

Can a Single Species Challenge Paradigms of Salt Marsh Functioning?

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Abstract Over the history of ecology, well-established generalizations were refined or even changed after the appearance or consideration of new evidence. Here, we review results obtained in Southwestern Atlantic salt marshes (between southern Brazil $-32^{\circ} 1' S$ - and the Argentinean Patagonia $-53^{\circ} 48' S$ -). Most of these salt marshes are inhabited by the intertidal burrowing crab *Neohelice granulata*, a species that influences many ecological processes through bioturbation and herbivory. The experimental evaluation of these processes shows that in some cases, the results were not consistent with generalizations and models of salt marsh ecological functioning. However, this does not imply that the generalizations grounded mainly on the results from North American sites are not valid. In turn, we suggest that these apparently conflicting results emerged because two major processes, herbivory and bioturbation, have been overlooked until recently. Thus, their relative contribution has not been included in the models of salt marsh functioning. In conclusion, we believe that there is a need for performing parallel and simultaneous experiments comparing distant sites with varying environmental (i.e., abiotic and biotic) conditions to be able to uncover common processes and causes of contingencies. Particularly, Southwestern Atlantic salt marshes could lead the way in providing information to better incorporate herbivory and bioturbation into current models or paradigms about how salt marshes work.

Keywords Salt marsh functioning · Bioturbation · Herbivory · Southwestern Atlantic · Burrowing crab · *Neohelice granulata*

Introduction

As it is nicely written in a recent editorial (“An elegant chaos”, *Nature*, 507, 139–140), it is doubtful that the generalities that underlie the complex patterns of nature will ever be phrased without describing contingencies. Indeed, the history of ecology is populated of generalities (at both, the community and the ecosystem scale) that were finally redefined when new information became available. For example, prior to the influential book *The theory of island biogeography* (MacArthur and Wilson 1967), biogeography had long remained in a natural history phase, mostly focusing on species distributions. Following the publication of the book, when the importance of colonization and extinction were highlighted as fundamental processes to understand biogeography, these ideas kept growing and evolving (Simberloff and Wilson 1969; Rosindell and Phillimore 2011). Additionally, even though positive interactions were considered in early ecological studies, they were largely ignored until the late twentieth century because they pre-dated the experimental ecology era (Bertness and Callaway 1994; Callaway 1997). Since then, many studies focused on the study of positive interactions, and nowadays, they are included with a significant role in the ecological theory (Bruno et al. 2003; Maestre et al. 2009). Analogously, in his famous paper, Nixon (1995) defined eutrophication as “an increase in the rate of supply of organic matter to an ecosystem” and argued that the most common cause was nutrient enrichment. Based on criticisms and new evidence, more than 10 years later (Nixon 2009), he highlighted the need of a “macroscope” (paraphrasing H.T. Odum) to understand the large-scale causes of eutrophication. Briefly, he

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recognized that climate change (i.e., temperature, wind, and cloud cover changes) could be a major force regulating or even driving to eutrophication. Particularly in salt marshes, it was assumed that the impact of invertebrate herbivores is irrelevant for salt marsh functioning (Pomeroy and Wiegert 1981; Odum 1988; Adam 1993; Daehler and Strong 1995). Since the late 1990s, a growing body of evidence challenged this paradigm, showing that it can strongly regulate marsh functioning (Bortolus and Iribarne 1999; Silliman et al. 2005). Here, we use Southwestern (SW) Atlantic salt marshes as a study system to show that the presence of a species can change the processes that govern ecosystem functioning and thus challenge the generalizations produced on systems with different drivers.

Characterization of SW Atlantic Salt Marshes

SW Atlantic salt marshes are found between southern Brazil (32° 1' S) and the Argentinean Patagonia (53° 48' S). The dominant plant species in these marshes are the dense-flowered cordgrass (*Spartina densiflora*), the smooth cordgrass (*Spartina alterniflora*), and the perennial glasswort (*Sarcocornia perennis*; Costa and Davy 1992; Isacch et al. 2006; Bortolus et al. 2009). These plant species cover ~70 % of salt marshes, and their relative abundance is tightly associated with freshwater inputs (*S. densiflora* dominates in freshwater influenced sites while *S. alterniflora* and *S. perennis* are more abundant in saltwater influenced sites; Isacch et al. 2006). The huge length of coastline (~2,500 km) harbors large variations in latitude (~21°), geomorphology, annual rainfall (>1,000 mm; Isacch et al. 2006), pore-water N content (Fanjul et al. 2007; Daleo et al. 2008; Cardoni et al. 2011), live plant and detritus production (Montemayor et al. 2011; 2014), and herbivore pressure (Alberti et al. 2007a). Results from a variety of experiments revealed (1) that most of these marshes are intensively consumed by small mammals (wild guinea pigs; Alberti et al. 2011a) and/or invertebrates such as intertidal crabs (Alberti et al. 2007a) and stem-borer moths (Canepuccia et al. 2010) and (2) that, in addition to the strong consumer control, plant production is also nutrient limited (Daleo et al. 2008; Alberti et al. 2011b). Particularly, most of these salt marshes (except for those located at the southernmost extreme, from 42° 25' S to 53° 48' S) are inhabited by the herbivorous and burrowing crab *Neohelice granulata* (formerly known as *Chasmagnathus granulatus*; up to 8 cm in carapace width: Luppi et al. 2002) where it can reach densities higher than 100 individuals m⁻² (Alberti et al. 2007a; Fig. 1). The extension of salt marshes inhabited by this crab species ranges from 356 to 82,055 ha (Isacch et al. 2006), while southernmost marshes range from 12 to 2,400 ha (Bortolus et al. 2009). Besides its striking herbivore role (can consume large amounts of plant biomass; Bortolus and

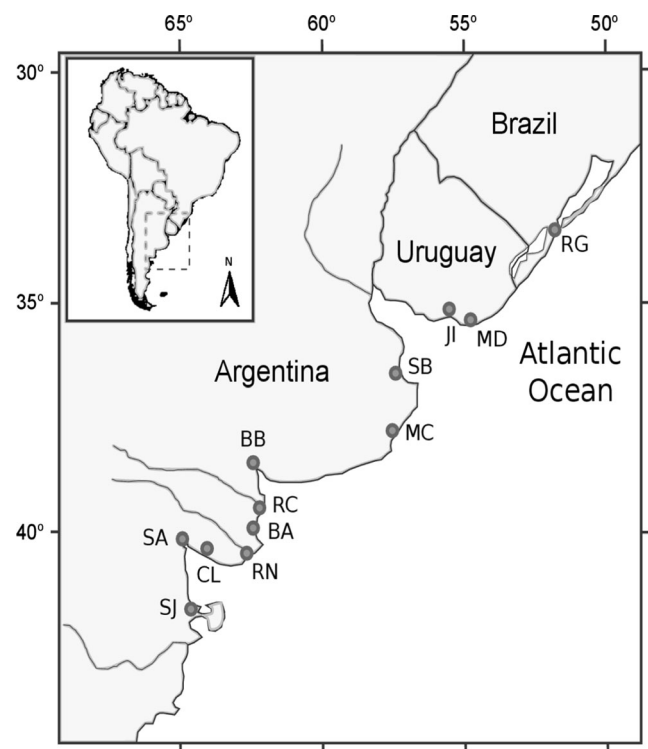


Fig. 1 Most extensive southwestern Atlantic salt marshes inhabited by the burrowing crab *Neohelice granulata*. RG Rio Grande; MD Arroyo Maldonado; JI José Ignacio; SB Bahía Samborombón; MC Mar Chiquita; BB Bahía Blanca; RC Río Colorado; BA Bahía Anegada; RN Río Negro; Caleta de los Loros; SA Bahía San Antonio; SJ Riacho San José

Iribarne 1999) particularly at lower intertidal heights (Alberti et al. 2007b), this crab is also a bioturbator capable of removing up to 2.4 kg m⁻² d⁻¹ of marsh sediment while creating and maintaining burrows (Iribarne et al. 1997). Burrows are found on areas that extend for several hectares (e.g., Iribarne et al. 1997; 2005) and can reach up to 1-m depth into the sediment (Iribarne et al. 1997), modifying nutrient dynamics (Fanjul et al. 2011), oxygenating the sediment and affecting plant growth strategies (Daleo and Iribarne 2009), as well as interactions between plants and other organisms (Daleo et al. 2007; Canepuccia et al. 2010).

Until the late 1990s, there were strikingly few studies about the functioning and organization of SW Atlantic salt marshes (Costa and Davy 1992). Since then, the processes that structure these salt marshes have received increasing attention, and many studied processes are, to some extent, coincident with prevailing paradigms of salt marsh functioning. For example, plant zonation in southernmost SW Atlantic salt marshes follows the classical model (e.g., Pennings and Bertness 2001): *Spartina alterniflora* (poor competitor) is displaced towards lower (more stressful) areas while *Sarcocornia perennis* (dominant competitor) occupies higher (more benign) areas (Idaszkin et al. 2011). However, increasing evidence suggests that most of these marshes, and particularly those inhabited by *N. granulata*, do not always follow the

predictions of salt marsh functioning models. Thus, we will focus here on these “conflicting” results produced by the crab and analyze whether these results challenge some salt marsh ecological theories or if they are just the product of some overlooked mechanisms.

Impacts of *Neohelice granulata* on Salt Marsh Functioning

Community-Scale Effects

Facilitation Through Reduced Herbivory

Even though there are several examples of herbivores affecting successions in marshes (e.g., Handa et al. 2002; Kuijper et al. 2004; Gedan et al. 2009; Daleo et al. 2014), it is generally accepted that the mechanism behind succession involves competition or amelioration of physical stress (e.g., Shumway and Bertness 1994; Pennings and Bertness 2001; Langlois et al. 2003). Given that salt marshes are physically stressful environments, it is now well known that facilitation plays a key role, determining zonation patterns, secondary successions, and plant production (e.g., Bertness 1985; Bertness and Hacker 1994; Bertness and Leonard 1997; Bortolus et al. 2002). Indeed, most examples and models of facilitative successions involve the direct or indirect amelioration of abiotic stressful conditions (e.g., Bertness 1991b; Bertness and Hacker 1994; Rand 2004). In this pathway, early colonizer species reduce the levels of abiotic stress (i.e., salinity, desiccation) and allow the establishment of late-successional competitively dominant species (e.g., Bertness 1991b; Pennings and Bertness 2001; but see Crain et al. 2008).

However, results from SW Atlantic do not fit with the generalized view that facilitative successions involve the amelioration of abiotic stress. During secondary succession after disturbance in SW Atlantic marshes, it is common to find patches composed by *S. densiflora* and *S. perennis* intermixed with large bare areas. This association between a pioneering species (*S. perennis*) that can tolerate and ameliorate stress levels and a less tolerant, dominant species (*S. densiflora*) follows the facilitation model of marsh succession. The removal of the pioneering species produces different outcomes on the dominant species depending on the size of the patch; when alone, small and young *S. densiflora* patches are completely consumed by crabs in a few months whereas larger and older patches grow faster than those associated with *S. perennis*. Crab exclusion experiments revealed that herbivory is the main driver of this pattern, as small *S. densiflora* patches can persist alone in the absence of crabs (Alberti et al. 2008). These results reveal that the amelioration of otherwise too severe biological stress can play a key role during secondary successions in salt marshes.

Herbivory and the Lower Zonation Limit Under High Abiotic Stress

The model of community organization proposed by Menge and Sutherland (1987), as well as its derivatives (e.g., Bertness and Callaway 1994; Bruno et al. 2003; Crain and Bertness 2006) argue that the relative importance of predation and competition diminishes as abiotic stress increases, while the importance of facilitative interactions between neighbors increases (stress amelioration). In concordance with these predictions, manipulative experiments showed an inverse relationship between competitive ability and stress tolerance: competitively superior plants occupy the least stressful zones of the salt marsh, displacing subordinate plants to more physically stressful zones (e.g., Snow and Vince 1984; Bertness 1991a, b; Pennings and Callaway 1992; Pennings et al. 2005b; Idaszkin et al. 2011).

The relative importance of different physical stresses in salt marshes varies both locally and geographically (Pennings and Bertness 2001; Pennings et al. 2005b). At the local scale, waterlogging increases towards the lowest reaches of the marsh, while salinity (when relevant) generally increases at intermediate to higher intertidal heights (e.g., Adam 1993; Pennings and Callaway 1992; Pennings and Bertness 2001). Indeed, tolerance to waterlogged and anoxic sediments determines the lower distributional limit of many marsh plants (e.g., Bertness 1991a; Pennings and Callaway 1992; Idaszkin et al. 2011). For example, *Spartina densiflora* is invading south-west Spain salt marshes, and flooding imposes severe restrictions in photosynthetic and growth rates and ultimately determines its lower distributional limit (Castillo et al. 2000). Overall, it is widely accepted that, for a given species, competition determines the distributional limit at the most benign end of a stress gradient, while physiological tolerance and positive interactions determine the zonation pattern at the stressful end (Bertness and Leonard 1997; Pennings and Bertness 2001).

Crab herbivory can play a major role influencing plant species zonation in SW Atlantic marshes. At microtidal sites where stress gradients are not persistent, crab herbivory seems to be a major factor that determines the distribution of marsh plants (Costa et al. 2003), but even at those marshes with clear gradients of salinity, submergence frequency, and anoxia, crab herbivory can strongly regulate the lower distributional limit of *Spartina densiflora* (Alberti et al. 2010b). When crab herbivory was prevented, transplants moved up to 28 cm below the natural distribution of *S. densiflora* grew even faster than at the original location. However, transplants that suffered crab herbivory were entirely eaten in a few months. Even more, without nutrient limitation, clonal expansion of natural *S. densiflora* stands into the mudflat was only possible after preventing crab herbivory. These results, coupled with the fact that a combination of crab bioturbation and herbivory

inhibits successful seedling establishments in mudflats (Alberti et al. 2010a; see the forthcoming sections), reveal that sexual or asexual colonization of areas below the natural lower distributional limit of *S. densiflora* is prevented by crabs. In concordance, similar results were obtained when the relative importance of crab herbivory and asexual propagation on the re-colonization of artificially created bare patches at the low marsh was analyzed (Daleo et al. 2011). Given the highly stressful conditions on those bare patches (high salinity, low sediment water content, and low redox potential), asexual propagation was essential for their closure, but it was impossible unless crab herbivory was impeded.

In SW Atlantic marshes, biological interactions can be extremely important even in physically stressful habitats, influencing the lower distributional limit of *S. densiflora*. Although the original model (Menge and Sutherland 1987) explicitly stands that its predictions are only valid when stressful factors affect all the involved species, neither this model nor its posterior widespread generalization (Bertness and Callaway 1994; Bruno et al. 2003; Crain and Bertness 2006) addresses what can be expected when stressful factors for different trophic levels are decoupled. Thus, results from SW Atlantic salt marshes suggest that when abiotic stress affects basal levels and not consumers (indeed, crab consumption rates increase with decreasing tidal height, because they mostly consume plants when under water; Alberti et al. 2007b), both will act in conjunction imposing even higher pressure upon primary producers. In this context, herbivory ends up controlling the lower distribution of marsh plants, as well as physical factors do. Analogous to the results shown in the famous Connell (1961) paper on rocky shores, abiotic stress (waterlogging) seems to impose limits to the distribution of *S. densiflora* (Castillo et al. 2000) determining its fundamental niche, but biotic interactions (herbivory) shortens the actual zonation, constituting its realized niche.

Bioturbation, Root Colonizing Fungi, and Plant Zonation

Even though the presence of arbuscular mycorrhizal fungi (AMF) on plants from wetlands is known since almost a century ago (Mason 1928; Bohrer et al. 2004), their impacts are generally assumed to be negligible because they are obligate aerobes and thus, they are negatively affected in waterlogged soils (Khan 1993; Miller and Sharitz 2000). In concordance, even though spores are frequently found in these ecosystems, they do not extensively develop due to the low oxygen conditions (Carvalho et al. 2004). Even more, the positive effect of AMF on plant performance is context dependent, as it varies with the species involved (Umbanhowar and McCann 2005), as well as with the nutrient scenario. The larger benefits of these fungi on plants are expected when nutrients are scarce, but as soon as nutrients become unlimited, the positive interaction may become parasitic due to the

large carbon transfer from plants to fungi (Johnson et al. 1997; Hart et al. 2003; Olsson and Tyler 2004).

Results from SW Atlantic marshes reveal that crab bioturbation can facilitate AMF which in turn can play important roles in salt marshes, affecting plant biomass (Daleo et al. 2007) and zonation (Daleo et al. 2008). Daleo et al. (2007) found that by increasing oxygen concentration in the sediment, crab burrows increased the proportions of *Spartina densiflora* roots infected with these fungi. When burrows or fungi were removed, live plant biomass experienced a 35 % reduction (influenced by both, reduced height and tiller densities). Even more, given that AMF do not form associations with *S. alterniflora* (McHugh and Dighton 2004) but do with *S. densiflora* (Daleo et al. 2007), this context dependency could influence salt marsh plant zonations under varying nutrient conditions. Removing fungi or adding fertilizer resulted in *S. alterniflora* moving upwards, invading the *S. densiflora* zone, while species zonation did not change when nutrients were added and fungi were removed, likely because the parasitic interaction was prevented. These results suggest that an otherwise subordinate species can become a dominant competitor if AMF are excluded from the natural system. Altogether, these results show that the interaction between bioturbators and these fungi can play a key but overlooked role in salt marshes by regulating both plant biomass and zonation patterns.

Ecosystem-Scale Effects

Crab Bioturbation Can Make Plants Speed Up Erosion Rates

It is well known that erodibility in intertidal systems is influenced by bio-stabilizers (e.g., macrophytes) and bio-destabilisers (e.g., bioturbators; de Deckere et al. 2001; Widdows and Brinsley 2002). Particularly, the existence of salt marshes depends essentially on the balance between sedimentation and erosion, and the net balance seems to be primarily controlled by interactions among biotic, hydrodynamic, and geomorphologic processes (Adam 1993; Allen 2000; Townend et al. 2011). Recent works dealing with biogeomorphological functioning of salt marshes denote the key role of biota on overall and internal marsh morphodynamics (D'Alpaos et al. 2012). When it comes to the biological control of sedimentary processes, salt marsh plants and animals are thought to have opposite effects. While in general, vascular plants promote sediment deposition and stabilization, animals are mainly showed as destabilization agents (Murray et al. 2002). For example, marsh vegetation plays a key role in marsh morphology as it traps and fixes sediments within the system, thus contributing to marsh aggradation in most cases. Sediment trapping efficiency of vegetation is modulated by their effect on water flow, depending on the species involved, their position in the intertidal,

architecture, and biomass (Leonard and Croft 2006; Neumeier and Amos 2006). The consensus is that marsh plants stabilize shorelines, protect coastal communities, and increase sedimentation by reducing the energy of incoming waters (Adam 1993; Bruno 2000; Gedan et al. 2011). In contrast, burrowing animals influence properties of sediments where they live (Murray et al. 2002), and they can often lead to sediment destabilization (Widdows et al. 2000) and even to marsh erosion (Talley et al. 2001; Hughes and Paramor 2004; Davidson and de Rivera 2010).

The perennial glasswort *Sarcocornia perennis* is a characteristic plant of SW Atlantic salt marshes, particularly those with little freshwater inputs (Isacch et al. 2006). This plant has very low ability to trap sediments, and thus it is not a major contributor to sediment deposition (Townend et al. 2011). In addition, this species shades the marsh surface, reducing abiotic stress (dryness and hardness) and facilitating the colonization by *N. granulata* (Bortolus et al. 2002). Once the crabs are established, they remove large quantities of sediment by depositing it on the marsh surface in mounds (Iribarne et al. 1997). These mounds are easily eroded in areas that experience high current speeds (i.e., basins, banks, and heads of tidal creeks), which promotes a net loss of sediment in those areas (Escapa et al. 2008). Furthermore, crab impacts on sediment erodibility coupled to sediment loss in creek basins increase inland growth rates of tidal creeks when compared with areas not inhabited by crabs (Escapa et al. 2007). Indeed, the experimental exclusion of crabs from creek heads and basins decreased the inland growth rates of creeks (Escapa et al. 2007). Even though *Sarcocornia perennis* could be stabilizing sediments, its net outcome is erosive under certain conditions, given that it can produce a comparatively much higher indirect increase in erodibility by facilitating the establishment of marsh crabs. As a result, and in contrast with common patterns observed in other salt marshes, sediment loss is higher in areas occupied by plants (and the associated crab burrows) than in unvegetated areas. Overall, approximately 62,436 ha (between Bahía Blanca $-38^{\circ} 50' S$, $62^{\circ} 30' W$ - and Anegada bay $-40^{\circ} 33' S$, $62^{\circ} 22' W$ -) of *Sarcocornia perennis* marshes with high tidal energy are endangered by this plant-bioturbator-facilitated erosive process.

Bioturbation and the Efficiency of Nutrient Filtering

Given that salt marshes are boundary systems located between the land and the sea, and are characterized by high rates of biogeochemical transformations (Alongi 1998), the classical paradigm stands that salt marshes act as nutrient filters intercepting land-derived nutrients, thereby reducing nutrient input to estuarine and coastal waters (Nixon 1980; Correl 1981; Valiela et al. 2002). In concordance, the loss of salt marshes is tightly related to the loss of eelgrasses which are extremely sensitive to eutrophication (Valiela et al. 2002).

Land-derived nutrients moving seaward can be intercepted due to the high rates of denitrification and nitrogen burial that occur in salt marshes (Valiela 2006). These increased nutrients after salt marsh losses can negatively affect seagrass meadows through the promotion of micro- and macroalgal growth that shade seagrasses or through nitrate toxicity (Valiela et al. 2002). Thus, there is consensus that salt marshes are highly effective nutrient filters that intercept land-derived nutrients, diminishing nutrient inputs into coastal waters (Nixon 1980; Teal and Howes 2002; Kinney and Valiela 2013).

SW Atlantic marsh plants facilitate the establishment of *N. granulata* and their burrows by buffering harsh physical conditions (Bortolus et al. 2002). These crabs construct straight, long vertical tubular and permanently open burrows that reach the water table (up to 1-m depth; Iribarne et al. 1997; Bortolus and Iribarne 1999; Escapa et al. 2008). Moreover, they spend most of their time within their burrows (they are mostly active when submerged; Méndez Casariego et al. 2011), where they defecate and accumulate food (plants and detritus). This material accumulation, plus the high rates of organic matter degradation (Fanjul et al. 2007) and nitrogen remineralization (Fanjul et al. 2011), produce high quantities of remineralized nutrients that are accumulated and concentrated in the water contained within burrows (Fanjul et al. 2008). Thus, burrows may act as deep conduits that directly discharge dissolved nutrients into the phreatic water (Fanjul et al. 2008). As a consequence, bioturbation activities (i.e., burrow construction and maintenance) enhance vertical transport of solute and particulate substances by increasing water-sediment exchange areas (i.e., burrow walls), and fueling and speeding biogeochemical cycles (Fanjul et al. 2007). The effects of crab bioturbation just mentioned show a novel way in which bioturbators can affect the capacity of marshes to filter both upland-derived and marsh-remineralized nutrients. Even more, although this nutrient-export mechanism has not been described for other bioturbators and/or marshes around the world (but see Xin et al. 2009), we think that this altered nutrient filtering capacity could be a common phenomena occurring in marshes inhabited by bioturbator crabs with similar functional roles (Wang et al. 2010; Needham et al. 2010).

Modulation of Organic Matter Export

High production of detritus is a particular and common feature of salt marshes (e.g., Bouchard and Lefevre 2000), and the final destination of these detritus is one of the main concerns for estuarine ecologists (see reviews by Odum 2002; Valiela et al. 2002). This detritus exported during floods can be incorporated to the planktonic or benthic food webs during and after decomposition (Newell et al. 1989) and is the primary source of nutrition for meiofaunal organisms (Couch 1989), benthic fauna (Levin et al. 2006), and fish (França et al. 2011). Therefore, for many estuarine food webs, salt marsh

detritus is considered an important source of organic matter (e.g., Peterson and Howarth 1987; França et al. 2011). In other cases, however, nutritional quality of detritus is insufficient to maintain estuarine organisms (e.g., Deegan et al. 1990; Newell et al. 1995), and seagrass beds (Connolly et al. 2005), microphytobenthos (Sullivan and Moncreiff 1990; Galván et al. 2011), seagrass epiphytes, or macro algae and phytoplankton (Deegan and Garritt 1997) become more valuable energy sources. Also, decomposing plant materials may contribute to the dissolved nutrient pool (Gallagher et al. 1976; Mann 1988), which may enhance food resources by supporting growth of phytoplankton or bacteria in the water column (e.g., Shiah and Ducklow 1995). In summary, the amount and importance of organic matter export from salt marshes are generally thought to depend on some abiotic estuarine characteristics such as tidal regime and amplitude (Kwak and Zedler 1997), geomorphology (Odum 2002), type of marsh edge (Cicchetti and Diaz 2002), presence of ditches (Koch and Gobler 2009), or the relative extension of the area occupied by salt marshes (Valiela et al. 2002) and watersheds (McClelland and Valiela 1998).

The production of detritus in SW Atlantic salt marshes varies with the plant species considered (i.e., *S. alterniflora* has higher decomposition rates likely contributing towards more profitable detritus for estuarine food webs than *S. densiflora*; Montemayor et al. 2011). Nevertheless, the organic matter generated in SW Atlantic marshes does not support many species, but it is essential to support *N. granulata* (Botto et al. 2005; Botto et al. 2011). Crab bioturbation plays another key role, affecting the detritus dynamics into coastal areas. Mudflats are boundary systems between marshes and the open waters, where the crabs are known as “deposit feeders”, mostly consuming the detritus of *Spartina* (Iribarne et al. 1997; Botto and Iribarne 2000). There and in creek banks, their funnel-shaped burrows occur in very high densities (Iribarne et al. 1997; Botto et al. 2006) and efficiently trap detritus (Botto et al. 2006). Even more, crab bioturbation causes an overall reduction in the concentration of carbon in the superficial sediment layers and, thus, a net decrease in the amount of carbon that can be exported from the marsh by tidal action (Gutiérrez et al. 2006). In this context, crab bioturbation seems to reduce the export of particulate organic matter to estuarine and coastal waters and its transfer to the food web.

Conclusions

Does a Single Species Challenge Salt Marsh Paradigms?

There are no reasons to believe that the processes playing key roles in these salt marshes (i.e., herbivory and bioturbation)

cannot influence marsh functioning elsewhere. All the novel results we report here are driven by herbivory and/or bioturbation, processes that are common in many different and distant salt marshes throughout the world (e.g., bioturbation by various crab species: Bertness 1985; Wang et al. 2010; Wilson et al. 2012; polychaetes: Paramor and Hughes 2005; herbivory by cattle: Bakker et al. 1993; feral horses: Furbish and Albano 1994; hares and geese: Kuijper and Bakker 2005; snails: Silliman et al. 2005; geese: Jefferies et al. 2006; grasshoppers and leafhoppers: Bertness et al. 2008; crabs: Holdredge et al. 2009). As an example, models of secondary succession in salt marshes (Pennings and Bertness 2001) predict that sexual reproduction plays a relatively minor role, being important mostly at areas with low environmental stress. Indeed, factors influencing seedling establishment were believed to be mostly abiotic (Shumway and Bertness 1992; Rand 2000). However, recent evidence challenged this classic view, showing that herbivory and bioturbation (by the polychaete *Nereis diversicolor*) can also play a fundamental role during seedling establishment (Paramor and Hughes 2005). Similar results were observed in SW Atlantic salt marshes, with a combination of crab (*N. granulata*) bioturbation and herbivory affecting seed availability and seedling establishment (Alberti et al. 2010a).

Even more, some of the “novel” results found in SW Atlantic salt marshes were recently found in other salt marshes from the Northern Hemisphere. For example, Wilson et al. (2012) found that bioturbation and herbivory by the crab *Sesarma reticulatum* accelerates plant decay and thus marsh erodibility in Cape Romain (SC, USA). Even though the whole process is not exactly the same because marsh plants do not seem to be facilitating the establishment of crab burrows, the process to reach the increased erodibility is strikingly similar (see Escapa et al. 2007). Moreover, examples from North America (e.g., Handa et al. 2002) and northern Europe (e.g., Esselink et al. 1997; Kuijper et al. 2004) reveal that herbivory can delay successions and patch recovery after disturbance, as it occurs in SW Atlantic marshes (Alberti et al. 2008; Daleo et al. 2011; 2014). Overall, this new information suggests that the “surprising” results obtained in SW Atlantic salt marshes might have been overlooked or are comparatively less important in other systems, rather than only being the product of a particularly important key species. Nevertheless, rather than rejecting prevailing paradigms, all these evidence suggest that paradigms need to be refined to include bioturbation and herbivory.

Context Dependency and Paradigms of Salt Marsh Functioning

We have shown here that the presence of *Neohelice granulata* makes SW Atlantic salt marshes work differently than current models and generalizations of salt marsh functioning. Many of

these generalizations are grounded on experimental studies conducted at relatively few sites (mostly at the east coast of North America: Pennings and Bertness 2001). However, many salt marsh studies have shown varying results with varying biotic and abiotic context even at relatively small scales (Dunson and Travis 1991; Bertness and Hacker 1994; Crain 2008). Indeed, the use of meta-analysis revealed that many aspects of ecology can be strongly context dependent (e.g., Burkepile and Hay 2006; Hillebrand et al. 2007; Hoeksema et al. 2010). Particularly, in salt marshes, several context dependent results have been identified. For example, the response of individual plant species to increased nitrogen availability varies as a function of the biotic and abiotic environment (Pennings et al. 2005a). Other studies showed that the direction and strength of plant interactions vary with the abiotic (Pennings et al. 2005b) and biotic context (Alberti et al. 2008; Crain 2008). As mentioned above, most SW Atlantic salt marshes experience intense herbivory and bioturbation, and this contingency could lead to the described differences with other salt marshes (Fig. 2). Then, the study of SW Atlantic salt marshes could provide valuable information to better incorporate herbivory and bioturbation into current models or paradigms about how salt marshes work. This is essential because SW Atlantic salt marshes are likely not unique, given that several marshes along East Asia and Oceania, as well as Northeast USA, are inhabited by similar burrowing crabs (see for example, Holdredge et al. 2009; Wang et al. 2010; Needham et al. 2010; Zhang et al. 2013).

Time for a Change of (Meta) Paradigm

Results from SW Atlantic salt marshes by no means imply that the paradigms described above are necessarily wrong; they rather emphasize the strong context dependency of community ecology results. This is not a novel finding, it has been often mentioned in the literature (e.g., Lawton 1999; Pennings et al. 2003; 2005a, b). Indeed, when the models of positive interactions and physical stress (developed mostly in New England salt marshes, USA) were evaluated at different geographic locations, the results supported those theories only after addressing the different biotic and abiotic context (Pennings et al. 2003; 2005b). Based on these frequent contingencies, Lawton (1999) argued that laws are rare in community ecology, but when they emerge, we must treasure them. However, there are some theories largely supported by empirical data, like the stress-gradient hypothesis (Bertness and Callaway 1994), which predicts the relative importance of facilitation and competition across environmental stress gradients. This theory was then refined by adding to the model the life history of the species involved (Maestre et al. 2009). In addition, Silliman et al. (2013) recently expanded the community organization model originally proposed by Menge and Sutherland (1987) to include the impact of consumers when stressful factors for

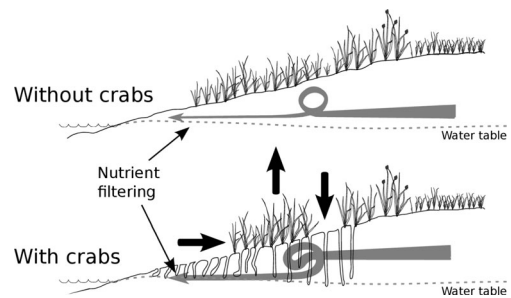


Fig. 2 Schematic representation of the predicted organization of south-western Atlantic *Spartina* salt marshes based on current paradigms of salt marsh functioning, if burrowing crabs were not present (without crabs), and actual functioning based on experimental results (with crabs). The *right pointing arrow* denotes that crab herbivory plays a key role establishing the lower distributional limit of *Spartina densiflora*. The *upward arrow* denotes that crab burrows can promote *Spartina densiflora* production through increased oxygenation that facilitates the growth of root colonizing fungi. The *downward pointing arrow* denotes that crab bioturbation and herbivory can dramatically retard the either sexual or asexual establishment of vegetation on unvegetated areas. The *twisted gray arrow* denotes that crabs and their burrows can increase nutrient cycling and diminish the ability of salt marshes to retain land-derived nutrients

primary producers and herbivores are decoupled (i.e., both physical stress and herbivory act synergically, imposing an even higher pressure upon plants; previously highlighted but not modeled by Alberti et al. 2010b and Daleo et al. 2011).

However, prior to the development of a framework that addresses the impacts of herbivores and bioturbators across physical stress gradients, we need a better understanding of how, where, and why these forces interact with those well-modeled interactions. To achieve this, we urgently need to analyze multiple interactions at much wider geographic ranges. Of course, this is almost impossible for a given laboratory or institution mainly due to logistic constraints. However, we might be experiencing a turning point, given that the evolution of communications is allowing geographically distant scientific groups to collaborate, to simultaneously design and run experiments, and to share, analyze, and interpret the results almost on real time. In any case, there is a need of global comparative studies to really understand how herbivory and bioturbation (as well as other potentially overlooked processes) affect the generalities about the functioning of salt marshes.

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