ENSO episodes modify plant/terrestrial–herbivore interactions in a southwestern Atlantic salt marsh

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ABSTRACT

Hemisphere scale events such as El Niño-Southern Oscillation (ENSO) can alter rainfall regimes worldwide, with important effects on species abundance and distribution. The evidence of ENSO effects on terrestrial communities is, however, restricted to a few ecosystem types. We explored the effects of ENSO episodes on plant/terrestrial–herbivore interactions through changes in the rainfall regime in a southwestern Atlantic salt marsh (Mar Chiquita coastal lagoon, Argentina. 37° 40′S, 57° 23′W). Surveys showed a positive relationship between winter rainfall and the abundance of the wild guinea pig *Cavia aperea*. The highest salt marsh abundances of *C. aperea* were associated with rainy periods during El Niño episodes, and the lowest ones were associated with the driest La Niña episodes. Rainfall was negatively associated with marsh sediment salinity, and experiments revealed that increased salinity reduces growth and increases mortality of cordgrass (*Spartina densiflora*). Salt increase also causes the highest percentage of dry area in *S. densiflora* leaves and reduced carbon content, and more salt content and secretion in *S. densiflora* stems. A factorial experiment in which we manipulated *C. aperea* presence and salinity along the edges of *S. densiflora* patches showed that plants can asexually invade unvegetated areas when salinity is reduced and *C. aperea* is excluded. Conversely, *S. densiflora* edges retracted when salinity was increased or there was *C. aperea* herbivory. Changes in nutritional quality of *S. densiflora* could explain the low herbivory of (and lack of impacts from) *C. aperea* in plots with high salinity. Thus, plant distribution responds directly to climate oscillations through changes in salt stress, and indirectly, through changes in plant–herbivore interactions. Herbivores respond indirectly to climate oscillations through changes in plant food quality, which suggests that top-down effects increase when bottom-up stressors are relaxed. ENSO events have direct and indirect effects on marsh communities that modulate the relative importance of top-down and bottom-up effects and have a considerable effect on the primary productivity of *S. densiflora* marshes.

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1. Introduction

Within the last centuries, alterations in rainfall regimes caused by global climate change have become pronounced worldwide (Collischonn et al., 2001; Karl and Trenberth, 2003; Berbery et al., 2006). Hemispheric scale events, such as El Niño/La Niña Southern Oscillation (ENSO), can alter global rainfall regimes. Climate models suggest that the frequency of ENSO episodes is expected to increase in the coming decades (Timmermann et al., 1999; IPCC, 2007; Bates et al., 2008). Complex relationships between global climate change and multiyear climatic oscillations will undoubtedly have a major effect on worldwide rainfall

intensity on an interannual timescale (Ropelewski and Halpert, 1996; Timmermann et al., 1999; Giannini et al., 2000), and will produce complex outcomes on species abundance and distribution in natural systems.

Rainfall patterns play an important role in spatial synchrony and in the dynamics of natural populations (Ostfeld and Keesing, 2000; Sala, 2006; Holmgren et al., 2006). Consequently, changes in rainfall regime may have diverse impacts by altering interspecific and species/environment interactions (e.g., Martin, 2001; Duffy, 2003; Canepuccia et al., 2008a). There is increasing evidence that extreme rainfall events affect processes in terrestrial communities (Holmgren et al., 2006). However, most information comes from a limited number of ecosystem types (e.g., arid regions, Lima et al., 1999; Holmgren et al., 2001; Farias and Jaksic, 2007; wetland, Canepuccia et al., 2008a). This raises a difficult issue for ecologists because species responses to climate drivers are contingent on a complex array of environmental

and biological variables (Harmon et al., 2009; Tylianakis, 2009). The limited information on different ecosystem types makes predictions about the impact of rainfall change on a given ecosystem uncertain.

Not all terrestrial ecosystems are equally affected by changes in rainfall regime. For example, in arid and semiarid environments of South America (e.g., Lima et al., 1999; Jaksic, 2001; Farias and Jaksic, 2007), North America (e.g., Polis et al., 1997), and Australia (e.g., Letnic et al., 2005) increased rainfall caused by the El Niño episodes triggers surges in plant growth. These productivity fluctuations are transmitted up through the food web (bottom-up effects, Polis et al., 1997), and may also interact with top-down processes (i.e., predators–herbivores–plants, Polis et al., 1998; Lima et al., 2002). Effects of increased rainfall are not only restricted to arid lands. Rainy periods promoted by the El Niño have also been associated with mangrove defoliation (McKillup and McKillup, 1997), changes in growth of boreal forests (Black et al., 2000), alpine forbs (Walker et al., 1995) and agroforests (Vincent et al., 2009). In ecosystems where plants do not undergo frequent intense water constrains (e.g., freshwater wetlands), floods caused by increased rainfall may produce terrestrial habitat loss that results in biodiversity loss and alteration of community interactions (Canepuccia et al., 2007, 2008a, 2009). In salt marshes, prolonged rainfall increase can enlarge the area of the submerged marsh, which may increase marsh plant herbivory by aquatic organism (Alberti et al., 2007). However, effects of rainfall increase could be different at the middle and high salt marsh where tides do not flush regularly.

Salt marshes are highly stressed ecosystems, mainly due to sediment salt accumulation (Bertness et al., 1992). Stress caused by sediment salinity can strongly affect marsh plant growth (e.g., Bertness et al., 1992; Shumway and Bertness, 1992) by limiting water uptake (Grattan and Grieve, 1999; Hu and Schmidhalter, 2005). Many plants can secrete salt through specialized glands to compensate for salt stress (Bradley and Morris, 1991a). However, the nutrient imbalance from salt stress, a consequence of the osmoregulatory function, can modify plant tissue composition (e.g., Cavalieri and Huang, 1981; Bacheller and Romeo, 1992), which can in turn affect consumer preference (e.g. Crain, 2008). If rainfall modifies salt accumulation in the marsh sediment through changes in freshwater input (e.g., Gross et al., 1990; De Leeuw et al., 1991; Miller et al., 2005), rainfall may also change plant growth (e.g., Minchinton, 2002), nutritional value for herbivores (e.g., Gross et al., 1990) and plant–herbivore interactions. Whereas the effects of salt stress on marsh plants have been relatively well studied (e.g., Partridge and Wilson, 1987; Bertness et al., 1992), the link between ENSO and plant/terrestrial–herbivore interactions in marshes have not.

Southwestern Atlantic salt marshes are dominated by the cord-grasses Spartina densiflora and S. alterniflora (Isacch et al., 2006). The wild guinea pig Cavia aperea is the largest mammalian herbivore, found most conspicuously in winter (pers. obs.), in most of these marshes. Cavia aperea feed mostly at the edges of S. densiflora patches. They cut stems at ground level and ingest stem bases including the basal meristematic tissue (pers. obs.), which has a thin primary cell wall (Evert, 2006) with a low proportion of refractory carbon. As a result of this feeding preference, the stems do not regenerate, and C. aperea is therefore likely to affect the extension of S. densiflora patches. We hypothesize that rainfall alteration by ENSO episodes can change growth and nutritional quality of S. densiflora, through changes in marsh sediment salinity, which affects C. aperea food choice and in turn alters the effects of its herbivory. Then ENSO episodes can drive direct and indirect effects on marsh communities by modulating the relative importance of top-down and bottom-up effects. The goal of this study was to evaluate whether plant/herbivore interactions depend on rainfall changes produced by ENSO episodes. Specifically, we examined (1) if rainfall alterations produced by the El Niño episodes (2003 and 2007) and the La Niña (2008) modify abundances of C. aperea, (2) if rainfall changes affect marsh sediment salinity, (3) if changes in sediment salinity alter conditions, growth, and nutritional

quality of S. densiflora, and (4) how all of these affect the interaction between C. aperea and S. densiflora.

2. Materials and methods

2.1. Study site

We worked in the Mar Chiquita coastal lagoon salt marshes (Argentina, 37° 40′S, 57° 23′W; an UNESCO Man and the Biosphere Reserve) during the southern hemisphere winters from 2003 to 2009. During this period, El Niño episodes occurred in 2002–2003 (AGU, 2007) and 2006–2007 (Anyamba et al., 2006), and one La Niña episode occurred in 2008 (see also Climate Prediction Center, September 2009). These marshes are dominated by the cordgrass S. densiflora (Isacch et al., 2006), and the wild guinea pig C. aperea is a frequent winter herbivore in both intermediate and high S. densiflora marsh (see Results section).

2.2. Effects of rainfall alterations by ENSO episodes on C. aperea abundance

We used the daily rate of C. aperea pellet deposition (pellets $m^{-2} day^{-1}$) to study the relationship between abundance of C. aperea and rainfall. Pellet deposition rate is a good indicator of abundance and habitat use by birds and mammals when other natural conditions are similar between habitats (Litvaitis et al., 1994; e.g., Owen, 1971 for geese; Langbein et al., 1999 for hares; Kuijper and Bakker, 2005 for geese and hares; Canepuccia et al., 2008a for fox and wild cat; Cassini and Galante, 1992 for C. aperea). Also, for our study site, the pellet count, instead of direct census, have the advantage that it is not affected by the height of the vegetation (above 1 m; for similar design see Cassini and Galante, 1992) and that includes all population segments (e.g., Litvaitis et al., 1994). The rate of C. aperea pellet deposition was estimated at middle marsh elevations across ten 4 m^2 plots set 10 m apart in areas with similar vegetal cover (differences in cover <5%). These plots were sampled at the end of the austral winter (September) from 2003 to 2009. Before each sampling, we removed all C. aperea pellets from each plot and counted all new pellets deposited over 24 h. Precipitation values were obtained from the Servicio Meteorológico Nacional Argentino for the Mar del Plata station (37° 56′ S; 57° 35′ W), located 25 km south of our study site with similar geographic characteristics. Winter rainfall was correlated (Zar, 1999) with the mean rate of C. aperea pellet deposition for the 7 years studied.

2.3. Effect of rainfalls on marsh sediment salinity

We also studied the relationship between sediment salinity and rainfall at the middle marsh. For this purpose we monitored sediment salinity during the winter of 2007 by sampling a core (4 cm diameter, 3 cm deep) of sediment in the center of each plot described previously. The sediment samples were weighed and dried to constant weight. The dried samples were then mixed with a known volume of distilled water, and salinity was measured after 24 h with a refractometer (precision of 1‰). The value was corrected by the initial sample water volume to reflect the original salt concentration (e.g., Goranson et al., 2004). We performed a correlation analysis (Zar, 1999) to study the relationship between sediment salinity and weekly rainfall.

2.4. Effects of sediment salinity on growth and nutritional quality of S. densiflora, and on plant/herbivore interactions

During five months, starting in May 2007, we manipulated sediment salinity (adding salt) and C. aperea presence (using exclosures) to evaluate the effects of salinity on growth and nutritional quality of S. densiflora and on plant/herbivore interactions. The experiment had fifty experimental plots (0.25 m^2 in area) located in

the middle marsh (for similar experimental units see Daleo et al., 2008, 2009; Alberti et al., 2010). In each plot, approximately 70% of the area enclosed was covered by *S. densiflora* separated by an edge of 30% bare surface. We randomly assigned plots to the following treatments: (1) salt addition, (2) *C. aperea* exclusion, (3) salt addition and *C. aperea* exclusion, (4) non-manipulated plots (controls), and (5) cage control (two-sided exclosures). Salt supplementation was added weekly to the sediment surface (for similar design see Bowdish and Stiling, 1998; Moon and Stiling, 2000; Silliman et al., 2005) of the salt addition plots to keep salinity (here and thereafter expressed as parts per thousand) close to values observed during dry winters (60). We added salt gradually to avoid sudden changes: 30 the first week, 40 the second week and then maintained 60 until the conclusion of the experiment. Salinity was monitored weekly in each plot as described previously. *Cavia aperea* exclusion plots were surrounded by a 2 cm mesh plastic fence 50 cm high. All plots were delimited, including the places of the exclusion fence, without sediment removal to prevent alter the substrate dynamics under the action of rainfall and tidal runoff, and consequently alter plant growth. The 2 cm mesh aperture excluded *C. aperea* and allowed free movement of all other herbivores (i.e., invertebrate herbivores, Canepuccia unpubl. data).

2.4.1. Effects of sediment salinity on growth and nutritional quality of S. densiflora

We compared stem size, plant condition and tissue composition of *S. densiflora* stems from the plots with and without salt addition to analyze the effect of salt stress on growth and nutritional quality of plants. At the end of the experiment (September 2007), we randomly cut one live stem from the non-exclosure plots with and without salt addition. Stem samples were taken at the edge of plant patches, in the side of the plot that limit with bare surface. To estimate stem growth, we measured the basal width and the entire length of each stem. To evaluate plant conditions, we estimated the percentage of total dry area in the four youngest leaves of each stem, including live: all or some part of leaves are green; or dead: whole leaves are dry. To analyze nutritional quality of stems, we cut a set of five live stems from the non-exclosure plots with and without salt additions. Given that *C. aperea* typically removes only a few centimeters at the stem base, we analyzed tissue composition at the basal 5 cm of collected stems. The basal sections were dried (48 h at 65 °C) and total nitrogen (N), phosphorus (P) and carbon (C) content (% DW) measured. Nitrogen and carbon content was measured using a CHN Carlo Erba auto-analyzer (see Strickland and Parsons, 1972), and phosphorus content was measured through combustion of organic phosphorus into inorganic phosphorus with subsequent analysis by Skalar Auto-Analyzer (see Solorzano and Sharp, 1980; Fourqurean et al., 1992).

We also analyzed the salt content of *S. densiflora* tissue and salt deposits on the epidermis of *S. densiflora* stems from the non-exclosure plots with and without salt additions. At the end of the experiment we cut one live stem from each of the plots and, as with nutrient content analysis, only the first 5 cm of the stem were analyzed. The external salt deposited on the stem epidermis (likely excreted salt) was estimated by washing the surface with a known volume of distilled water and then measuring salinity in the washed-off water. These measured salinities were corrected by the volume of washed-off water to reflect the concentration of salt per stem area. We used these washed stems to estimate tissue salinity. Stem tissue salinity was estimated by rehydrating the stems from ground dry weight (48 h at 65 °C) in a known volume of distilled water. Salinity of the supernatant was measured after 24 h and corrected by the initial water volume to reflect the tissue salinity (e.g., Goranson et al., 2004). We used Welch's approximate *t*-test (Zar, 1999) to evaluate the null hypothesis of no differences (1) in stem width and length, (2) percentage of dry area in

leaves, (3) tissue composition (i.e., N, P, C and salt content) and (4) salt on the epidermis of *S. densiflora* stems.

2.4.2. Effects of sediment salinity on plant/herbivore interactions

We compared the use of plots by *C. aperea* (those with and without salt addition) to evaluate if sediment salinity modified *C. aperea* marsh habitat use. We used the rates of *C. aperea* pellet deposition as an indicator of the use of these plots. Every week during the experiment, before adding the new salt ration, we counted and removed all *C. aperea* pellets from each plot. To evaluate herbivory on *S. densiflora*, each week we also counted the number of *S. densiflora* stems consumed by *C. aperea* in plots with and without salt addition. The foraged stems were easily recognized given that *C. aperea* has a peculiar grazing mode, cutting stems at the base, consuming only a few centimeters and discarding the rest on the ground. We evaluated the null hypothesis of no differences between plots with and without salt addition in the number of *C. aperea* pellets and the number of consumed stems collected during the experiments, using Welch's approximate *t*-test (Zar, 1999).

Because both herbivory and salinity can affect *S. densiflora* patch expansion (interface between marsh plants and bare surfaces), we marked the edge of each plot between the vegetated and unvegetated area using 10 plastic flags. At the end of the experiment, we quantified the average distance between the new edge and the position of the flags. We assigned positive values to the asexual colonization of unvegetated areas and negative values to the reduction of vegetated area. We then compared edge movement with and without rodents and salt addition using Tukey tests after a two-way ANOVA (Zar, 1999). To detect exclosures effects, we compared edge movement between control and cage control plots using Welch's approximate *t*-test (Zar, 1999).

3. Results

3.1. Effects of rainfall alterations by ENSO episodes on C. aperea abundance

Pellet deposition by *C. aperea* was maximum during the El Niño episodes, with the highest winter rainfall values (El Niño 2003: mean = 6.4, SE = 1.9 pellets m^{-2} day^{-1}; El Niño 2007: mean = 6.0, SE = 2.7 pellets m^{-2} day^{-1}, Fig. 1A). In contrast, the minimum pellet deposition occurred during winters with the lowest rainfall values (2006: no pellets were found; La Niña 2008: mean = 0.4, SE = 0.2 pellets m^{-2} day^{-1}; Fig. 1A). There was a positive relationship between winter rainfall and pellet deposition across the study period (from winter of 2003 to winter of 2009; $r^2 = 0.80$, $F = 15.63$, $p = 0.01$, $n = 7$, Fig. 1A).

3.2. Effect of rainfall on marsh sediment salinity

In the winter of 2007, sediment salinity in the middle marsh ranged between 11 and 53 and was negatively correlated with weekly rainfall. ($r^2 = 0.58$, $F = 14.06$, $p < 0.05$, $n = 11$, Fig. 1B).

3.3. Effects of sediment salinity on S. densiflora condition and growth, and on plant–herbivore interactions

3.3.1. Effects of sediment salinity on growth and nutritional quality of S. densiflora

There were no differences in basal width (mean = 2.63 mm, SE = 0.52 mm) or length of *S. densiflora* stems (mean = 214.40 mm, SE = 52.00 mm) between salt addition and control plots (width: mean = 3.09 mm, SE = 0.58 mm, $t_{17.8} = -1.86$, $p = 0.08$; stem length: mean = 266.53 mm, SE = 117.50 mm, $t_{12.4} = -1.28$, $p = 0.22$). However, plants from salt addition plots decreased their photosynthetic area due to a higher percentage of senescent area in their leaves (mean = 50.53%,
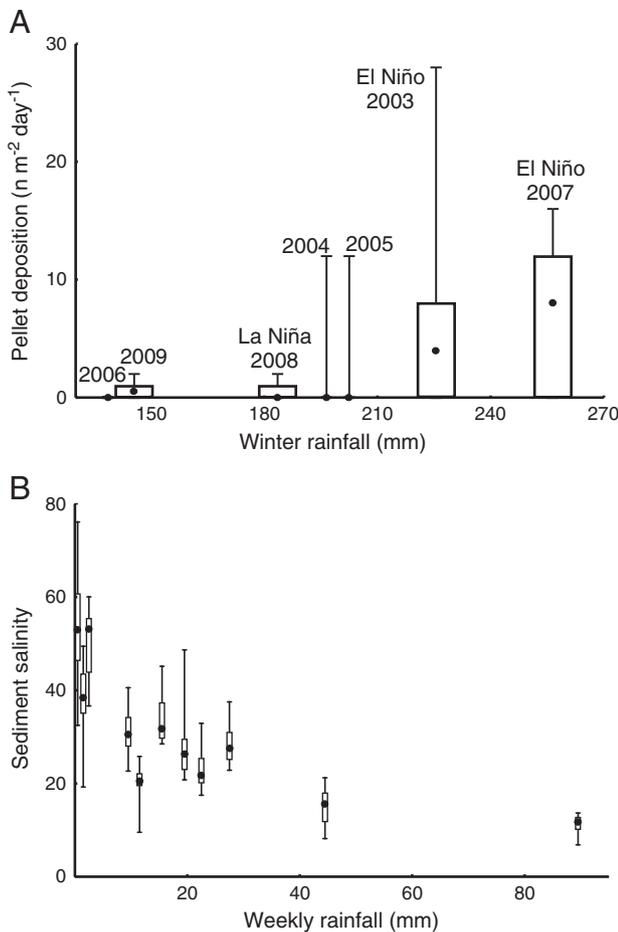
A

B

Fig. 1. Relationship between (A) winter rainfall and mean *C. aperea* pellet deposition between 2003 and 2009; and (B) weekly rainfall and mean sediment salinity at the middle marsh in the winter of 2007. Here and thereafter, boxes represent 25th and 75th percentiles, vertical lines represent 1st and 99th percentiles, and point inside boxes represents the median.

SE = 13.26) than did plants from control plots (mean = 32.93%, SE = 11.91, $t_{17.8}$ = 3.12, p < 0.05). Tissue composition analyses revealed that *S. densiflora* from plots where salinity was increased showed a higher water content (mean = 47.35%, SE = 1.48%), lower C content (mean = 40.03%, SE = 0.23%), and higher salt content (mean = 0.11%, SE = 0.01%) than plants from control plots (water: mean = 38.94%, SE = 2.02%, $t_{16.5}$ = 3.35, p < 0.05; C: mean = 41.74%, SE = 0.34%, $t_{15.9}$ = −4.07, p < 0.05; salt: mean = 0.07%, SE = 0.01%, $t_{17.5}$ = 2.27, p < 0.05). There were no differences in N and P content between the plants in plots with salt addition (N: mean = 0.29%, SE = 0.02%; P: mean = 0.045%, SE < 0.01%) and those in control plots (N: mean = 0.27%, SE = 0.02%, $t_{17.9}$ = 0.59, p = 0.56; P: mean = 0.04%, SE < 0.01%, $t_{16.1}$ = 0.43, p = 0.67). *Spartina densiflora* stems had more salt on the epidermis in plots with salt addition (mean = 40.97, SE = 10.53 µg mm^{-2}) than in control plots (mean = 10.53, SE = 4.83 µg mm^{-2}, $t_{9.3}$ = 2.50, p < 0.05).

3.3.2. Effects of sediment salinity on plant/herbivore interactions

During the experiment we removed less *C. aperea* pellets in salt addition plots (mean = 4.9, SD = 1.3, pellets per week^{-1}) than in the control plots (mean = 18.5, SD = 4.9 pellets per week^{-1}; $t_{10.4}$ = −2.69, p < 0.05). We also found lower stem consumption by *C. aperea* in salt addition plots (mean = 1.8, SD = 0.5 stems per week^{-1}) than in control plots (mean = 10.8, SD = 2.3 stems per week^{-1}; $t_{9.8}$ = −3.74, p < 0.05).

As expected from the low abundances of *C. aperea* during dry winters and the low use of plots where salinity was increased, the herbivore did not have any impact on *S. densiflora* edge expansion rates in plots where

salinity was increased. Under increased salinity, expansion rates tended to be negative regardless of whether the plot was open to *C. aperea* or not, due to increased stem mortality (Fig. 2). In contrast, *C. aperea* strongly influenced *S. densiflora* edge expansion rates in plots without salt addition; in those plots, marsh patches only expanded their perimeter towards the bare surfaces if herbivory by *C. aperea* was prevented (interaction effect: F = 5.82, p < 0.05; Fig. 2, Table 1). There were no cage effects (control: mean = −0.70, SE = 0.20 cm; cage control: mean = −0.67, SE = 0.20, t_{18} = −0.09, p = 0.93).

4. Discussion

Our study shows that the abundance of *C. aperea* in the marsh increased during rainy periods caused by El Niño episodes and decreased during dry periods including La Niña episodes. Dry periods are also associated with increased salinity in marsh sediment. Following increased salinity, the proportion of dry *S. densiflora* leaves, water and salt content, and salt deposited on the epidermis increases and C content decreases. Our experimental manipulation in 2007 suggests how these rainfall-induced changes may affect the role of *C. aperea* as a control of *S. densiflora* patch expansion rates. In dry years, *C. aperea* is not present in the marsh, possibly because of low marsh palatability due to high salt content, and does not influence patch expansion rates. In rainy years, however, *C. aperea* is a prominent control of patch expansion rates due to intense grazing induced by higher palatability (i.e., lower salt content). It is interesting to note that the low expansion rates observed in plots with high salinity (both open and caged and therefore likely due to the deleterious effects of high salt content on plant growth) do not differ from the low expansion rates observed in plots without salt addition and open to *C. aperea*, suggesting that precipitation and herbivory by *C. aperea* are equally strong controls of *S. densiflora* patch expansion rates.

High and intermediate salt marsh elevations are usually characterized by relatively high sediment salinity due to irregular tidal flushing and high evapotranspiration (e.g., Bertness et al., 1992). El Niño episodes increase rain events, resulting in a decrease of sediment salinity. In fact, mean sediment salinity was five times higher after dry periods than after heavy rainy periods. The frequency and intensity of ENSO episodes can modify the growth (e.g., Minchinton, 2002) and nutritional condition of marsh plants through oscillations in sediment salinity and salt content in plants. Due to the toxicity of Na$^+$ and Cl$^-$ (Hu and Schmidhalter, 2005), higher sediment salinity can reduce N uptake by plants, with consequences to growth and survival (e.g., Bradley and Morris, 1991b;
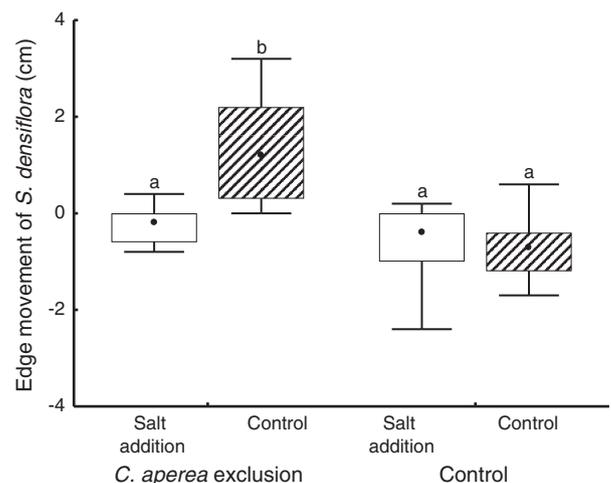

Fig. 2. Effects of salt addition, by stems mortality increases, and exclusion of *C. aperea* herbivory, on the expansion or contraction of patch edge of *Spartina densiflora* after 5 experiment months. Different letters indicate significant differences (p < 0.05) by Tukey test after two-way ANOVA.

Table 1
Results of the two-way ANOVA analyzing the effect of salt addition and *Cavia aperea* exclusion on the expansion or contraction of *S. densiflora* cover in the edge between plant patches and bare sediment.

	SS	df	MS	F	p
C. aperea exclusion	17.56	1	17.56	19.48	<0.01
Salt addition	8.03	1	8.03	8.91	<0.01
C. aperea exclusion x Salt addition	5.24	1	5.24	5.82	0.02
Error	32.44	36	0.90		

Bowdish and Stiling, 1998; Hu and Schmidhalter, 2005). However, in our experiment, N content in plant stems did not differ between high salinity and control plots. Plant growth at higher salt stress can allocate a greater proportion of available N to the production of osmolites (e.g., proline), resulting in reduced plant growth, leaf expansion and carbon gain, but with no noticeable change in total N content (e.g., Cavalieri and Huang, 1981; Richardson and McCree, 1985). The specific mechanisms by which N content remained unaltered with increased sediment salinity have not been determined, but *S. densiflora* was negatively affected by the increase in sediment salinity, showing a lower carbon gain and higher senescent tissue in leaves. The increase of the senescent area in *S. densiflora* leaves under high salinity may result in decreased photosynthetic capacity, which might also explain the higher stem mortality in those treatments that finally led to a retraction of the plant patch edge. As an adaptation to salt stress plants can increase salt excretion, which contributes to a decrease in tissue salt concentration (Bradley and Morris, 1991a). In our study, plants exposed to increased salinity increased their salt content by about two times and the amount of salt deposited on the epidermis by about four times. These changes most likely affected the nutritional quality of *S. densiflora* for consumers, which explains the low abundance of *C. aperea* in the marsh during dry years and the low herbivory in (and lack of *C. aperea* impact on) the plots with high salinity.

Palatability of marsh plants usually changes in relation to salinity gradients within marshes (e.g., Hemminga and van Soelen, 1988; Goranson et al., 2004) and to salinity gradients on a geographic scale (e.g., Pennings et al., 2001; Salgado and Pennings, 2005). In fact the abundance and diversity of vertebrate herbivores feeding in salt marshes is lower than in freshwater marshes (Odum, 1988; Greenberg et al., 2006). Body mass of herbivores generally decreases as salt content in their grass diets increases (Kam and Degen, 1993; Shanas and Haim, 2004). Some herbivores change their behavior and habitat use to minimize salt stress. For example, meadow voles *Microtus pennsylvanicus* consume dew and rain drops, and selectively eat grasses with low salt content (Getz, 1965). Our observations suggest that *C. aperea* mainly inhabits areas upland from the marsh (areas with lower salinity, e.g., Odum, 1988; Bertness et al., 1992) during non-ENSO and La Niña winters, but moves into the salt marsh during El Niño episodes when *S. densiflora* is more palatable.

Herbivores can have important effects on marsh ecosystems (Hik et al., 1992; Jefferies et al., 2006; Kuijper and Bakker, 2005). Among them, small mammals can have important though underappreciated effects on marsh habitat (e.g., Howell, 1984; Canepuccia et al., 2008b; Crain, 2008). Our factorial experiment, manipulating *C. aperea* presence and salinity in the edge of *S. densiflora* patches, showed that this herbivore drastically reduced patch expansion rates if salinity remained within typical values for rainy years. Grazing at the perimeter of plant patches can have important consequences for plant colonization and patch closure (e.g., Bishop, 2002), limiting the potential for primary production (e.g., Silliman et al., 2005) and function in marsh ecosystems (e.g., Fagan and Bishop, 2000). Grazing can also increase the area of open spaces, which in turn can increase the diversity of ecological niches within the ecosystem. *Cavia aperea* produced these impacts in our study, but only during rainy years. This finding is consistent with models that show that consumer effects are only noticeable within certain domains of environmental gradients

(Menge and Sutherland, 1987; Bertness and Callaway, 1994; Bruno and Bertness, 2001). We found that herbivory by *C. aperea* during rainy years has an important top-down effect on *S. densiflora*.

The frequency of ENSO episodes and associated rainfall oscillations are predicted to increase in the coming years across all continents (Timmermann et al., 1999; Giannini et al., 2000; IPCC, 2007; Bates et al., 2008). The impact of these rainfall oscillations on terrestrial ecosystems is still largely unknown. It might be profound and complex (Holmgren et al., 2006; Farias and Jaksic, 2007 for desert; Canepuccia et al., 2008a, 2009 for fresh water wetlands, our study for salt marshes). We expect an increased frequency of the El Niño episodes will increase *C. aperea* herbivory on *S. densiflora* (with an inverse response during La Niña episodes), which appears to be an important control of the plant's growth and productivity. Increased frequency of ENSO episodes may, by altering herbivore/plant interactions, alter bottom-up effects and top-down pressure, and substantially affect the primary productivity and ecological functions of *S. densiflora* in southwestern Atlantic marshes.

Acknowledgements

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