

Beyond competition: the stress-gradient hypothesis tested in plant–herbivore interactions

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Abstract. The stress-gradient hypothesis predicts that interactions among plants are context dependent, shifting from facilitation to competition as environmental stress decreases. Although restricted to facilitation/competition, the mechanistic model behind the hypothesis is easily modified to include other negative interactions that are as important as competition in structuring natural communities, e.g., herbivory. To evaluate this hypothesis we experimentally tested if the balance between the facilitative and trophic effect of an intertidal, burrowing, herbivorous crab in marsh plants is context dependent and shifts from positive to negative as stress decreases. By sampling salt marshes differing in sediment size characteristics, we show that sites with larger sediment particle size had less stressful oxygen levels than sites with fine sediment particles, and that the level of stress was reduced by the presence of crab burrows. We then conducted a factorial experiment manipulating sediment size and crab presence. Results show that, by decreasing soil anoxic stress, crabs increase plant growth in stressful zones, but their ecological importance as herbivores increases in more benign zones. Our findings suggest that the balance between positive and negative interactions along stress gradients is more important than previously perceived and also applies to facilitation and herbivory between animals and plants.

Key words: burrowing crabs; ecosystem engineers; environmental gradients; herbivory; *Neohelice (Chasmagnathus) granulata*; positive interactions; southwestern Atlantic salt marshes (Argentina); *Spartina*; stress-gradient hypothesis.

INTRODUCTION

The structure of natural communities is usually the result of a complex combination of interactions among their components, where the relative importance of each interaction can be a function of both physical and biological conditions (Callaway 1995, Callaway and Walker 1997, Bruno et al. 2003). In this context, the environmental-stress model predicts where competition and predation would be important relative to environmental stress (Menge and Sutherland 1987). Given that high trophic-level species are expected to be more susceptible to environmental stress than species from more basal levels, the model predicts that, as stress increases, the importance of structuring variables will shift from predation to competition and then to abiotic stress. Later, this model was modified to include positive interactions in the stress-gradient hypothesis (SGH; Bertness and Callaway 1994, Callaway and Walker 1997; see also Brooker et al. 2008). The SGH predicts that the importance of negative competitive effects is higher under benign environmental conditions, whereas positive facilitative effects increase in importance as

environmental stress (either biotic or abiotic) increases (Bertness and Callaway 1994, Callaway and Walker 1997). The SGH is supported by various studies conducted in a wide variety of plant systems and with different environmental gradients (e.g., Pugnaire and Luque 2001, Callaway et al. 2002, Wright et al. 2006, Eränen and Kozlov 2008). Most of those studies involved some kind of environmentally mediated positive interaction performed by a potential competitor, as habitat amelioration, physical protection from enemies, nutrient enrichment, or chemical protection vs. light, nutrient, or space competition (see Callaway 1995, Stachowicz and Hay 1999). The balance of interactions between species that are not potential competitors but have a trophic relation, although initially suggested to behave in similar way (Connell 1975, Menge and Sutherland 1987, see also Bruno et al. 2003), remains poorly studied.

Ecosystem engineers affect other species through environmentally mediated interactions (Jones et al. 1994, 1997, Hastings et al. 2007), thus their effects and impacts upon natural communities may be strictly context dependent. Ecosystem-engineer species are not only engineers, but can also be competitors, predators, or prey within their communities (Wilby et al. 2001). Thus, their ecological importance (see Jones et al. 1997) may be a balance between their roles as ecosystem engineers and their roles as trophic or competitive

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components (Wilby et al. 2001). Shrub mounds in arid systems, classic examples of ecosystem engineers, are known to have great effect on plant growth, species richness, and community composition by increasing soil moisture (Wright et al. 2006). However, the magnitude of this effect is a function of water availability (Wright et al. 2006) and, as precipitation increases (and growing conditions improve), shrubs are no longer ecosystem engineers and, as SGH predicts, their ecological importance as competitors increases (see Guo and Berry 1998). This balance between facilitative and negative effects is not necessarily restricted to competitors. Species that modulate environmental factors can have great positive effects upon other species under some conditions (see Jones et al. 1997), but the engineering activity or feature can become ambiguous under other conditions (i.e., the engineering activity can have no effect upon physical factors). Therefore the relative importance of those species as predators, prey, or competitors may increase. The mechanistic model behind the SGH is, thus, easily modified to include other interactions beyond facilitation/competition, such as facilitation/herbivory (see also Bruno et al. 2003).

Salt marshes along the southwestern Atlantic coast are characterized by the presence of salt-tolerant grasses of the genus *Spartina* (*S. densiflora* and *S. alterniflora*) that grow year-round, forming dense monospecific stands across the entire intertidal (see Bortolus 2006, Isacch et al. 2006). Within these marshes, burrowing crabs of the species *Neohelice* (*Chasmagnathus*) *granulata* commonly occur at high densities, (often >60 crabs/m²; e.g., Iribarne et al. 1997). Burrowing activities of this crab can transport up to $2.5 \text{ kg}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ of sediment from deeper soil layers to the surface (Iribarne et al. 1997) and result in dense matrices of burrows (up to 0.1 m in diameter and 1 m deep) that comprise up to 25% of the top 0.5 m of soil volume. The presence of crabs greatly impacts sediment chemistry (e.g., nitrification, denitrification, organic-carbon oxidation) and enhances both soil drainage and aeration (Gutierrez et al. 2006, Fanjul et al. 2007). As happens with burrowing organisms in other salt marshes (e.g., Bertness 1985), their soil oxygenation can positively affect plant growth (Daleo et al. 2007). However, the crabs are also herbivores (Iribarne et al. 1997, Bortolus and Iribarne 1999) and can exert strong control over marsh plant production (Costa et al. 2003, Alberti et al. 2007). This simultaneous dual role (ecosystem engineer and herbivore) generates an apparent contradiction because experimental results show positive effects of crabs upon plant production in some cases (Daleo et al. 2007), but negative effects in others (i.e., Bortolus and Iribarne 1999, Alberti et al. 2007).

The objective of this work was to evaluate if the balance between the negative effect, produced by herbivory, and the positive effect, produced by ecosystem-engineering activities, of the burrowing crab *N. granulata*, upon plant growth, is regulated by the

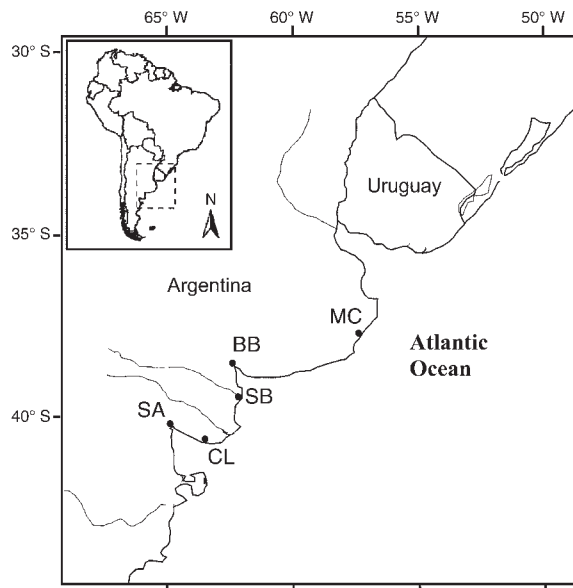


FIG. 1. Map of the southwestern Atlantic coast showing the location of the five salt marshes studied in this work: MC, Mar Chiquita coastal lagoon; BB, Bahía Blanca estuary; SB, San Blas Bay; CL, Caleta Los Loros; SA, San Antonio Bay.

physical context where interactions occur. We expected that the positive effect of burrowing activities would depend on the sediment levels of anoxia. Anoxic stress, for instance, may be important in zones with fine-grain sediment, where the presence of crabs may affect sediment oxygenation, allowing plant growth. Sediments with large grain size, in contrast, may have better oxygenation, thus suppressing the possible positive effect of burrows but retaining the negative effect of herbivory.

METHODS

To evaluate if the effect of crabs in sediment aeration was context dependent, we selected five salt marshes along the southwestern Atlantic coastline, all located in Argentina (see Fig. 1): Mar Chiquita Coastal Lagoon ($37^{\circ}32' \text{ S}$), Bahía Blanca ($38^{\circ}41' \text{ S}$), and Caleta los Loros ($41^{\circ}01' \text{ S}$), characterized by sediments of fine grain size; and San Blas Bay ($39^{\circ}48' \text{ S}$) and San Antonio Bay ($40^{\circ}45' \text{ S}$), characterized by sediments of large grain size (P. Daleo, *personal observation*). At each salt marsh, and to confirm the expected differences in sediment granulometry, the grain size distribution was estimated by the extraction of three samples of sediment (0.3 m depth, 0.1 m diameter). Sediment was sieved and fractions $>1000 \mu\text{m}$ (cobble and pebble), $1000\text{--}125 \mu\text{m}$ (sand), and $<125 \mu\text{m}$ (silt and clay) were separated and dried (60°C , 72 h), and then the relative mass of each fraction was measured. Vertical profiles of sediment redox potential (Eh) were measured in sites both with ($n = 3$) and without crabs ($n = 3$) at 0–10 mm, 10–20 mm, 30–40 mm, 50–60 mm, 70–80 mm, and 90–100 mm depth intervals, at each salt marsh. Eh was measured in situ by

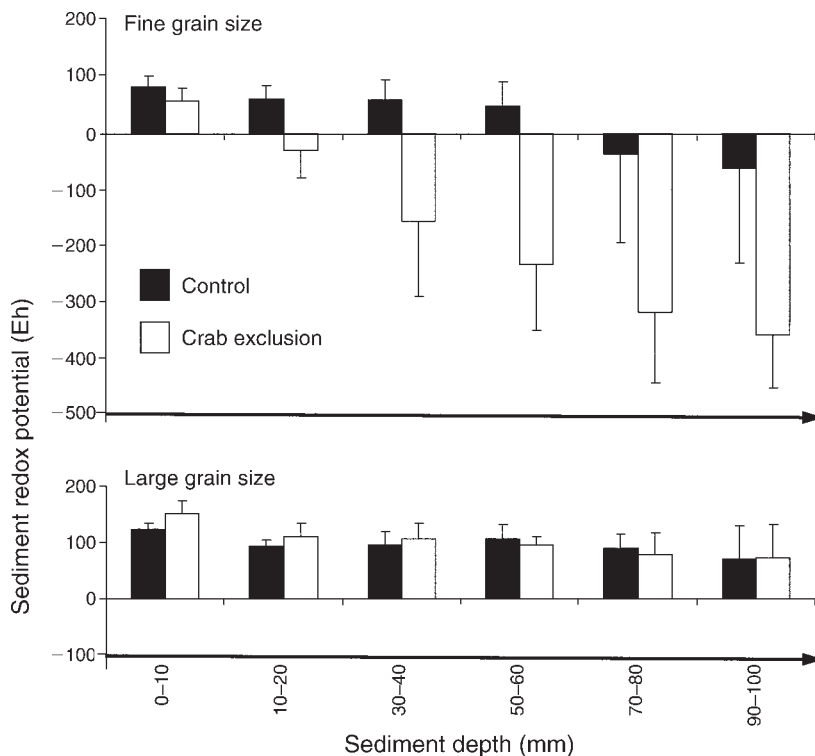


FIG. 2. Effect of experimental exclusion of the crab *Neohelice (Chasmagnathus) granulata* and sediment grain-size manipulation on sediment redox potential (1 Eh = 1 mV).

pushing into the sediment a combined Pt electrode with Ag/AgCl internal reference (HI-3230B, Hanna Instruments [Buenos Aires, Argentina]; see Daleo et al. [2007] for further description). The null hypothesis of no difference on grain size between salt marshes was evaluated with ANOVA (Zar 1999). For each salt marsh, the null hypothesis of no effect of crab burrows on sediment redox potential was evaluated with nested ANOVA with crab burrows, vertical profile (nested in crab burrows), and depth as main factors (Zar 1999).

To evaluate the effect of the sediment grain size on the balance between negative and positive effects of the crabs on plant growth, a factorial experiment was carried out at San Antonio Bay. This is a $\sim 80\text{-km}^2$ embayment with up to 9 m semidiurnal tides. The intertidal zone is characterized by sandy-pebble flats at lower tidal elevations (i.e., 0–3 m above mean low tidal level, hereafter MLTL) and salt marshes dominated by the smooth cord grass *Spartina alterniflora* occurring higher in the intertidal slope (i.e., 3–10 m above MLTL). The experiment was performed at ~ 5 m above MLTL (i.e., middle marsh) in a location near San Antonio Oeste town, at the western portion of the Bay. The experiment consisted of 28 experimental units (0.7×0.7 m). In each unit, sediment was removed to a depth of 0.5 m. In 14 of those units, sediment was replaced by sediment of large grain size (characteristic of the surrounding environment), whereas in the remaining

14 units, sediment was replaced with fine sediment obtained by sieving the ambient sediment through a $1000\text{-}\mu\text{m}$ mesh. In half of the experimental units of each group (i.e., large and fine grain size), crabs were excluded using exclusion cages. Exclusion cages ($0.7 \times 0.7 \times 0.7$ m, 0.3 m deep) were constructed with a plastic mesh (10-mm opening) and supported by iron stakes in each corner. In the remaining seven units of each crab group, crabs were not excluded. Once sediment manipulation was concluded, *S. alterniflora* transplants were moved to those experimental units. Transplants (0.3×0.3 m, 0.5 m depth of sediment containing ~ 20 live and intact stems of *S. alterniflora*) were placed in the center of each experimental unit. Seven control cages that consisted of exclusion cages but with two open walls (allowing crabs to freely move in and out) were set up to test for caging artefacts. Seven additional units were marked and left unchanged (with the sediment and plants originally present) as references to evaluate the existence of artifacts associated with sediment manipulation and plant transplant. The experiment began on 12 June 2007, and after 11 months (10 May 2008) sediment redox potential in each experimental unit was measured as explained above. The number of live and dead stems in a 0.3×0.3 m square centered in each unit was quantified, and the mean height of stems (estimated by averaging the height of five randomly chosen stems per plot) was measured. Aboveground plant material was

harvested and classified as dead and live material. Both fractions were dried (60°C, 72 h) and weighed (precision: 0.0001 g). The null hypotheses of no effects of crab exclusion and sediment manipulation on sediment redox potential was evaluated with three-way ANOVA with crab presence, sediment grain size, and depth as main factors. The null hypotheses of no effects of crab exclusion and sediment manipulation on stem height, stem density, and plant biomass were evaluated with two-way ANOVA with crab presence and sediment grain size as main factors (Zar 1999). To evaluate the presence of possible artifacts associated with enclosures, the null hypotheses of no difference in all measured variables between control cages and control units were evaluated with *t* tests (Zar 1999). To evaluate the existence of possible artifacts associated with sediment manipulation and plant transplant, the null hypotheses of no differences in any measured variable between control units and experimental units that correspond to large-grain sediment and no exclusion of crabs were evaluated with *t* tests (Zar 1999). To evaluate if sediment manipulation or grain size affected crab herbivory, we counted the number of leaves with distinctive damage from herbivory (see Alberti et al. 2007). The null hypothesis of no differences in the proportion of leaves with herbivory damage between large sediment, fine sediment, and control plots was evaluated with ANOVA (Zar 1999)

RESULTS

As expected, the proportions of each sediment fraction were different between salt marshes (cobble/pebble, log-transformed data, $F_{4,10} = 300.61$, $P < 0.0001$; sand, $F_{4,10} = 6.21$, $P < 0.01$; silt/clay, $F_{4,10} = 61.39$, $P < 0.0001$). The two salt marshes chosen for their large-grain sediments (San Blas Bay and San Antonio Bay) were characterized mainly by cobble and pebble whereas the three salt marshes chosen by their fine-grain sediment (Mar Chiquita, Bahía Blanca, and Caleta los Loros) were characterized by a mix of sand, silt, and clay. Crab presence increased sediment redox potential only at salt marshes characterized by fine sediments (i.e., Mar Chiquita, Bahía Blanca, and Caleta los Loros). At those salt marshes, redox potential rapidly decreased with depth in the absence of burrows but remained higher and relatively constant in zones with burrows (Appendix A). At San Blas Bay and San Antonio Bay, in contrast, redox potential was higher and less variable with depth, without effects of burrows (Appendices A and B).

Sediment manipulation was effective and led to a significant change in the frequency distribution of grain size. At the end of the experiment, plots intended to have fine grain size were characterized mainly by sand, silt, and clay whereas sediments intended to have large grain size were mainly characterized by pebble, cobble, and sand. There were no differences in the proportion of leaves with distinctive herbivory marks between plots

TABLE 1. Results of two-way ANOVA evaluating the effect of experimental exclusion of the crab *Neohelice (Cahsmagnathus) granulata* (Crabs) and manipulation of the sediment grain size (Sediment) on *Spartina alterniflora* growth.

Source of variation	df	MS	F	P
Height				
Crabs, C	1	54.32	2.98	0.097
Sediment, S	1	100.32	5.50	0.027
C × S	1	160.32	8.79	0.0067
Error	24	18.23		
Live stems				
C	1	63	4.36	0.047
S	1	206.29	14.29	0.0009
C × S	1	195.57	13.54	0.0012
Error	24	14.44		
Total stems				
C	1	41.20	1.31	0.26
S	1	132.14	13.73	0.0011
C × S	1	31.46		
Error	24			
Live biomass				
C	1	1.46	0.19	0.66
S	1	42.58	5.69	0.025
C × S	1	151.15	20.20	0.0001
Error	24	7.48		
Dead biomass				
C	1	17.64	1.82	0.19
S	1	2.78	0.29	0.6
C × S	1	54.97	5.68	0.025
Error	24	9.68		
Total biomass				
C	1	8.96	0.33	0.57
S	1	67.10	2.49	0.13
C × S	1	388.44	14.43	0.0009
Error	24	26.92		

with fine sediments, large sediments, and controls ($F_{2,18} = 0.26$, $P > 0.5$), thus, sediment manipulation or size did not affect crab herbivory. There was no difference in number of crab burrows between fine and large sediments ($F_{1,12} = 2.82$, $P > 0.1$). The presence of crab burrows increased the sediment redox potential only in plots with fine grain size whereas, with large grain size, redox potential was higher and constant among depths, without effects of crab burrows (sediment × crabs × depth: $F_{5,96} = 2.334$, $P < 0.05$; Fig. 2). There were no differences in the measured variables between partial cages and control plots (evaluation of artifacts associated with the exclusion cages) or between control plots and plots with large grain size without exclusion (evaluation of artifacts associated with sediment and plant manipulation; Appendix C).

The effect of crab presence on plant growth was dependent on the type of sediment. With large grain size sediments, crab exclusion positively affected *Spartina alterniflora* growth, increasing stem height as well as live and total biomass of plants but having no effect on live and dead stem density or dead biomass (Table 1, Fig. 3). In sediments with fine grain size, in contrast, crab

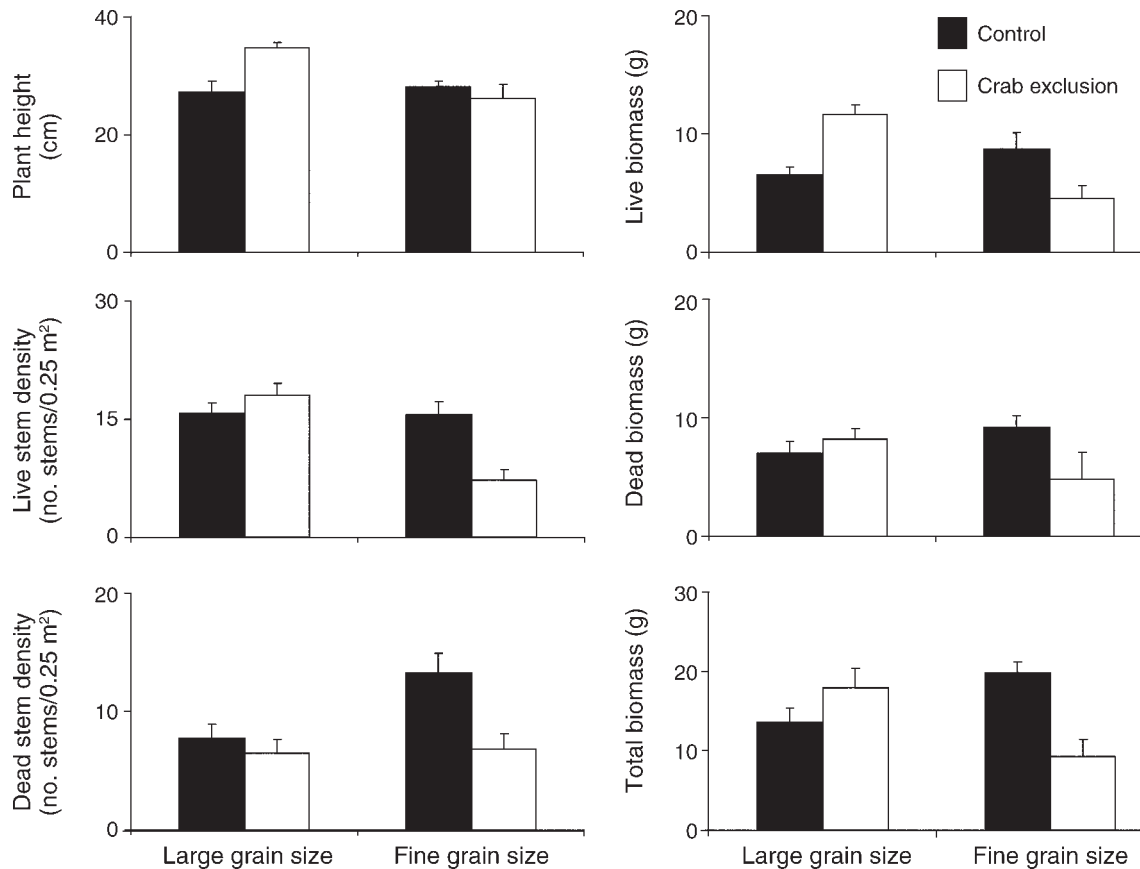


FIG. 3. Effect of crab exclusion and grain-size manipulation on *Spartina alterniflora* plant height, stem density, and plant biomass.

exclusion negatively affected plant production, decreasing stem density as well as dead, live, and total biomass, but having no effect on plant height (Table 1, Fig. 3).

DISCUSSION

Consistent with the stress-gradient hypothesis (SGH), our results show that the balance between positive and negative effects of the burrowing crab *Neohelice granulata* upon *Spartina alterniflora* is context dependent, being regulated by the physical characteristics of the local environment where interactions take place. While crab presence increases sediment aeration at stressful zones, its presence has no physical effect at zones where the naturally high porosity allows a better oxygenation. The effect of crabs, thus, changed from positive at zones with fine-grain sediments to negative at zones with large-grain sediments (i.e., the result of crab exclusion on *S. alterniflora* growth changed from negative at fine sediments to positive at large-grain sediments).

Facilitation is a critical force in the structure of salt marshes (Bruno et al. 2003). Previous experiments reveal that nearly 35% of the vascular plant production of southwestern Atlantic salt marsh communities is dependent on crab burrowing activities (through habitat

amelioration and facilitation of mycorrhizal infection; see Daleo et al. 2007). Given that this burrowing crab and *Spartina* co-occur across a large spatial scale (between southern Brazil, 28° S, and the northern part of the Argentinean Patagonia, 42° S) at similarly high densities, this interaction is likely to have regional ecosystem effects. Moreover, since crabs and other burrowing and deposit feeding organisms have been shown to increase plant growth in many coastal salt marsh communities (Montague 1982, Bertness 1985, Lee 1998), this facilitative mechanism may be a critical force generating the high primary productivity of wetlands and the many ecosystem services they provide worldwide. Herbivory, on the other hand, is now recognized as an important force that can also affect salt marsh plant production (see Silliman and Bortolus [2003] for a review), and our work shows that environmental conditions can balance the relative importance of both forces.

More generally, our work shows that the relative importance of engineering vs. trophic or competitive effects of ecosystem engineers can be a function of environmental conditions. The ecological importance of ecosystem engineers is already hypothesized to change predictably along environmental stress gradients, being

more important at both extremes (Crain and Bertness 2006). This occurs because engineers can ameliorate physical conditions at the physically harsh extreme of the gradient but also can create protection from enemies or competitors at the benign extreme (Crain and Bertness 2006). This theoretical model, nevertheless, applies to ecosystem engineers as a functional group, and not to individual species. By definition, all species can be characterized as ecosystem engineers (an ecosystem engineer is an organism whose presence or activity changes the resource flux or alters the physical surrounding; see Wilby 2002) but, as with all ecological processes, the key is to determine when, where, and which organisms engineer habitats with important outcomes for community and ecosystem processes (see Reichman and Seabloom 2002, Wright et al. 2006). Probably all organisms can have significant effects as ecosystem engineers (and thus be part of the functional group), depending on the environmental context where the presence or activity of the organism occurs. The environmental context is what determines the ecological importance of organisms as trophic or competitive components or as ecosystem engineers.

It has become clear that facilitative interactions can be fundamental in structuring natural plant communities (see Callaway and Walker 1997, Brooker et al. 2008, Chu et al. 2008), and our understanding of how positive and negative interactions affect community structure has improved rapidly since the approaches changed from the analysis of a single specific mechanism to the notion that structure is the result of complex, context-dependent combinations of interactions (Menge and Sutherland 1987, Callaway 1995, Callaway and Walker 1997, Bruno et al. 2003, Alberti et al. 2008). As initially suggested by the environmental stress model (Connell 1975, Menge and Sutherland 1987), our results show that the balance between positive and negative effects along different stress conditions applies not only to facilitation and competition between plants (or sessile organisms, see Kawai and Tokeshi 2007), but also to the balance between facilitation and herbivory between animals and plants.

Our results raise two questions: (1) Is this example of salt marsh crabs a particular case? (2) To what extent can this model be generalized beyond our specific example? In gradients of nutrient availability, for instance, herbivores can have a positive effect on plant production by speeding up nutrient cycling in areas of low fertility, but they can have a negative effect in areas with higher nutrient supplies (where the suppressing effect of consumption exceeds the enhancement of nutrient cycling; see Belovsky and Slade 2000, Barot et al. 2007). This pattern may also be common in arid systems where burrowing activities of small herbivorous organisms tend to have a positive effect on plant growth when precipitation is low (see Wilby et al. 2001, Wesche et al. 2007). Summing up, those results suggest that the SGH is more general than previously perceived and can

be applied to the balance between facilitation and herbivory.

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APPENDIX A

Results of nested ANOVA evaluating the effect of burrow presence and depth on the redox potential of five southwestern Atlantic salt marshes (*Ecological Archives* E090-167-A1).

APPENDIX B

Graph of the effect of burrow presence and depth on the redox potential of five southwestern Atlantic salt marshes (*Ecological Archives* E090-167-A2).

APPENDIX C

Statistical results of the comparison between cage controls and total controls and the comparisons between total controls and plots with large grain size but without crab exclusion (*Ecological Archives* E090-167-A3).