization (C)	1	2,792.2	9.26	0.0078
H × C	1	1,927.8	6.39	0.0223
Error	16	301.6		
Time (T)	2	5,534.2	19.40	<0.0001
H × T	2	5,268.3	18.47	<0.0001
C × T	2	837.0	2.93	0.0676
H × C × T	2	722.5	2.53	0.0952
Error	32	285.2		
<i>Sarcocornia perennis</i>				
H	1	16,202.7	5.78	0.0287
C	1	3,389.3	1.21	0.2879
H × C	1	1,298.4	0.46	0.5060
Error	16	2,805.2		
Time (T)	2	28,348.5	21.18	<0.0001
H × T	2	1,415.6	1.06	0.3590
C × T	2	2,354.5	1.76	0.1884
H × C × T	2	550.1	0.41	0.6664
Error	32	1,338.2		
<i>Distichlis spicata</i>				
H	1	125	17.17	0.0008
C	1	52.4	7.19	0.0164
H × C	1	44.9	6.17	0.0244
Error	16	7.3		
Time (T)	2	12.7	2.34	0.1121
H × T	2	13.0	2.40	0.1065
C × T	2	12.8	2.36	0.1108
H × C × T	2	12.9	2.38	0.1090
Error	32	5.4		
<i>Cressa truxillensis</i>				
H	1	44.1	0.27	0.6098
C	1	474.7	2.92	0.1070
H × C	1	470.7	2.89	0.1084
Error	16	162.8		
Time (T)	2	969.3	9.71	0.0005
H × T	2	1,352.6	13.55	<0.0001
C × T	2	58.6	0.59	0.5617
H × C × T	2	9.2	0.09	0.9122
Error	32	99.8		

Statistically significant values ($p < 0.05$) shown in bold

Sexual and clonal colonization of disturbed zones

In terrestrial systems, plant species composition during the early stages of secondary succession is generally determined by species differences in sexual reproduction strategies,

as seed dispersal, soil seed storage, and germination rates (Grime 2001). However, large belowground occupation by rhizomes, efficient clonal growth, and clonal integration between colonizers and well-established individuals are sometimes the only way to re-colonize empty zones, particularly in systems with relatively high disturbance frequency or strong environmental stress (see Shumway 1995; Pennings and Callaway 2000). Colonization of salt marsh disturbed zones, for example, is known to be strongly dependent on asexual reproduction and clonal integration (Bertness 1999; Pennings and Bertness 2001). Seedling establishment, in contrast, is rare and does not influence recovery (Bertness et al. 1987; Bertness 1999; Angelini and Silliman 2012), as seed germination and seedling survival are strongly limited by the increased soil salinity (Shumway and Bertness 1992). Our results show that sexual reproduction can be important in SW Atlantic salt marsh patch recovery dynamics, as subordinate species are capable of sexually colonizing disturbed zones. Although *S. densiflora* was also capable of sexually colonizing disturbed plots, its importance was very low. This might be in part due to increased soil salinity levels and low seed viability (Bertness et al. 1987; Bortolus et al. 2004), but our evidence shows that colonization was relatively high when herbivores were excluded and clonal colonization was impeded. These results suggest that herbivory is a fundamental force in suppressing *S. densiflora* sexual colonization, thus increasing the importance of clonal integration in patch recovery.

Models of succession and herbivory in salt marshes

Connell and Slatyer (1977) proposed three pathways of succession: (1) facilitation (when pioneer species ameliorate stressful environmental conditions promoting the establishment of late successional species), (2) tolerance (when early successional species do not modify the arrival and establishment of late successional species), and (3) inhibition (first established plants reduce the success of forthcoming species). Particularly in salt marshes, the great majority of examples follow the facilitative pathway, with pioneer species reducing the otherwise too harsh abiotic conditions, and, thus, allowing the establishment of late successional species (Bertness and Leonard 1997; Pennings and Bertness 2001; Angelini and Silliman 2012). Farrell (1991) incorporated the role of herbivores to these succession pathways and predicted that their impact on the rate of succession would depend on herbivore preferences. When herbivores consume early successional species, their impact on the rate of species replacement should vary depending on the succession pathway. However, when herbivores prefer late successional species, they should retard succession regardless of the succession pathway. If competitively superior species are preferred, selective foraging

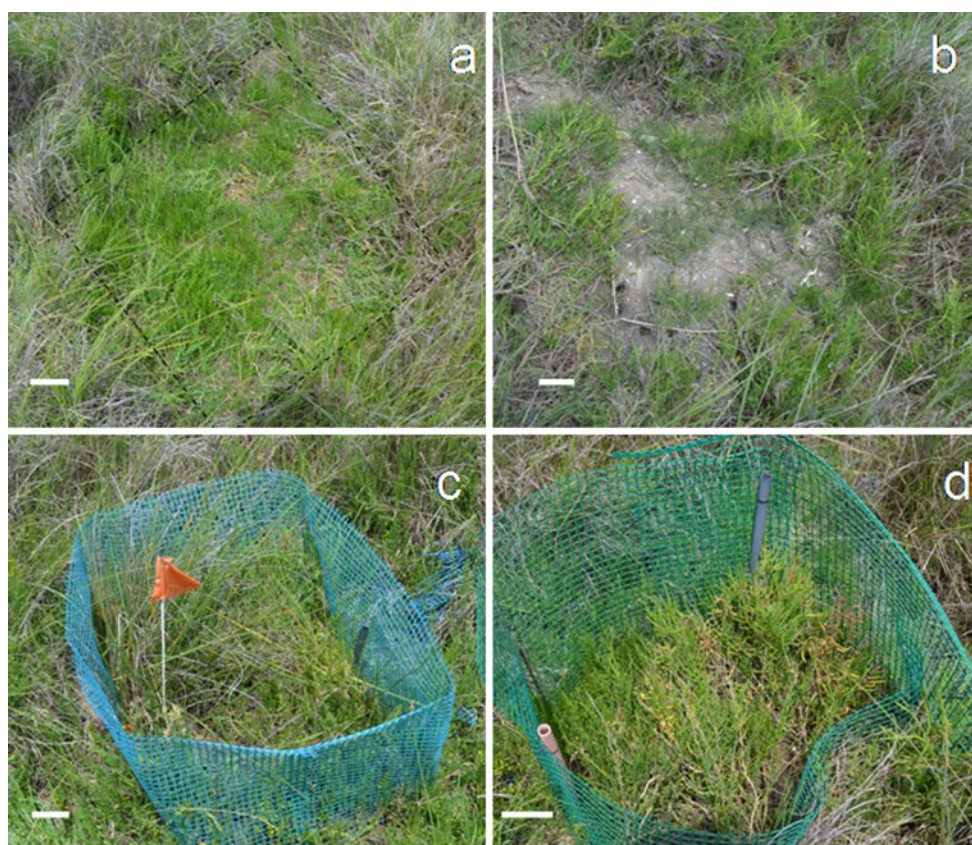


Fig. 2 Photographs of experimental bare patches after 6 years of recovery; **a** unmanipulated controls with extensive colonization of *Sarcocornia perennis* and *Cressa truxillensis*, **b** prevention of clonal colonization with patches of bare space and some colonization of *Sarcocornia perennis* and *Cressa truxillensis*, **c** herbivore exclosures

with extensive colonization of *S. densiflora* and *S. perennis*, similar to background vegetation. **d** Herbivore exclosures and prevention of clonal colonization with strong dominance of *S. perennis* and no *S. densiflora*. White bars 0.1 m

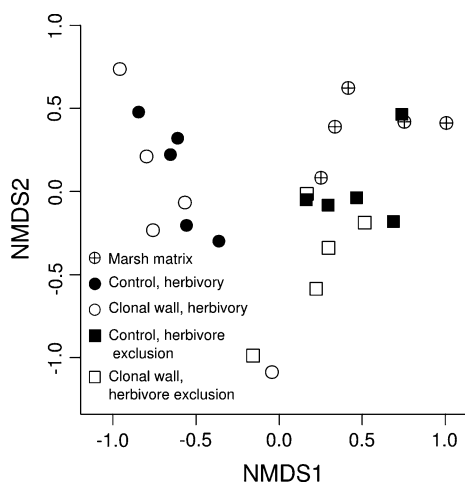


Fig. 3 Non-metric multidimensional scaling (nMDS) plot comparing plant species assemblages across treatments of experimental bare patches after 6 years of recovery. Stress = 0.096

on dominant species is expected to increase plant diversity by slowing down temporal gap closure, avoiding overgrowth of competitively inferior species (Olf and Ritchie 1998). In grassland systems, nevertheless, fast growing, competitively inferior species like annuals and forbs are usually more palatable than matrix grass species (Cates and Orians 1975), and herbivory is expected to decrease plant diversity and even increase the rate of secondary succession. Our results, and others from different salt marshes, are coincident with Farrell's (1991) predictions: when herbivores prefer late successional species, they end up slowing down species replacement, allowing early successional species to dominate disturbed zones for longer periods of time (see Kuijper et al. 2004; Bromberg Gedan et al. 2009). Our results further suggest that the relatively high abundance of *S. perennis* in the higher zones of SW Atlantic salt marshes (see Isacch et al. 2006) can be, in part, the result of the interaction between disturbance and herbivory.

Herbivory as a structuring force in salt marshes

Abiotic stress and nutrient competition were, for a long time, considered to be the only important factors in determining salt marsh community structure (Pomeroy and Wiegert 1981; Adam 1993), but herbivory is now also considered as a force strong enough to influence marsh functioning (Silliman et al. 2005; Jefferies et al. 2006). In contrast with the classic model of marsh secondary succession (Bertness and Shumway 1993; Pennings and Bertness 2001), our evidence shows that herbivores can also have strong effects on this succession dynamic by maintaining the dominance of subordinate species. When herbivores were not excluded, the recovery of *S. densiflora* was negligible even 6 years after initial disturbance, suggesting that patches will hardly return to *S. densiflora* dominance and that herbivores can drive (and maintain) the community to an alternative state (a consumer-driven state; see Bertness et al. 2002; Jefferies et al. 2006; Bromberg Gedan et al. 2009). However, previous results indicate that dominance of *S. densiflora* in the long term can be possible, as (1) *S. perennis* can facilitate *S. densiflora* colonization by protecting young susceptible stems from herbivory (Alberti et al. 2008), and (2) intensity of herbivory is coupled with long-term weather cycles (Alberti et al. 2007; Canepuccia et al. 2010). Years with low herbivory pressure, and *S. perennis* facilitation, can thus allow *S. densiflora* to slowly recover. Therefore, although results of the present study suggest that herbivores can maintain disturbance patches far from pre-disturbance states, the process of succession can be longer than our experimental time frame. If recovery of *S. densiflora* dominance can be achieved in the long term, the general model of facilitation would still hold and explain succession dynamics but, in this case, driven by biological stress (herbivory) instead of physical stress.

Prevailing paradigms of salt marsh functioning have emerged from many experimental studies conducted at relatively few north western Atlantic coastal sites (Pennings and Bertness 2001). In this context, it is uncertain if these generalizations are valid at geographically distant marshes, with different biotic and abiotic contexts (Pennings et al. 2003; Fariña et al. 2009). Current conceptual models of secondary succession in salt marshes (Pennings and Bertness 2001) predict that, either by clonal propagation (at harsh environmental conditions) or by sexual reproduction (at more benign conditions), the complete recovery of disturbance-generated patches occurs in less than 4 years (Bertness and Ellison 1987; Ellison 1987). However, results from southwestern Atlantic salt marshes reveal that, at different intertidal heights (low: Daleo et al. 2011; and high: this study), full recovery after disturbance, if achieved, might take longer than a decade.

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