

South West Atlantic salt marshes as model systems for community and ecosystem ecology

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ABSTRACT. Just as some species are used as model systems in organismal biology (e.g., physiology, genetics), many ecosystems are commonly used as model systems in ecology. Salt marshes, for instance, are great models to perform manipulative field experiments, and thus, were historically used to understand the drivers of community and ecosystem function. Decades of experimental work, indeed, made a strong contribution to community ecology as a discipline, but most of the emerged hypotheses and models were grounded in a few sites. When studies from new sites came onboard, looking to enlarge generalities, their results challenged the prevailing ideas. Here, we review more than 25 years of intense experimentation in South West Atlantic salt marshes, which helped not only to increase the knowledge about salt marsh functioning, but also to expand this knowledge beyond salt marshes helping to refine community and ecosystem function theory. We show that results coming from SW Atlantic marshes significantly contribute to understand 1) the separate and interactive effect of biotic and abiotic stress for species distribution and even for ecosystem stability, 2) the integrated role of species that can function as ecosystem engineers and as consumers, 3) the balance between stochastic and deterministic forces as drivers of community structure, and 4) the regulation of cross-ecosystem fluxes. Nevertheless, we believe SW Atlantic salt marshes still have a lot more to offer, not only as conceptual models that help satisfy our intellectual curiosity, but also as key ecosystems that provide valuable benefits to our societies.

[Keywords: drivers of community organization, ecological theory, ecosystem function]

RESUMEN. Las marismas del sudoeste atlántico como sistemas modelo en ecología de comunidades y ecosistemas. El uso de ciertas especies como sistemas modelo es común en algunas ramas de la biología (e.g., fisiología, biología molecular, genética). De manera similar, existen ecosistemas muy usados como modelo en ecología. Las marismas, por ejemplo, son sistemas relativamente simples, lo que los hace ideales para realizar experimentos manipulativos de campo. Por ello, son muy utilizadas para entender los determinantes de la estructura y el funcionamiento de comunidades y ecosistemas. Históricamente, la influencia de trabajos realizados en marismas tuvo gran impacto sobre el desarrollo de la ecología de comunidades como disciplina. Sin embargo, la mayor parte de los trabajos que dieron lugar a teorías y modelos generales provienen de unos pocos lugares, por lo que muchas veces, al querer ponerlos a prueba en otros sitios geográficos, los resultados obtenidos parecen no ajustarse a las predicciones. En este artículo hacemos una revisión de algunos trabajos, realizados en las marismas del sudoeste Atlántico durante más de 25 años, que ayudaron no sólo a que entendamos mejor el funcionamiento de las marismas en sí, sino también a extender el conocimiento más allá de estos sistemas en particular. En esta revisión mostramos cómo los resultados obtenidos en las marismas del SO Atlántico contribuyeron al entendimiento de 1) los efectos aislados e interactivos de factores bióticos y abióticos sobre la distribución de especies y hasta la estabilidad de los ecosistemas, 2) el rol integral de especies que pueden actuar simultáneamente como ingenieras y como consumidoras, 3) el balance entre procesos neutrales y determinísticos como reguladores de la estructura comunitaria, y 4) la regulación de los flujos entre ecosistemas. Sin embargo, estas marismas tienen mucho más para ofrecer, no sólo como modelos conceptuales que ayudan a calmar nuestra curiosidad intelectual, sino como ecosistemas clave en la provisión de servicios ecosistémicos.

[Palabras clave: reguladores de la estructura de comunidades, teoría ecológica, funciones ecosistémicas]

INTRODUCTION

Model organisms, such as fruit fly, yeast, house mice and mustard plants, are extensively used in biology to answer a wide range of questions, with the hope that their answers will be generally applicable (i.e., valid for other organisms). The main reason behind the choice of these particular organisms as models

is usually related with the fact that they are somehow simpler than the other options (i.e., cheaper, easier to grow, easier to manipulate) (Matthews and Vosshall 2020), thus, facilitating research performance. Community ecology does not stand aside from this logic, as some model systems are extensively used to develop and expand ecological concepts and theory. Among these systems, salt marshes

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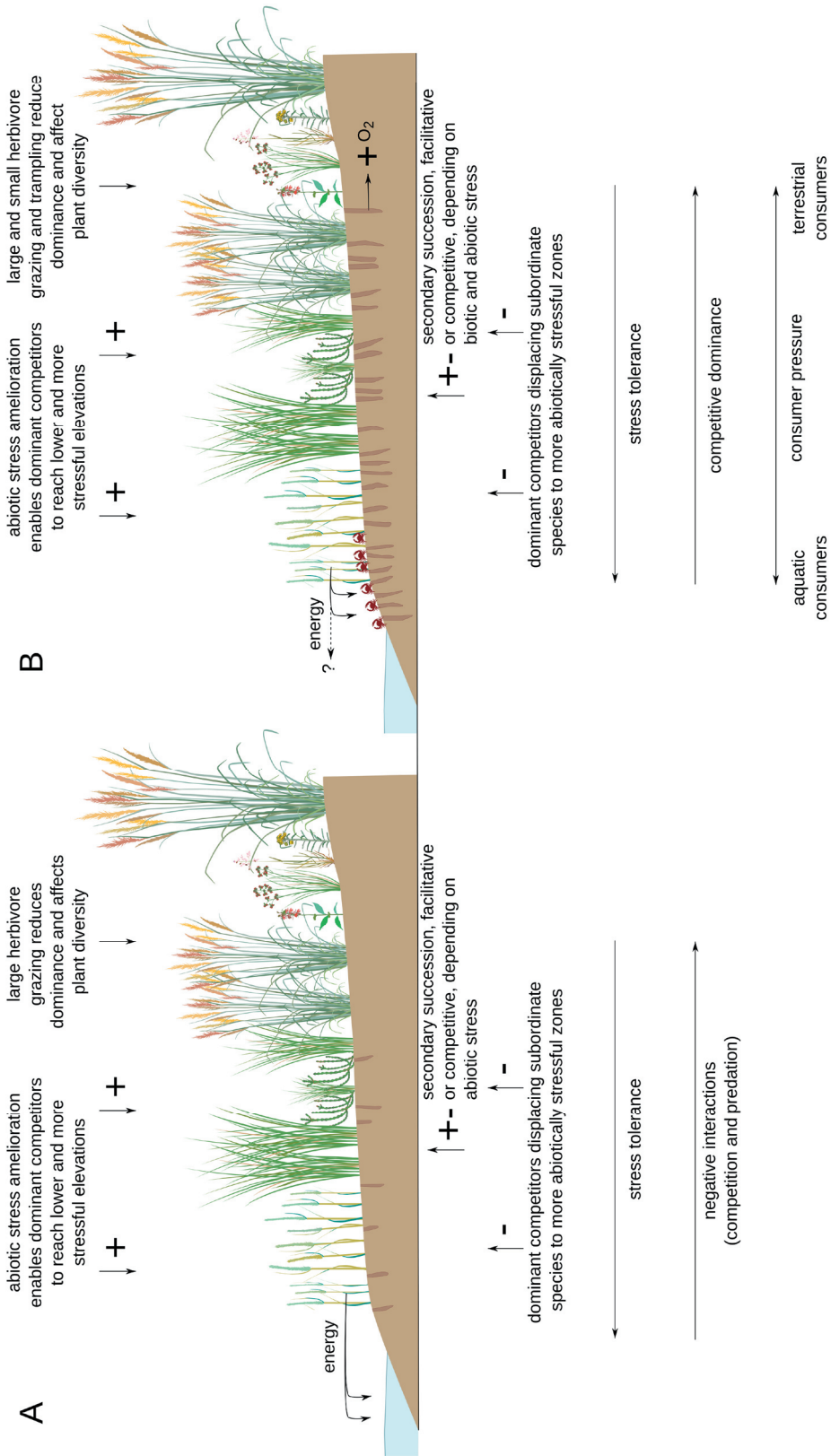


Figure 1. (A) Classical model of salt marsh community structure, adapted from Bertness and Leonard (1997), showing zonation patterns determined by competition in the upper edge of a given species' distribution, and by abiotic stress and facilitation in the lower edge. (B) Modified version including findings from SW Atlantic salt marshes, where herbivory and bioturbation/trampling play a more prominent role.

Figura 1. (A) Modelo clásico de la estructura de una marisma, adaptado de Bertness and Leonard (1997), en el que se muestra el patrón de zonación con los límites superiores de la distribución de las especies determinado por competencia y los límites inferiores determinados por el estrés abiótico y facilitación. (B) Versión modificada donde se incluyen los cambios surgidos a partir de las evidencias obtenidas en los estudios de marismas del Sudoeste Atlántico, donde la herbivoría y la bioturbación juegan un rol más importante.

are runners-up (just behind rocky shores) for experimental approaches that made significant contributions to our understanding of the forces that shape the structure and function of natural communities.

But why are salt marshes great model systems? The answer to this question can be puzzling, as salt marshes are usually a tangled jungle of grasses with sharp blades, strategically located at muddy swamps full of mosquitoes, gadflies and ticks. Working in coastal systems can sound great, but you will be bitten, punctured and sunk into the mud, and you will probably suffer extreme heat wearing full clothes in the middle of the summer to protect yourself from the bugs. Those clearly non-ideal features had a strong influence in the way that people historically perceived marshes: wastelands needing to be dredged and waiting to be filled (Davy et al. 2009). This negative perception of marshes resulted in a long-lasting denial of their intrinsic value. But after the first studies of pioneering scientists, as Eugene and Howard Odum, John Teal, and more recently Ivan Valiela and Mark Bertness among others, it turned out that, despite the mud and the smell, salt marshes are not only great models for intellectual exercises, but they are also fundamental systems that provide numerous and valuable key ecosystem services crucial for human development (Barbier et al. 2011).

Let's go back to our question by first answering what salt marshes are. Salt marshes are vegetated coastal marine/estuarine systems widely distributed in middle and high latitudes worldwide. These ecosystems are highly dynamic, given that they experience tidal regimes, which imply that they are periodically flooded by saline or brackish water (see Figure 1A). They develop in the upper intertidal zone, usually neighbored in their downward edge by tidal flats, and in their upward edge by other vegetated systems such as grasslands or forests at wet environments, and shrublands or sparse xeric bushes at arid environments (Pennings and Bertness 2001). The tidal flooding generates an elevational gradient of edaphic factors, in which lower zones are generally characterized by stronger physical stress (i.e., waterlogged, anoxic sediments) (Pennings and Bertness 2001). Vegetation is constrained to those species that can cope with the harsh abiotic conditions, and mostly includes halophytic grasses, short statured shrubs and herbs, with usually a few dominant species typically distributed

in distinctive zonation patterns across the compact elevation gradient (Bertness 1991). In addition to the high levels of stress, and despite salt marshes being highly productive systems, plant growth is also nutrient limited (Valiela et al. 1975; Daleo et al. 2015). Indeed, the conspicuous vegetation zonation pattern is generally the result of a trade-off between nutrient competition and flooding-related stress toleration (Bertness 1991); more stressful (i.e., generally lower) zones are characterized by stress tolerant, competitively inferior species, while more benign (i.e., generally higher) zones are dominated by less stress-tolerant, but competitively superior species (Bertness 1991). At arid zones, nevertheless, this pattern changes as the higher zones can also be quite stressful due to abiotic stress (i.e., desiccation, salinity) (see Idaszkin et al. 2011). Thus, a brief summary of why salt marshes are so amenable to perform ecological research may include that they are 1) great systems to evaluate how different biotic and abiotic drivers interact, as they present sharp small-scale elevation changes leading to environmental gradients determined by tidal flooding; 2) fairly simple communities, with a relatively reduced number of species ordered in conspicuous zonation patterns, which simplifies the measurement of eventual changes in community structure, and 3) inhabited by relatively small-sized organisms (plants and animals), what makes them easy to manipulate (e.g., translocate, remove, exclude or include) in order to perform experiments.

The description we provided above (and in Figure 1A) is based on popular models of salt marsh community structure that emerged after decades of experimental work. But those works were mostly performed at a few sites (i.e., North Eastern coast of USA). The initial formulation of theories and hypotheses based on single-site experiments is quite common in ecology and, as a result, usually does not account for the roles of particular environmental contexts and contingencies. After this initial formulation, other researchers around the globe usually rush to include those exciting new theories into their research programs, but soon discover that results coming from their study sites do not fit well within the theory. As no-fit examples accumulate, what starts out as a black swan slowly becomes a very colorful flock of swans, forcing the theory to be redefined. As we will see, South West (SW) Atlantic salt marshes have, indeed, some features that make them quite different from the 'mainstream' marshes

described above. These distinctive features can even change the processes that govern community structure and functioning, and thus challenge the generalizations produced elsewhere (Alberti et al. 2015). Here, we summarize some examples of how different theories and hypotheses, driven by well-established generalizations, were refined or expanded after the result of more than 25 years of work at SW Atlantic salt marshes. Although in the following text we focus on the contribution of salt marshes (and those from the SW Atlantic in particular) to the community ecology theory, by no means we are implying that other systems or locations did not make similar or even more important contributions. Instead, we highlight that our salt marshes have something to say in terms of our ecological comprehension of the natural world.

South West Atlantic salt marshes

There are extensive and diverse salt marshes distributed from southern Brazil to the southern tip of Patagonia. These salt marshes (we will call them SW Atlantic salt marshes) are diverse from a geomorphological standpoint, including areas dominated by tidal flats of

ivers, lagoons, creeks, coves and protected bays (see Figure 2). Their long coastline (~3500 km) also harbors large variations in environmental conditions, including rainfall, temperature, tidal amplitude, sediment composition and nutrient availability (Isacch et al. 2006; Fanjul et al. 2007; Daleo and Iribarne 2009). The Northern part, for example, receives high annual rainfall (~900-1200 mm) and presents extensive marshes characterized by brackish water conditions, while the southern part receives low annual rainfall (<650 mm) and marshes are restricted to the presence of large bays or small river mouths (Isacch et al. 2006). Not surprisingly, this variability in environmental conditions is linked to some variability (that can reach up to an order of magnitude between extremes) in productivity, standing biomass and density of burrowing organisms, among other biological features (Martinetto et al. 2016). Vegetation, for instance, is generally dominated by three species; the intertidal cordgrass *Spartina densiflora* (now known as *Sporobolus densiflorus*), the cordgrass *Spartina alterniflora* (now known as *Sporobolus alterniflorus*) and the glasswort *Sarcocornia* sp. (= *Salicornia* sp.) (Figure 2). Although these three plant species usually cover ~70 % of salt marsh areas, their relative abundance is tightly

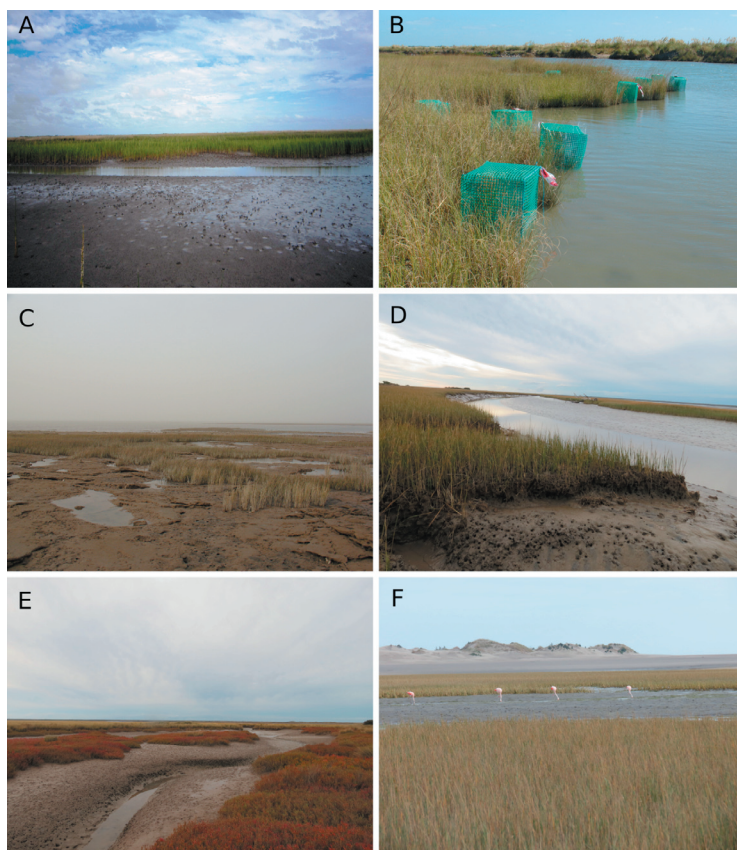


Figure 2. SW Atlantic salt marshes are quite diverse in terms of geomorphology, including areas dominated by tidal flats of rivers, lagoons, creeks, coves and protected bays. The variability in environmental conditions is linked to some variability in the biological features as species dominance or composition. Examples of salt marshes dominated by *S. alterniflora* (A: Samborombón Bay; C: San Blas Bay, D: Río Negro estuary, F: Caleta de los Loros), *S. densiflora* (B: Mar Chiquita) and *Sarcocornia* sp. (E: Río Negro estuary).

Figura 2. Las marismas del Sudoeste Atlántico son muy diversas en términos de geomorfología e incluyen áreas de planicies de marea de ríos, lagunas, arroyos, caletas y bahías protegidas. La variabilidad en las condiciones ambientales determina cierta variabilidad en algunas características biológicas importantes, como la dominancia e incluso la composición de especies. Se muestran ejemplos de marismas dominadas por *S. alterniflora* (A: Bahía Samborombón; C: Bahía San Blas, D: estuario del Río Negro, F: Caleta de los Loros), *S. densiflora* (B: Mar Chiquita) y *Sarcocornia* sp. (E: estuario del Río Negro).

associated with environmental conditions, as freshwater inputs (*S. densiflora* dominates in freshwater influenced sites while *S. alterniflora* and *Sarcocornia* sp. are more abundant in saltwater influenced sites) (Isacch et al. 2006) or temperature (*Sarcocornia* sp. dominates at the southernmost, colder marshes) (Idaszkin and Bortolus 2011). Here, we will mainly focus on studies performed on the Northern part (from 31°48' S to 42°25' S) as salt marshes are 1) more intensively studied and 2) larger in extension, but we acknowledge that southernmost salt marshes have significant differences in terms of structure and function (see Supplementary Material S1). Despite their environmental and biological variability, there is a distinctive and conspicuous feature that characterize these Northern salt marshes; they are densely inhabited by the burrowing crab *Neohelice granulata*. This crab (up to 8 cm in carapace width) can reach densities higher than 100 individuals/m², forming massive crab beds that extend into the tidal flats (Figure 2A, D, E). Throughout this text, some of the discrepancies with the generalizations and models grounded in other salt marshes that we will highlight, are indeed directly or indirectly related with the presence of this crab species (see also Alberti et al. 2015). These initial discrepancies turned to be just the more conspicuous, and triggered the discovery of other important actors and novel interactions. They ultimately redefined the way in which we perceive salt marsh organization, leading to Figure 1B, but wait, don't look at it before reading the text below!

HERBIVORES CLAIM THEIR PLACE

In this section, we will review how inclusion of herbivores into the conceptual model of salt marsh structure and function helped to redefine some concepts, showing how the relative importance of different forces can be context dependent. For a long time, one prevailing paradigm was that salt marsh community structure and function were mainly determined by abiotic drivers, with consumers having negligible effects. This idea comes from early experimental work performed at rocky shores, and was materialized into the stress-gradient hypothesis (or environmental-stress model) (Menge and Sutherland 1987). This hypothesis postulated that the importance of consumption, as a structuring force, should decrease as stress increases. The cornerstone of this model was simple; high trophic-level species are expected to be more susceptible

(and more responsiveness) to environmental stress than species from more basal levels. In addition, the ability of plants to tolerate abiotic stresses (such as salinity) is linked to their inherently low growth rates. Finally, as wild herbivores are not quite conspicuous at salt marshes (at least not as conspicuous as in African savannas), it is not very surprising that, at that time, herbivory was assumed as a non-important driver of salt marsh structure and function. There were, however, studies with large domestic herbivores on salt marshes (Bakker 1978, 1985), but for some reason (likely because they do not involve wild herbivores) these studies were set aside. Then, it was not until the early years of this century that parallel works at southern US and Argentinean marshes started to suggest that, at least at some sites, this assumption needed to be inspected more carefully (Silliman and Bortolus 2003).

First, evidence accumulated suggesting that small vertebrates and invertebrates could affect salt marsh plants by trophic effects (Bortolus and Iribarne 1999; Silliman and Zieman 2001), at least under certain conditions. Soon, it became clear that herbivores commonly reduce plant productivity directly, by feeding (Silliman and Bortolus 2003; Bortolus et al. 2004; Vera et al. 2009; Alberti et al. 2011), but also indirectly by facilitating pathogen infection at the grazer-induced wounds (Silliman and Newell 2003; Daleo et al. 2009), resulting in a significant decrease in plant standing biomass. As the number of studies addressing the impact of herbivores on salt marshes grew, it was evident that, despite the expectations under the stress-gradient hypothesis, many times the peak of consumption was concentrated in areas or periods characterized by high abiotic stress. For example, herbivory is usually highest during drought or floods, or at the lowest edges of the marsh (Silliman et al. 2005; Alberti et al. 2007a, 2007b). As a consequence of these investigations, it is now clear that grazing pressure and environmental stress can act synergically to regulate plant production. Being fair, this does not necessarily contradict the environmental-stress model, because one of its assumptions was that both, consumers and prey, are affected in the same direction by abiotic stress. Instead, the results described above contributed to expanding the stress-gradient hypothesis, clarifying that the impact upon producers can be magnified (i.e., additive stress) if environmental stress does not directly affect consumers (Alberti et al. 2010).

More or less simultaneously, the stress-gradient hypothesis was modified to include positive interactions (Bruno et al. 2003). Until then, community regulation was largely explained by physical factors, recruitment/dispersal and negative species interactions (predation and competition). Although the existence of positive interactions between species was known for decades, they were largely ignored (or considered inconsequential) by the ecological theory (not to say ecologists). Perhaps the models of ecological succession proposed by Connell and Slatyer (1977) were the only widely accepted formalization that included positive interactions as possible drivers of community organization. Nevertheless, even those authors stated that facilitative successions, although possible, should be uncommon and unlikely.

During the last decade of the 20th century, experimental evidence supporting a prominent role of positive interactions accumulated in a variety of systems. In this context, rocky shores and salt marshes made a substantial contribution to visibilize the importance of positive interactions as structuring force (Bertness and Leonard 1997). Inherited from the stress-gradient hypothesis, nevertheless, biotic and abiotic stress were still thought to be mutually exclusive, and thus, amelioration of biotic stress (e.g., protection against strong herbivory pressure) was not expected in abiotically harsh environments (Bertness and Callaway 1994; Bruno et al. 2003). Indeed, successional models for salt marshes were either facilitative (mediated by abiotic stress amelioration) where environmental stress was high, or competitive in mild environments (Bertness and Ellison 1987; Ewanchuk and Bertness 2003, 2004). In accordance with theoretical models (Farrell 1991), herbivores were only thought to be responsible for retarding or speeding up succession dynamics depending on the successional model (i.e., facilitative, neutral or competitive) and/or on whether the consumed plants were early or late successional species (van der Wal et al. 2000; Kuijper et al. 2004). Studies conducted in SW Atlantic salt marshes challenged this established idea, showing that associational resistance to herbivory could be highly important, even in abiotically stressful environments (Alberti et al. 2008; see also Graff et al. 2007 for similar results in the Patagonian steppe). In particular, they showed that, in recovering zones after disturbance, *S. densiflora*

seedlings need to grow within *Sarcocornia* sp. patches to be protected from the otherwise too strong crab herbivory rates. Moreover, to our knowledge, experiments conducted in Argentinean salt marshes showed for the first time that herbivores can turn an otherwise competitive succession into a facilitative succession, because *S. densiflora* grows faster in isolation in the absence of herbivory (Alberti et al. 2008).

Going back to the past, the development of the theory behind ecological zonation somehow mimicked that of ecological successions, and of course, was then largely covered by the 'stress-gradient hypothesis' umbrella. More than a century ago, ecologists already knew that the abiotic environment played a central role (Clements 1916). Competition gained importance as a driver of species zonation (particularly at the most abiotically benign ends of species' distribution) some decades later (Connell 1961). Afterwards, the focus shifted from negative interactions and the abiotic environment shaping communities, towards a more broad view that included amelioration of both biotic and abiotic stress (Bruno et al. 2003). Again, salt marshes made a significant contribution to this last step, revealing that stress amelioration can allow the expansion into areas otherwise outside the fundamental niche (*sensu* Hutchinson 1957). Specifically, negative interactions commonly dominate in the most benign end of abiotic gradients, while abiotic stress, and positive interactions that ameliorate it, usually dominate in the opposite end of the gradient (Bertness and Leonard 1997; Pennings et al. 2005) (Figure 1A). However, as previously mentioned, negative interactions (and herbivory in particular) can have prominent roles even under abiotically stressful conditions (see also Smit et al. 2009). Can these negative interactions be strong enough to constrain plant zonation across the environmental stress gradient even more? Well, evidence from SW Atlantic salt marshes suggested that this biotically defined zonation edge in harsh environmental conditions can be possible (Alberti et al. 2010), something that was later confirmed in other salt marshes (He et al. 2015). However, in science answering one question raises many more. For example, now that herbivores are recognized as important actors, can they have other significant roles (i.e., as ecosystem engineers)? If so, which forces mediate the relative importance of trophic and non-trophic effects?

UNEXPECTED OUTCOMES FROM ECOSYSTEM ENGINEERING

In addition to their trophic effects, herbivores can also modify community dynamics by ecosystem engineering (EE) effects (Wilby et al. 2001). Ecosystem engineering involves modulation of resources from one species to another through non-trophic effects that directly or indirectly change the abiotic environment (Jones et al. 1994). Burrowing by organisms such as crabs, earthworms and polychaetes are classic examples of EE, and the effect, known as bioturbation, is a well-known process that caught the attention and even led to the last scientific book of Charles Darwin (Meysman et al. 2006).

As we previously noted, despite the high levels of productivity, marsh plant growth is usually limited by oxygen availability (Mendelssohn et al. 1981). Burrowing organisms, thus, can facilitate plant growth by increasing sediment oxygenation (Bertness 1985; Fanjul et al. 2007). This facilitation was thought to be quite direct; burrows increase the surface of the sediment in contact with air, enhancing soil drainage, decreasing sulfurs and increasing oxygen availability (Bertness 1985). But this facilitation can be more complex, involving previously cryptic actors such as plant root endophytes (Daleo et al. 2007). Plant root endophytes, as mycorrhizal fungi, can increase nutrient uptake of associated plants (Klironomos et al. 2000) but in flooded ecosystems, such as seagrasses, mangroves and marshes, their effects were assumed to be negligible since they are obligate aerobes (Miller and Sharitz 2000). However, field experiments in SW Atlantic marshes confirmed that a significant part of the positive effect of burrowing activities by crabs on *S. densiflora* growth was indeed mediated by increases in root colonization by fungal endophytes (Daleo et al. 2007), highlighting that ecosystem engineers can function as ecological linchpins activating and maintaining key mutualisms between species.

This is not the only example of how bioturbation can affect the way in which community structure regulates ecosystem functioning. Commonly, plants contribute to soil/sediment stabilization by increasing soil cohesion and reducing the energy of erosive agents (Schmidt et al. 2001; Duarte et al. 2013; Feagin et al. 2015). But again, as we will be

seeing throughout this text, things could work a little bit differently in SW Atlantic salt marshes. Unlike other marsh plants, *Sarcocornia* sp. (highly abundant in many SW Atlantic marshes) has a low ability to trap sediments and does not contribute to sediment deposition (Townend et al. 2011). However, this plant reduces desiccation stress and thus facilitates crab colonization (Bortolus et al. 2002). Thus, when *Sarcocornia* sp. settles on bare sediments, it forms clonal patches that facilitate the establishment of crabs (Escapa et al. 2015). And here comes the twist in the story: due to their intense burrowing activity, crabs decrease sediment stability, becoming unstable for *Sarcocornia* sp. roots, and leading to plant death and subsequent salt pan formation, which eventually collapse and promote creek expansion and erosion (Escapa et al. 2015). Thus, plant facilitation of crab establishment leads the system to an unexpected condition, since by negatively affecting *Sarcocornia* sp. and increasing sediment erosion, crabs promote creek formation in previously vegetated patches.

The opposite mechanism of bioturbation (i.e., biocompaction of soils, also known as trampling) has also been studied for a very long time (Keen and Cashen 1932). While bioturbation was largely attributed to small-sized animals (invertebrates) in marine systems (Meysman et al. 2006), biocompaction was mostly studied with large terrestrial mammals (e.g., Howison et al. 2017). As trampling is more important in loamy or clay soils, like those found in many salt marshes (Tanner and Mamaril 1959; Howison et al. 2017), and given that soil compaction reduces soil porosity (thus increasing anoxia), its potential effect in salt marshes are expected to be high. However, animals inhabiting salt marshes are usually small-sized, and trampling was long assumed inconsequential. Field experiments, nevertheless, showed that the wild guinea pig (*Cavia aperea*) can indeed affect soil compaction through trampling, affecting plant community structure, at least in runaways (Pascual et al. 2017). It is worth mentioning that, as expected, the scale at which these effects take place (runaways cover ~15% of the high marsh surface) is smaller than the compaction produced by large mammals on intensively managed grasslands or in African savannas, but enough to affect plant diversity at marsh scale.

ALL THE SMALL THINGS... THE BALANCE OF DETERMINISTIC AND STOCHASTIC DRIVERS

In this section, we will move to a less conspicuous group of organisms that were largely ignored in community ecology. The use of this group of organisms, nevertheless, is rapidly gaining momentum, and will probably have a strong influence during the next decades, likely challenging the way we

understand community assembly rules. Given their dispersal potential, microbes had been thought to be ubiquitous. Thus, the only filter determining the presence/absence of each species in a given location should be the environment (Fenchel and Finlay 2004). Under this view, environmental conditions should function as a strong filter, creating predictive and limited-membership communities with low site-to-site variability in species composition (community convergence)

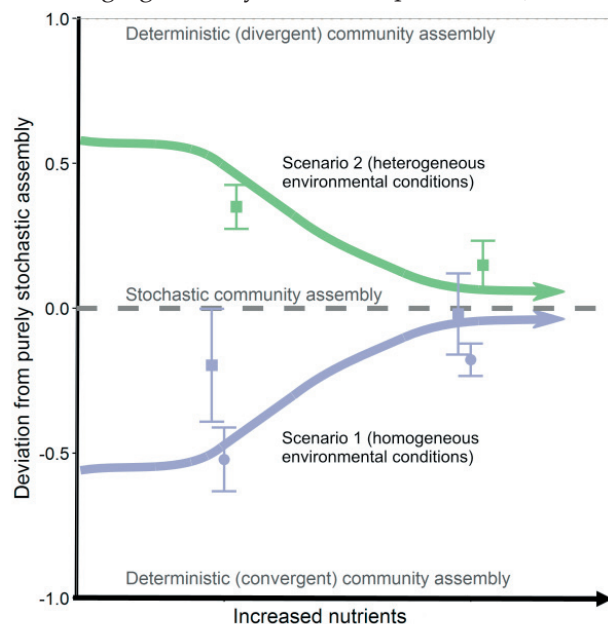


Figure 3. Conceptual model of two proposed basic scenarios in which the enhanced stochasticity, associated with increased resources, should lead to convergence or divergence of communities. Deviation from purely stochastic assembly is expressed as the Raup-Crick metric, that ranges from -1 to 1, indicating whether communities are less dissimilar (approaching -1), as similar (approaching 0) or more dissimilar (approaching 1) than communities randomly assembled. In scenario 1, greater nutrient inputs should increase divergence of communities when the initial environmental conditions are spatially homogeneous. Without enhanced nutrient inputs, niche selection determines which species from the regional pool can be present, creating predictive and limited-membership communities with low site-to-site variability in species composition (community convergence). In such situations, greater nutrient inputs weaken niche selection and increase compositional stochasticity. In scenario 2, in contrast, greater nutrient inputs should increase convergence of communities when the environmental conditions are spatially heterogeneous because increased stochasticity reduces the importance of deterministic filters. The interaction between niche selection and environmental heterogeneity deterministically creates divergent communities. Similarly to the situation in scenario 1, greater nutrient inputs decrease niche selection, but drive communities to convergence instead of divergence. Bars represent mean \pm SE of data from Daleo et al. (2018) and from Zhou et al. (2014). Position of data with respect to the x axis is arbitrary. This model is a free adaptation of that proposed by Dini-Andreote et al. (2015).

Figura 3. Modelo conceptual de dos escenarios básicos en los que aumentos en la estocasticidad, asociados a una mayor disponibilidad de recursos, deberían llevar a una mayor convergencia o divergencia de las comunidades. Las desviaciones de un ensamble puramente estocástico se expresan con el índice de Raup-Crick, que toma valores entre -1 y 1, indicando si los ensambles son más similares (hacia el -1), tan similares (cercano a 0) o más disímiles (hacia el 1) que ensambles generados aleatoriamente. En el escenario 1, aumentos en la disponibilidad de nutrientes deberían aumentar la divergencia de las comunidades cuando las condiciones ambientales son espacialmente homogéneas. En condiciones de bajos recursos, el nicho ecológico determina cuáles especies pueden estar presentes, creando comunidades predecibles con baja variabilidad entre sitios (convergencia). En estos casos, una mayor cantidad de nutrientes lleva a que se relajen los filtros del nicho ecológico aumentando la estocasticidad. En cambio, en el escenario 2, más nutrientes deberían llevar a una mayor convergencia de las comunidades cuando las condiciones ambientales son espacialmente heterogéneas, ya que la mayor estocasticidad reduciría la importancia de los filtros determinísticos (que de otra forma llevarían a ensambles divergentes). Al igual que en el escenario 1, al aumentar la disponibilidad de nutrientes disminuye la importancia de los filtros determinísticos, aunque llevando en este caso a ensambles más convergentes. Las barras representan la media \pm SE de los datos publicados por Daleo et al. (2018) y por Zhou et al. (2014). La posición de los datos con respecto al eje x es arbitraria. Este modelo es una adaptación libre del modelo propuesto por Dini-Andreote et al. (2015).

among sites with similar conditions, and high site-to-site variability in species composition (community divergence) among sites with different conditions (Chase and Myers 2011). Indeed, at SW Atlantic salt marshes, environmental drivers such as greater salinity stress, presence of consumer damage and nutrient loadings, can interact and drive to clearly different fungal leaf communities (Daleo et al. 2018). As we will discuss in the next paragraph, nevertheless, our results also show that stochastic forces, together with these deterministic filters, are important drivers of these assemblies.

It is now widely accepted that the assembly of species into natural communities is the result of a combination of both deterministic and stochastic forces that act simultaneously (Leibold and McPeck 2006). During the last decade, the focus shifted to understand the mechanisms underpinning their relative influences (see Chase 2007; Vellend et al. 2014). In some systems (especially plant systems), increases in resource availability usually lead to community homogenization and diversity loss by deterministic processes such as light competition (see Hautier et al. 2009). In other systems, however, enhanced resources can increase community divergence by enhancing the relative importance of stochastic processes, such as ecological drift (Chase 2010). In contrast, our results show that increased nutrient inputs enhanced the relative importance of stochastic processes but driving to community convergence. As stated before, without increased nutrient inputs, different environmental conditions generate distinctive communities, but increased nutrient inputs canceled this divergence, driving communities to similar endpoints regardless of other environmental drivers. These results provided evidence from an unusual scenario that can be used to extend some models on the balance between deterministic and stochastic drivers (Figure 3).

SCALING UP COMMUNITY STRUCTURE TO ECOSYSTEM FUNCTION

So far, we have shown different ways in which a variety of factors change salt marsh community structure, but what are the consequences of those changes? The structure of communities and their function can be tightly linked, but the mechanisms behind this linkage are not always obvious, and can be hard to recognize. In this section we review

a few ways in which altered communities modify ecosystem functioning.

In the last decade, salt marshes, together with mangroves and seagrasses, were identified as environments with a great capacity of sequestering and storing carbon (McLeod et al. 2011). Within the context of global climate change and the greenhouse effects due to the large atmospheric emissions of carbon, it is of particular interest to understand how this type of ecosystems works in order to be able to preserve them. One of the main processes related to the global carbon budget is litter decomposition because it directly contributes to CO₂ flux in the atmosphere. Most of the work evaluating litter decomposition in salt marshes was oriented towards comparing nutrient content of litter from different plant species (e.g., Simões et al. 2011) and the effect of different environmental variables (e.g., Kirwan and Mudd 2012), but very few evaluated the effect of changes in the biodiversity of soil decomposers and the plant community.

As mentioned before, salt marshes usually have one or a few dominant plant species structuring the whole environment, thus, any change in biodiversity or composition can potentially have important cascading effects for ecosystem functioning. This feature is especially relevant as salt marsh communities (i.e., species composition) are being altered by anthropogenic drivers such as altered nutrient inputs, species invasions, shoreline development and climate change. Despite this global scenario, there is comparatively poor empirical data testing how changes in composition can affect decomposition. To our knowledge, there are some studies that evaluated the effects of changes in soil decomposer communities (e.g., Zimmer et al. 2004), and changes in plant litter composition (Treplin et al. 2013), but very few evaluating *in situ* changes in the plant community (Liao et al. 2008). We already went through how herbivory can decrease *S. densiflora* dominance (Daleo et al. 2017), especially at recovering patches after disturbance, which, in turn, can allow subordinate plant species to colonize, generating a different and persistent plant community (Daleo et al. 2014). Litter produced at this new community decomposed quicker than that produced at *S. densiflora* dominated patches, in part due to more labile composition, but also because of key changes in the microenvironment, such as enhanced solar radiation and increased soil temperature (Daleo et al. 2020). Thus, evidence found from

SW Atlantic salt marshes shows that changes in plant dominance or composition can significantly change the carbon cycle and, thus, the role that these salt marshes have as carbon storage areas. These results joined previously isolated pieces of evidence to show how drivers of community structure can have effects on ecosystem functioning through both changes in species composition (litter quality) and the microenvironment they generate (Daleo et al. 2020).

In addition to the effects caused by changes in species composition, community function can be also altered by changes in the interaction strength between species. Climate change, for instance, is magnifying temperature and rainfall extremes, making harsh environmental conditions even harsher, and thus, potentially generating stronger biotic interactions. If high enough, these interactions may drive persistent community or ecosystem state shifts. For example, and extending the concepts mentioned in the preceding paragraph, in Chinese and US salt marshes, severe droughts can intensify herbivore grazing leading to massive die-off zones, where vegetation could not recover after abiotic conditions were reestablished (Silliman et al. 2005; He et al. 2017). Similarly, climate change is also expected to promote consumer front formation (a concentration of consumers, grazers or predators, in a specific time and place) (Silliman et al. 2013). Can you imagine this? Hundreds and thousands of individuals moving together through the landscape towards food resources. Consequences of consumer fronts for the community can be extraordinary (see Silliman et al. 2013 to learn more about consumer fronts in different ecosystems). However, to our knowledge there was no clear evidence of consumer front formation induced by climate change that could lead to persistent zonation changes in species distributions. A recent work combining historical weather data with field samplings and experiments showed how extreme precipitation can promote consumer (crabs) fronts, thus generating the retraction of the lowest salt marsh edge (Rocca et al. 2021). This occurred because extreme rainfall events (becoming more common in recent decades) promote floods, which enhance crab herbivory pressure at the lower edge of the marsh. While the mudflat is underwater, crabs concentrate on the marsh-mudflat edge, and exert a pressure excessively high on those plants. This can scale up, not only changing

zonation patterns, but also the geomorphology of the area, given that the consumer fronts accelerated vertical soil erosion in the salt marsh edge, probably washing away the carbon sequestered in the top layers of the sediment. Analogous parts of this process were also found in US salt marshes (Coverdale et al. 2014; Vu et al. 2017; Vu and Pennings 2021). Hence, consumer fronts, triggered by extreme weather events, have consequences that go beyond communities, potentially changing salt marsh resilience. Together, these results support the general call that models of future climate scenarios should integrate the indirect effects on ecosystem-regulating food web interactions.

TO ECOSYSTEMS AND BEYOND: CROSS-ECOSYSTEM FLUXES OR CRAB INTERCEPTION?

We mentioned in the last section that salt marshes are now known to have a great capacity of sequestering and storing carbon. More than half a century ago, however, the focus was not on their role as C sinks, but as important sources of C subsidies for other systems. Indeed, since the outwelling hypothesis was proposed in the 60's (Teal 1962; Odum 1968), one of the most important functions that were assigned to salt marshes has been the support of fisheries. This idea persists nowadays, as evidence was accumulated therein, showing that primary production of salt marshes support an important portion of the secondary production of many estuaries and their adjacent marine environments (Childers et al. 2000). However, the mechanisms involved in the cross-system energy subsidy, and in the importance of this supply for the receiving environment, is variable (Ziegler et al. 2021). Subsidies can occur via direct transportation of salt marsh detritus through tidal or fluvial flooding (Teal 1962; Nixon 1980; Odum 2000), or it can involve an indirect increase of marine primary production through an enhanced supply of dissolved nutrients, in the form of reactive inorganic N generated by organic matter decomposition in marsh sediments (e.g., Krest et al. 2000; Santos et al. 2019). Another usual but indirect mechanism involves the flux of energy through animal movements between environments, as marine juvenile fishes feeding on salt marsh habitats (Colombano et al. 2021). This hypothesis of salt marshes as supporters of the secondary production of

marine environments (especially fisheries of commercial interest) was, for years, the most important argument for the conservation and restoration of these habitats worldwide.

In SW Atlantic marshes, however, crabs can affect most of the processes involved in C fluxes (Martinetto et al. 2016) and, consequently, impact the possible support of marine food webs. For example, even though detritus production in these marshes is high (Montemayor et al. 2011), crab burrowing activities trap a large amount of detritus into the marsh and the surrounding tidal flats sediments (reducing the amount exported), limiting the direct exportation pathway (Gutiérrez et al. 2006). Some energy fluxes from marshes could still be expected through the indirect pathway, given that crabs are mobile organisms. But crab movement is mainly restricted between the marsh and the tidal flats (Mendez-Casariago et al. 2011). On the other hand, juvenile fishes use tidal creeks and marsh habitats, but mainly during flooding events (Valiñas et al. 2010) and evidence suggests that the amount of energy moved through this mechanism is limited; only a few species feed on benthic fauna in these habitats, and none seems to consistently feed on crabs (Valiñas et al. 2012). Thus, putting all the pieces together, there is no evidence that SW Atlantic salt marshes are acting as suppliers of energy for estuarine food webs. Indeed, stable isotopes analyses (Botto et al. 2005) suggest that this marsh-derived organic matter does not support juvenile fishes nor other members of the estuarine food webs, but instead this production is mostly used by the burrowing crabs. Most of the primary production seems to be stored and recycled inside the salt marsh-crab system.

THE FUTURE OF SALT MARSHES

As we mentioned, given their position just in the edge of terrestrial and marine systems, salt marshes are particularly exposed to the increasingly frequent extreme weather events (He and Silliman 2019) and to chronic high nutrient loads coming from agriculture and other human activities (Adam 2002; Bertness et al. 2004). In addition, salt marshes are also suffering increased pressures associated with

both land reclamation and domestic livestock grazing (Bromberg Gedan et al. 2009). In this context of enhanced pressure from diverse (and potentially interacting) drivers, it is imperative to understand how these drivers are affecting salt marsh structure and function, and thus the ability to maintain the provision of key ecosystem services (Bromberg Gedan et al. 2009; Montoya and Raffaelli 2010). To achieve this, we need to raise our heads and understand that marshes are not isolated 'natural sanctuaries' but part of diverse landscapes where different stakeholders have different perspectives. This necessarily forces us to think in larger spatial and temporal scales, and to find a way to be more efficient in a context of limited resources to perform research (see Supplementary Material S1 for a brief overview of the future directions that, in our opinion, can help us to move forward).

In summary, we made a general review of some results that, we believe, helped to increase the knowledge about salt marsh functioning and also to expand this knowledge beyond this specific system to build community and ecosystem function theory. We believe SW Atlantic salt marshes still have a lot more to offer, not only as conceptual models that help satisfy our intellectual curiosity, but also as key ecosystems that provide valuable benefits to our societies. We hope that our effort will continue to yield useful results for the development and expansion of ecological theory. We also hope these results will help to predict possible future response scenarios and to design mitigation actions, thus producing information valuable for decision makers regarding management of these endangered systems.

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