



Crab Bioturbation and Herbivory May Account for Variability in Carbon Sequestration and Stocks in South West Atlantic Salt Marshes

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Coastal vegetation plays an important role for climate change mitigation. Compared with terrestrial ecosystems, coastal vegetation shows higher rates of atmospheric CO₂ uptake and a more efficient retention of carbon (C) in sediments. Salt marshes present the highest values as C binders, although a global estimation of these values is still pending due to regional gaps in the records predominantly from the southern hemisphere. There are no clear patterns or dominant processes with enough evidence to account for the observed variability, suggesting that context dependent processes are likely greatest influencers on C storage. Salt marshes in the South West Atlantic (SWA) coast are densely populated by the intertidal burrowing and herbivore crab *Neohelice* (= *Chasmagnathus*) *granulata*. Many ecological processes related to C transformation occurring in these salt marshes are influenced by crab activities, either through bioturbation or via herbivory. We hypothesize that *N. granulata* could have a significant role in the capacity of SWA salt marshes to bind C. Reduction of plant biomass, increased aerobic decomposition in the sediment and facilitation of erosion are some of the multiple effects exerted by *N. granulata* that can directly and indirectly modify the capacity of salt marshes to bind C. Here, we compiled information available regarding C sequestration and accumulation in SWA coastal salt marshes and propose a hypothetical model including the mechanisms mediated by *N. granulata* that interfere the transformation paths of C in salt marshes. The data suggest that mechanisms that are top-down regulated, negatively affect C accumulation in the form of aboveground biomass especially in salt marshes dominated by *Spartina alterniflora*. While, mechanisms mediated by bioturbation can negatively (increasing oxygenation and thus facilitating aerobic degradation) affect as well as positively (increasing retention of macrodetritus) affect the accumulation of C, the latter being of greater magnitude in *Spartina densiflora* salt marshes.

Keywords: Blue C, salt marshes, herbivory, bioturbation, coastal vegetation

INTRODUCTION

Vegetated coastal ecosystems (salt marshes, mangroves, seagrass meadows) provide many goods and services. For instance they play a fundamental role dissipating wave energy and limiting the effects of sea level rise (Gedan et al., 2011), act as filters, cycling the excess of land-derived nutrients (McGlathery et al., 2007), and provide a habitat for many economically important species (Beck et al., 2001). However, although these benefits are well recognized, degradation and loss of these ecosystems are continuously occurring at accelerating rates (Duarte et al., 2008; Valiela et al., 2009).

Recently, a new service derived from coastal vegetation has been identified concerning the role that these ecosystems play in climate change mitigation, with particular focus on the role of coastal plant communities in sequestering and storing atmospheric CO₂ (Nellemann et al., 2009; Duarte et al., 2013). Vegetated coastal ecosystems are efficient carbon binders exceeding the well know capacity of terrestrial forests. Reported average C burial rates (CBR) for coastal vegetation range between 138 and 244 g C m⁻² year⁻¹ while temperate, tropical and boreal forests range between 4 and 5 g C m⁻² year⁻¹ (McLeod et al., 2011; Ouyang and Lee, 2014). In addition to the efficient CBR, marine vegetated ecosystems can store C for millennia (Mateo et al., 1997; Lo Iacono et al., 2008; Chmura, 2009), while terrestrial vegetation does so for decades or centuries (Chambers et al., 2001). Thus, preservation and restoration of coastal vegetated ecosystems represent a win-win scenario for climate change mitigation implementation: on the one side the preservation and restoration of these ecosystems secure an active and efficient uptake of atmospheric CO₂, and in the other, their preservation prevents the emission of greenhouse gases by exposing to degradation the large amount of carbon stored in sediments and live biomass. In this context, the term “blue carbon” has emerged to indicate C that is sequestered and stored in coastal marine environments (Nellemann et al., 2009).

Blue carbon is the most recently acknowledged ecosystem service provided by salt marshes (Chmura, 2013). Historically, the high productivity of salt marshes has been more linked with the export of energy to adjacent systems and the support of a significant fraction of the metabolism that takes place within the water column rather than binding organic matter (OM) in salt marsh sediments (Valiela et al., 2000). There are some characteristics that make these ecosystems particularly good as C binders. For instance, every CO₂ molecule stored in salt marsh and mangrove soils has an added value due to the negligible rate of emission of others greenhouse gases such as methane (Chmura, 2009). Marine sediments present large concentrations of sulfate which inhibits the activity of methanogen bacteria (Winfrey and Ward, 1983) limiting, thus, the emission of methane. The average CBR reported for salt marshes is quite similar to that found in mangroves and over 1.75 fold higher than that reported for seagrasses (244.7, 226 and 138 g C m⁻² year⁻¹ for salt marshes, mangroves and seagrasses respectively; McLeod et al., 2011; Ouyang and Lee, 2014). Nevertheless, there is a huge variability in CBR for salt marshes around the world, ranging from 18 to 1713 g C m⁻² year⁻¹ (Ouyang and Lee, 2014). The

maximum CBR reported for salt marshes is almost twice than the maximum reported in mangrove ecosystems (949 g C m⁻² year⁻¹) and 9 times higher than the maximum CBR for seagrass meadows (190 g C m⁻² year⁻¹; McLeod et al., 2011). This difference among systems highlights the potential of salt marsh ecosystems for binding C as well as the need for further studies on the determinant factors for sequestration and remobilization of C from marsh sediments.

In spite of the effort to estimate global C storage and sequestration rates in salt marshes, there is a gap in data mostly from the southern hemisphere (Chmura, 2013; Ouyang and Lee, 2014). Given the enormous variability in CBR registered in salt marshes worldwide, global estimations calculated with the current data available is probably biased. There are not yet clear general patterns or a dominant process with enough evidence to account for this variability. Some of the main factors described to influence C sequestration in coastal wetland habitats are: local geomorphology, nutrient availability, hydroperiod, salinity, and suspended sediment supply. For instance, sediment grain size has recently found to be a good predictor of C storage in SE Australian salt marshes (Kelleway et al., 2016). There are also inherent characteristics to plant species that dominate within different salt marshes that are linked to the C burial capacity, such as allocation of plant parts, decomposition rates and primary productivity. These characteristics are, in turn, influenced by physical factors such as temperature, precipitation, tidal range, nutrients, and granulometry; as well as biological (plant competition, bioturbation, trophic cascades; McLeod et al., 2011). A previous study attempting to explain the variability in CBR was based on the type of halophyte dominating the salt marsh. In that analysis, *Distichlis* was found to have the lowest average CBR, while *Spartina* had the highest (Ouyang and Lee, 2014). However, when the data is carefully examined, both maximum and minimum CBR reported correspond to *Spartina* dominated salt marshes. This pattern suggests that there are more site specific characteristics to explain such a large variability related to the ecological functioning of each particular location.

Although, burrowing and herbivorous organisms often inhabit vegetated coastal ecosystems, their effects on C stocks are scarcely known, but evidence shows that they can be relevant to Blue C studies. For instance, the activity of intertidal burrowing crabs (*Ucides cordatus* and *Uca maracoani*) enhance the decomposition of OM in the soil of Brazilian mangroves reducing up to 70% the total organic carbon (Araújo et al., 2012). In salt marshes in Cape Cod (Mass, USA), the crab *Sesarma reticulatum* increases erosion by burrowing near-water sediment and reduces plant biomass by herbivory (Coverdale et al., 2014). These two examples are evidence that the activity of these organisms reduce the capacity of these environments to bind C.

Salt marshes along the Atlantic coast of South America are mostly dominated by two species of *Spartina* (*S. densiflora* and *S. alterniflora*) and *Sarcocornia* spp. (Figures 1A–C). Most of these salt marshes (except for those located at the southernmost extreme, from 42° 25' S to 53° 48' S) are highly bioturbated by the burrowing crab *Neohelice* (= *Chasmagnathus*) *granulata* (Figures 1D–F, Iribarne et al., 1997). This crab is also an

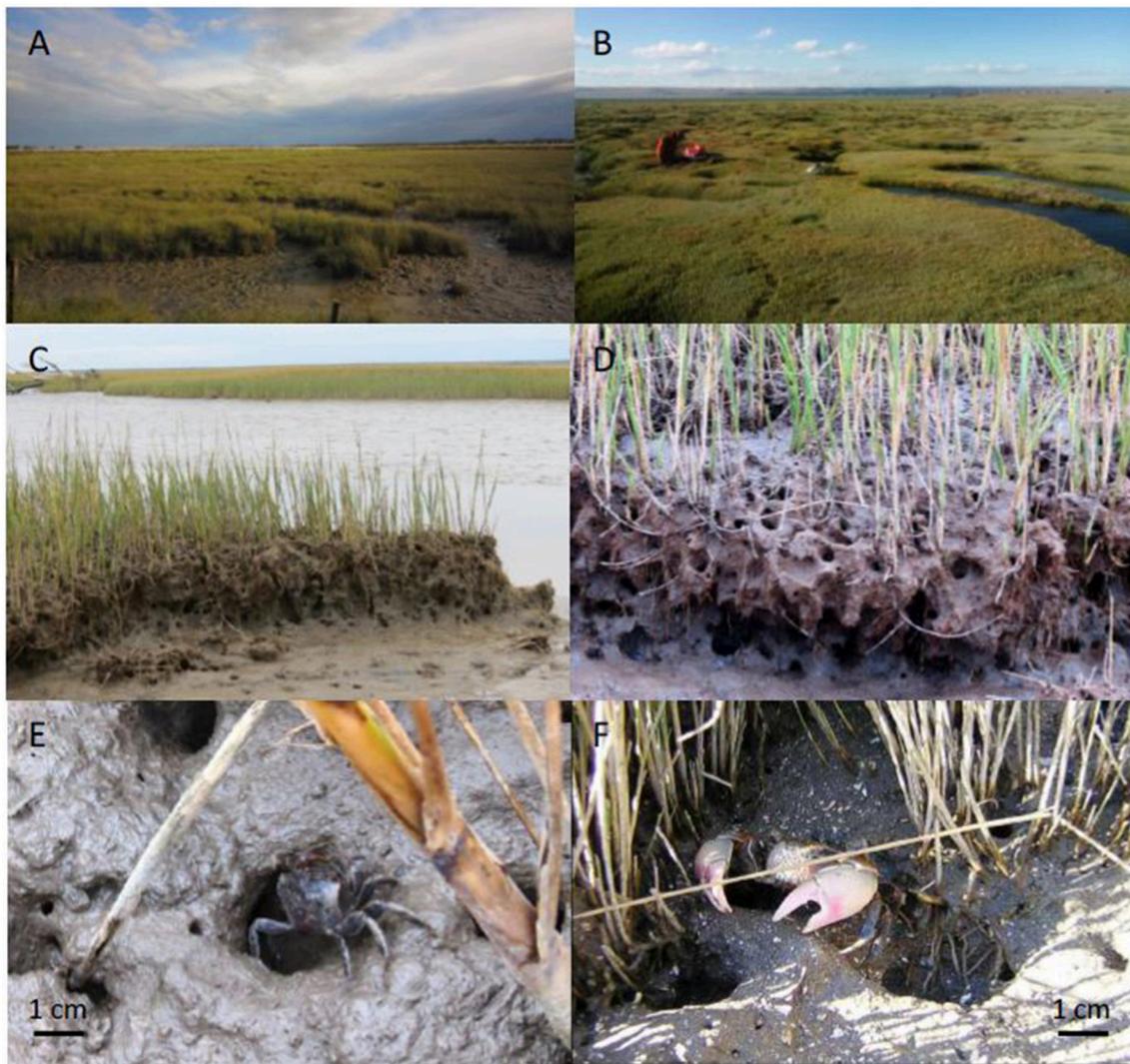


FIGURE 1 | Typical South American salt marshes dominated by *Spartina densiflora* (A), *Sarcocornia* spp. (B), and *S. alterniflora* (C). *Neohelice granulata* burrowing bed in a *S. alterniflora* salt marsh showing erosion and plant roots exposed through the burrows (D). *N. granulata* with burrow in *S. alterniflora* (E) and *S. densiflora* (F) salt marshes. Photo credits: P. Martinetto (A,C–E), J. Alberti (B), and P. Daleo (F).

herbivore (Iribarne et al., 1997) and exerts a strong top-down control on salt marsh plants (Costa et al., 2003; Alberti et al., 2007a). Many ecological processes related to C transformation occurring in these salt marshes are influenced by crab activities, either through bioturbation or via herbivory (Alberti et al., 2015). Thus, we hypothesize that *N. granulata* could have a significant role in the capacity of South West Atlantic salt marshes to bind C. Reduction of plant biomass, increment of aerobic decomposition in the sediment and facilitation of erosion are some of the multiple effects exerted by *N. granulata* that can directly and indirectly modify the C stored in these salt marshes.

In this study we compiled the available information regarding the processes affected by *N. granulata* linked to the pathways of C in South American salt marshes. Based on this information, we propose a model including the mechanisms that

regulate C transformation paths in salt marshes mediated by *N. granulata*.

The South West Atlantic Salt Marsh Environment

South West Atlantic (SWA) salt marshes span ~ 4300 km of coastline from Rio Mampituba (29° S) in Southern Brazil to Río Grande in the Southern Argentinean Patagonia (53° S, Table 1). The quite large latitudinal range of distribution (~24°) includes geomorphologic as well as climatic variations (Costa and Davy, 1992; Isacch et al., 2006). Dominant plant species are the cordgrasses *S. densiflora* and *S. alterniflora* and the glasswort *Sarcocornia* spp. (formerly named *Sarcocornia perennis*; Costa and Davy, 1992; Isacch et al., 2006; Bortolus et al., 2009). These plant species dominate ~70% of the SWA

TABLE 1 | Salt marshes in the South West Atlantic coast with dominant plant species, area and location.

	Major Macrohabitats (ha)				Total	Latitud (S)	Brackish species	Source
	<i>Spartina alterniflora</i>	<i>Spartina densiflora</i>	<i>Sarcocornia</i> spp.	Brackish species				
BRAZIL								
Rio Mampituba	–	+	–	44	44	29° 19' 35"	So Hp	(1)
Tramandaí	–	+	–	92	92	29° 58' 35"	So Jk	(1)
Lagoa do Peixe	–	228	+	166	394	31° 21' 31"	Ju	(1)
Lagoa dos Patos	110	675	+	6053	6838	31° 48'–32° 09'	Jk Sc	(1)
Rio Chuí	–	+	+	8	8	33° 44' 35"	Ju So	(1)
URUGUAY								
Arroyo Maldonado	+	550	111	1222	1883	34° 53'	Sc So Ju	(2)
Laguna José Ignacio	–	178	2	469	649	34° 53'	Sc So Ju	(2)
ARGENTINA								
Bahía Samborombon	5060	26,314	8336	42,345	82,055	35° 13'–36° 18'	Sc Ju Co	(2)
Laguna Mar Chiquita	–	3882	304	7382	11568	37° 29'–37° 46'	Ju Co	(2)
Bahía Blanca	9193	65	20376	+	29634	38° 41'–39° 30'	Ju Ph	(2)
Río Colorado	397	1344	731	4548	7020	39° 34'	Ph	(2)
Bahía Anegada	20,503	2908	42,060	2492	67,963	39° 48'–40° 42'	Ph	(2)
Río Negro	47	656	+	49	752	41° 00'	Ph	(2)
Caleta de los Loros	440	+	30	–	470	41° 01'	–	(2)
Bahía San Antonio	2068	+	2124	–	4192	40° 42'–40° 50'	–	(2)
Riacho San José	108	23	225	–	356	42° 24'	–	(2)
Caleta Valdés	89	25	329	–	443	42° 15'–42° 27'	–	(2)
Río Chubut	–	18	+	–	18	43° 20'	–	(2)
Tombo		+			+	43° 58' 40"	–	(3)
Bustamante			12		12	45° 05' 31"	–	(3)
Malaspina			+		+	45° 09' 20"	–	(3)
Puerto Deseado Complex			+		+	47° 44' 45"	–	(3)
Buque			625		625	48° 03' 31"	–	(3)
San Julian Complex			1369		1369	49° 16' 13"	–	(3)
Sta. Cruz Complex			117		117	50° 01' 26"	–	(3)
Coig Complex			+		+	51° 00' 20"	–	(3)
Loyola Complex			2400		2400	51° 37' 23"	–	(3)
Punta Dungeness			63		63	52° 23' 25"	–	(3)
Puerto Espora Complex			+		+	52° 28' 44"	–	(3)
San Sebastián Complex			+		+	53° 20' 26"	–	(3)
Río Grande			+		+	53° 48' 50"	–	(3)
Total	38,015	36,866	79,214	64,869	218,964			

Brackish species are: Sc, *Scirpus maritimus* L.; Hp, *Hibiscus pernambusensis*; So, *Scirpus olneyi*; Jk, *Juncus kraussii*; Ju, *Juncus acutus* L.; Co, *Cortadeira selloana*; Ph, *Phragmites australis*. Source: (1), Costa et al. (2007); (2), Isacch et al. (2006); (3), Bortolus et al. (2009).

salt marshes and their relative abundance is closely related to the input of freshwater in each location. *Spartina densiflora* is the dominant species in areas with higher freshwater input while *S. alterniflora* and *Sarcocornia* spp. dominate more saline sites (Isacch et al., 2006). In those salt marshes where both *Spartina* species coexist, *S. alterniflora* occupies low intertidal areas, being daily affected by tides while *S. densiflora* remains in the upper intertidal zone where the inundation only occurs during high spring tides. The loss of salt marsh area in the SWA coast is almost entirely related to degradation as

a result of anthropogenic activities. Eutrophication (Cardoni et al., 2011), land-fill (Costa et al., 2009; Marangoni and Costa, 2009; Pratolongo et al., 2013), fire to improve cattle forage as well as to prevent accidental fires (Bortolus and Iribarne, 1999; Isacch et al., 2004), and farming/ranching (Marangoni and Costa, 2010) are the primary causes of salt marsh loss and conversion.

Crab beds of *Neohelice granulata* constitute a conspicuous characteristic of SWA coastal areas from tidal flats to salt marshes. Crab density in the salt marsh is variable both within

TABLE 2 | Minimum and maximum means reported in the literature.

	<i>Spartina densiflora</i>	<i>Spartina alterniflora</i>
PRODUCTIVITY AG		
Lagoa dos Patos	2260 ¹	669–1707 ^{2,3,4}
Bahía Blanca	3674 ⁵	106–1792 ^{5,6}
Laguna Mar Chiquita	602–2599 ^{7,8}	
PRODUCTIVITY BG		
Lagoa dos Patos		1928 ¹
Bahía Blanca		526–744 ⁹
LIVE AG BIOMASS		
Lagoa dos Patos	1580 ¹	780–2079 ^{2,3,4}
Bahía Samborombón	1861 ¹⁰	367 ¹⁰
Laguna Mar Chiquita	888–1640 ^{7,8,11,12}	
Bahía Blanca	422–1153 ¹⁰	266–689 ^{6,10}
Bahía Anegada	534 ¹⁰	247 ¹⁰
Río Negro	411 ¹⁰	443 ¹⁰
Bahía de San Antonio	604 ¹⁰	364 ¹⁰
BG BIOMASS		
Lagoa dos Patos		3977 ²
Laguna Mar Chiquita	1244 ¹¹	
Bahía Blanca		850–950 ⁹
DEAD AG BIOMASS		
Lagoa dos Patos	1715 ¹	480–1188 ^{2,3,4}
Bahía Samborombón	1401–1857 ¹⁰	91–622 ¹⁰
Laguna Mar Chiquita	800–888 ^{11,12}	
Bahía Blanca	520–553 ¹⁰	25–416 ^{5,8}
Bahía Anegada	528 ¹⁰	211 ¹⁰
Río Negro	708 ¹⁰	334 ¹⁰
Bahía de San Antonio	1240 ¹⁰	478 ¹⁰
SENESCENCE		
Bahía Blanca	4179 ⁵	1481 ⁵
AG DECOMPOSITION		
Brazil	49 ¹³	73 ¹³
Bahía Blanca	27 ¹⁴	68 ¹⁴
CRAB BURROW ABUNDANCE		
Lagoa dos Patos	21 ¹⁵	15 ¹⁶ –77 ¹⁷
Mar Chiquita	56 ¹⁵	
Bahía Blanca	68 ¹⁵	70 ¹⁵
Bahía Anegada	100 ¹⁵	103 ¹⁵
Río Negro	107 ¹⁵	122 ¹⁵
Bahía de San Antonio	49 ¹⁵	
CRAB HERBIVORY		
Lagoa dos Patos	1–7 ¹⁸	2–25 ¹⁸
Bahía Samborombón	29–41 ¹⁸	51–75 ¹⁸
Laguna Mar Chiquita	17–37 ¹⁸	
Bahía Blanca	3–5 ¹⁸	8–25 ¹⁸
Bahía Anegada	17–46 ¹⁸	21–62 ¹⁸
Río Negro	21–24 ¹⁸	14–64 ¹⁸
Bahía de San Antonio	6–20 ¹⁸	29–47 ¹⁸
Caleta de los Loros		4–15 ¹⁸
Riacho San José	19–21 ¹⁸	0–1 ¹⁸
Río Chubut	0–2 ¹⁸	

(Continued)

TABLE 2 | Continued

	<i>Spartina densiflora</i>	<i>Spartina alterniflora</i>
FUNGUS INFECTION		
Bahía Samborombón	30 ¹⁹	30 ¹⁹
Laguna Mar Chiquita	28 ¹¹	
Bahía Blanca	16 ¹¹	34 ¹¹
Bahía de San Antonio	20 ¹¹	48 ¹¹

Superscript numbers indicate references sources of data: ¹Peixoto and Costa (2004), ²Cunha et al. (2005), ³Costa et al. (2004), ⁴Peixoto et al. (1997), ⁵Montemayor et al. (2015), ⁶González Trilla et al. (2009), ⁷González Trilla et al. (2010), ⁸Vera et al. (2009), ⁹Negrin et al. (2012), ¹⁰Montemayor et al. (2014), ¹¹Daleo and Iribarne (2009), ¹²Daleo et al. (2007), ¹³Hickenbick et al. (2004), ¹⁴Montemayor et al. (2011), ¹⁵Alberti unpublished results, ¹⁶Freitas et al. (2016), ¹⁷Freitas et al. (2015), ¹⁸Alberti et al. (2007a), ¹⁹Daleo et al. (2009).

Productivity: g*m⁻²*year⁻¹, biomass: g*m⁻², senescence: g*m⁻²*year⁻¹, decomposition: % of decomposed biomass in approximately 6 months, crab burrow abundance: burrows*m⁻², crab herbivory: % of leaves damaged by herbivory, fungus infection: % of leaves with damage from herbivory infected by *Phaeosphaeria spartinicola*. AG and BG indicate above and below ground respectively.

and among salt marshes ranging from 6 to more than 120 burrows per m² (Alberti et al., 2007a, Table 2). There is usually one crab and one entrance per burrow (Iribarne et al., 1997). Therefore, burrows density is a good proxy widely used to estimate crab abundance without using destructive sampling methods. *N. granulata* inhabits SWA salt marshes located above 42° 25'S, and these salt marshes correspond to ~98% of the total area covered by salt marsh in the SWA coast (Table 1). As a bioturbator, this crab can remove up to 2.4 kg of sediment per day per m² and their burrows can reach up to 1 m depth and range from 2 to 7.5 cm in entrance diameter (Iribarne et al., 1997). The impacts on ecological functions in SWA salt marshes are either via herbivory, consuming large amounts of plant biomass, or via bioturbation through the construction and maintenance of their burrows (Alberti et al., 2015).

Although there are other burrower (e.g., small invertebrates such as *Laeonereis culveri* in Argentinean salt marshes, Albano et al., 2012 and *Nephtys fluviatilis* and *Kalliapseudes schubartii* in Brazil C. Costa per. Obs.) and herbivore organisms (stem-borer moths, Canepuccia et al., 2010 and rodents in the upper marsh Pascual et al., 2015) inhabiting the SWA salt marshes, none have effects comparable to those of *N. granulata* on salt marsh ecological functioning (Alberti et al., 2015). Rodents can have a large impact via herbivory by reducing plant biomass, but these are restricted to the upper marsh (Costa et al., 2004; Pascual et al., 2015) and they inhabit fully terrestrial vegetation, thus play no role as burrowers in the salt marsh. *Cyrtograpsus angulatus* is a grapsid crab that builds burrows in salt marshes in Caleta Valdés, at the southern limit of *N. granulata* distribution (42° 15'S, Iribarne et al., 2003). However, when both species coexist in northern coastal areas, *C. angulatus* is limited to inhabit the low intertidal and it never inhabits salt marsh areas (Martinetto et al., 2007). *C. angulatus* burrows are similar in shape to those of *N. granulata*, and it has been proposed that these species play similar roles modifying sediment structure and affecting the infaunal community in soft-bottom intertidal areas (Martinetto et al.,

2011); however its effects on salt marsh sediments have never been explored.

Given the large variability in CBR estimated in salt marshes around the world and the difficulties in identifying a variable that can explain this variability (Ouyang and Lee, 2014), local conditions seem to be key, although the principal mechanisms are often unknown. In this context, crabs strongly influence almost every single step from primary production to carbon sequestration in SWA salt marshes and we believe that is a primary driver in modulating their CBR. Below we investigate the multiple ecological functions linked to C sequestration and storage in SWA salt marshes mediated by *N. granulata* through herbivory and bioturbation.

Effects Mediated by Herbivory

Neohelice granulata consumes large amounts of green *Spartina* spp. biomass (Bortolus and Iribarne, 1999), in particular at lower intertidal heights (Costa et al., 2003; Alberti et al., 2007a). Herbivory is particularly intense on *S. alterniflora* likely due to its lower position in the intertidal (up to 75% damaged leaves; Alberti et al., 2007a, **Table 2**). Reduction of aboveground biomass by herbivory on *S. densiflora* has been estimated in 20% (Alberti et al., 2010b) while the intensity of herbivory in *S. alterniflora* can double it (Alberti et al., 2007a; Daleo et al., 2009). In addition to the reduction in biomass by direct consumption, crabs can also reduce plant biomass by facilitating infection by fungi in those leaves damaged by grazing (Daleo et al., 2009; Freitas et al., 2015). This facilitative process amplifies the negative effect that crabs exert reducing plant biomass. Both, grazing and fungal infection suppress *S. alterniflora* production by more than 50% consequently decreasing the potential of C that can be accumulated in live plant biomass. Thus, herbivory could potentially modulate the amount of C stored in salt marshes dominated by *Spartina* spp. by reducing aboveground biomass.

Effects Mediated by Bioturbation

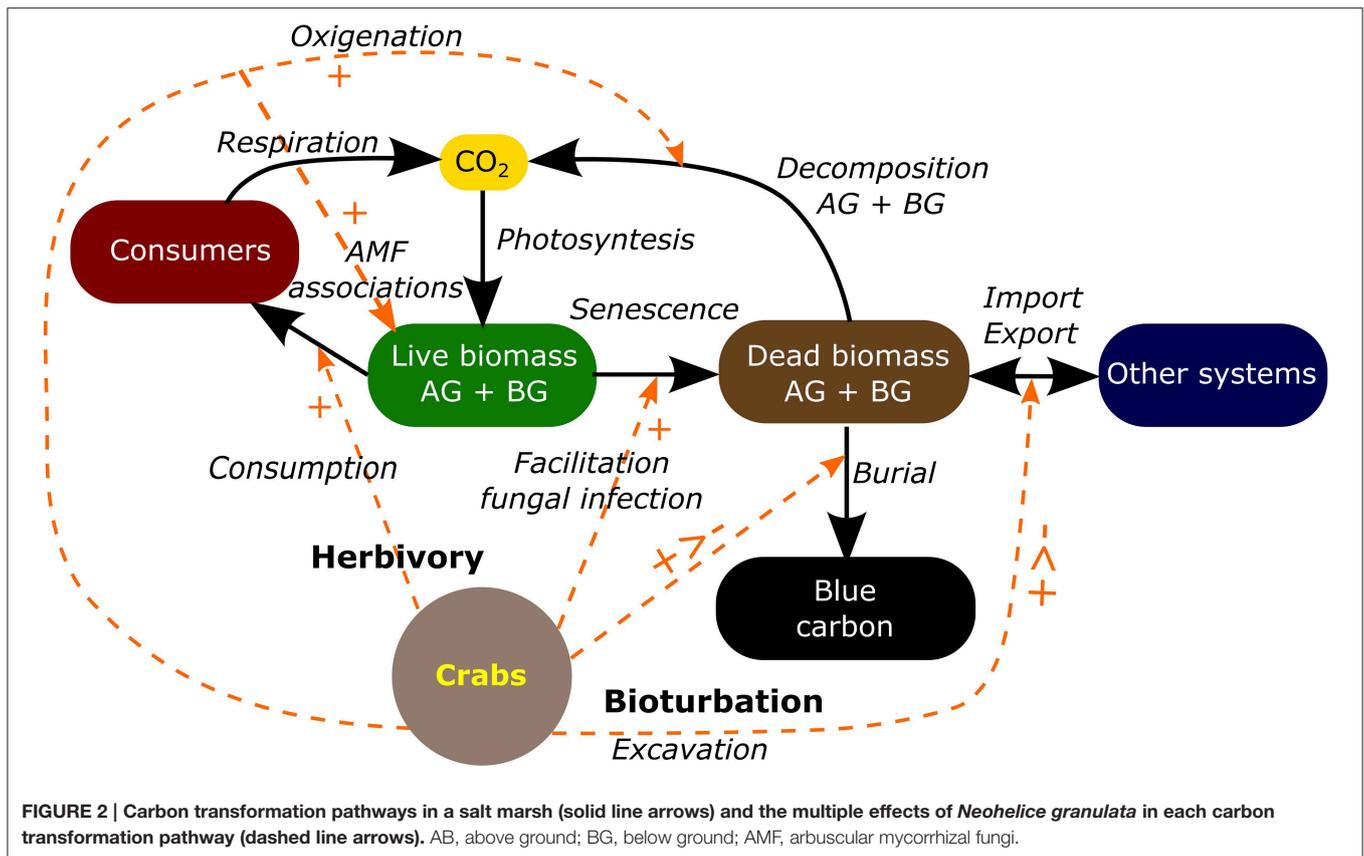
Crab burrows are mainly straight, vertical and tubular and long enough to reach the water table (up to ~1 m depth and 2.66 cm average diameter; Iribarne et al., 1997; Bortolus and Iribarne, 1999), and these are maintained permanently open (Escapa et al., 2008). The effects mediated by bioturbation comprise a complex interplay between direct and indirect effects with both positive and negative outcomes in terms of C sequestration and storage.

The presence of crabs and their burrows contributes to the increase of O₂ content within the sediments (Fanjul et al., 2008, 2011), which in turn could increase the aerobic decomposition rates of the OM present in the sediment (Hemminga et al., 1991). In fact, rates of OM degradation and nitrogen remineralization are accelerated in areas bioturbated by *N. granulata* (Fanjul et al., 2007, 2011). Given that crabs spend most of the time inside their burrows (Méndez Casariego et al., 2011), feces and plant and detritus accumulate there. As a consequence, high quantities of remineralized nutrients are accumulated and concentrated in the water within the burrows (Fanjul et al., 2008); detritus are efficiently remineralized and quickly exported to the water column as CO₂ and dissolved organic carbon (Fanjul et al., 2014).

In addition to this negative effect, increasing the sediment O₂ content also has a positive effect. Arbuscular mycorrhizal fungi (AMF) are obligate aerobes so their development is often limited in salt marshes. Even when their spores are present in the sediment, the waterlogged and consequently low oxygen conditions characteristic of salt marsh habitats limits extensive development. An increase in O₂ in the sediment due to the presence of burrows promotes AMF association with *Spartina densiflora* roots (Daleo et al., 2008). The occurrence of AMF has strong consequences in the structure of the salt marsh by increasing plant biomass (Daleo et al., 2007) as well as altering salt marsh species zonation (Daleo et al., 2008). When burrows or AMF were experimentally eliminated, the biomass of *S. densiflora* was reduced by 35% (Daleo et al., 2007). In those salt marshes where both *Spartina* species coexist, *S. alterniflora* is limited to more stressful low intertidal areas while *S. densiflora* dominates more benign high intertidal areas. However, when AMF is inhibited, *S. alterniflora* can move to higher elevation areas invading *S. densiflora* zone (Daleo et al., 2008). *S. densiflora* contributes more to the C accumulation than *S. alterniflora* due to its higher biomass per m² and primary production (Montemayor et al., 2014). Thus, a modification in the areas occupied by one or other species will have an impact in the ability of that marsh to accumulate C. These results indicate that the presence of crabs and their burrows can indirectly regulate biomass production by facilitating AMF association in *S. densiflora* salt marshes or by modulating the area inhabited by each species, which can affect a salt marsh capacity to sequester atmospheric CO₂ and to store C in live biomass.

Another indirect effect of crab bioturbation is related to the performance of *S. densiflora*. By increasing nutrient availability in bioturbated sediments, and promoting nutrient acquisition through AMF associations, *N. granulata* bioturbation enhances the performance of *S. densiflora*. Experimental manipulation of crab densities show that *Spartina densiflora* has lower fiber contents and C/N ratios and produces higher density of seeds at higher crab densities (Canepuccia et al., 2008). This indirect effect could be seen as positive; however, plants with better nutritional conditions are preferred by other herbivores than *N. granulata*. For instance, stem-borer moths (*Haimbachia* sp. nov) inhabit and consume a greater proportion of plants that grow in soils with higher burrow densities (Canepuccia et al., 2010). In terms of C stocks, the final outcome of this interplay of effects is variable and depends on the magnitude of the increase in *S. densiflora* performance, how much the herbivores reduce live biomass and how much of the litter production increased by herbivory is effectively trapped in the sediments or exported to adjacent systems.

Bioturbation also affects the retention and exportation of detritus, and again, it may have positive or negative effects on C balance. In salt marshes located in the Bahía Blanca estuary (**Table 1**) *Spartina* species produced the same amount of detritus (Montemayor et al., 2011). However, even though *S. alterniflora* is more frequently inundated, which could increase the export of detritus, it had a greater proportion of trapped detritus in the sediment than *S. densiflora*. This could be related to the larger number of crab burrows in that zone (Montemayor et al.,



2011). In fact crab burrows act as passive traps increasing detrita entrapment in the sediment (Botto et al., 2006). Moreover, the C content trapped inside the burrows as a result of tidal sediment deposition is greater than the C content in the sediment excavated by crabs and exposed in the surface resulting in a net decrease in the amount of C that can be exported from the marsh by tidal processes (Gutiérrez et al., 2006). In this context, crab bioturbation seems to reduce the export of particulate OM to estuarine and coastal waters.

The presence of vegetation in the SWA coast ameliorates harsh physical conditions in the sediment facilitating the establishment of *N. granulata* and their burrows (Bortolus et al., 2002). Particularly in SWA salt marshes dominated by *Sarcocornia* spp., these crabs and their burrows can then promote erosion (Escapa et al., 2008). The ability of *Sarcocornia* spp. to trap sediments is very low contributing very little to sedimentation (Townend et al., 2011). In addition, during the construction and maintenance of burrows, crabs remove large amounts of sediment depositing it in the surface as mounds in the burrow entrances (Iribarne et al., 1997). These mounds are easily eroded in areas subjected to high speed currents, especially at the head of tidal creeks, basins, and banks where a net loss of sediment occurs (Escapa et al., 2008). At a landscape scale, this process increases the inland growth rate of tidal creeks (Escapa et al., 2007). Furthermore, the experimental exclusion of crabs at the head of creeks and basins demonstrate a direct link between crab bioturbation and erosion by decreasing the

inland growth rate of tidal creeks (Escapa et al., 2007). In areas less affected by currents, such as mudflat plains and inside the salt marsh matrix, the sedimentary balance is positive showing a net increase in sediment deposited into burrows of 380 and 1200 g sediment per m² per day in salt marshes and mudflat plains respectively (Escapa et al., 2008). These studies demonstrate that the impact of bioturbation on *Sarcocornia* spp salt marshes is context dependent: it promotes sediment (and C) losses at the head of tidal creeks, basins and banks, while promotes sediment (and C) deposition in the marsh matrix.

Overall, bioturbation can both positively and negatively affect C sequestration and storage through direct and indirect mechanisms. This complex interplay of effects leads to large (between) and small (within salt marshes) context dependent variations in C sequestration and storage.

Carbon Stocks Gains and Losses

With all the previously summarized information we constructed a conceptual model showing C sequestration and storage pathways that involves: (1) CO₂ uptake by photosynthesis, (2) the transfer of C through the food web by herbivores and detritivores, (3) senescence of above and below ground plant biomass, (4) decomposition of dead plant biomass, (5) import and export of dead plant biomass from/to adjacent systems and, (6) burial of dead plant biomass and C accumulation in sediments. The crab *Neohelice granulata* affects all these processes through both herbivory and bioturbation (Figure 2). Summarizing, crabs eat

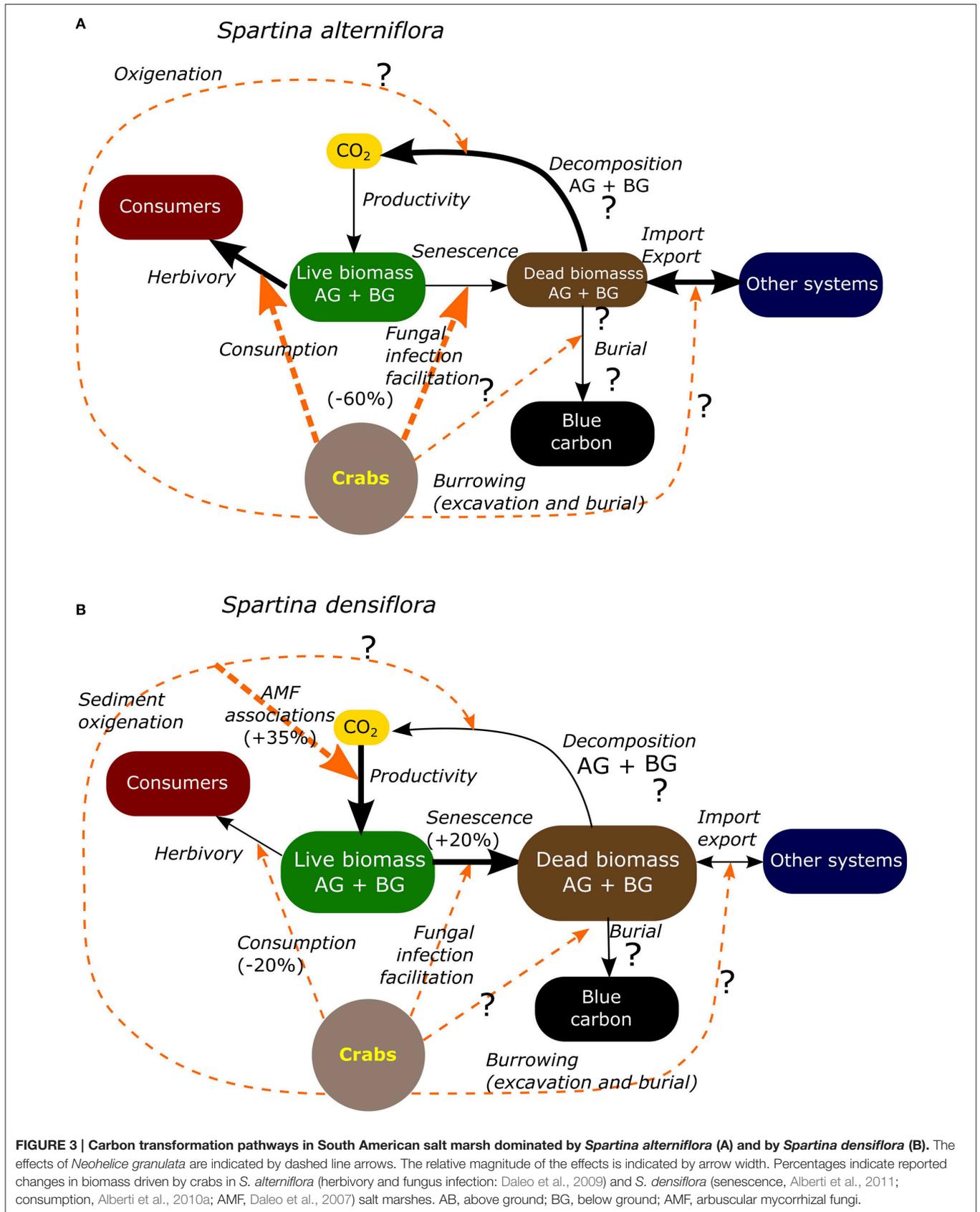


FIGURE 3 | Carbon transformation pathways in South American salt marsh dominated by *Spartina alterniflora* (A) and by *Spartina densiflora* (B). The effects of *Neohelice granulata* are indicated by dashed line arrows. The relative magnitude of the effects is indicated by arrow width. Percentages indicate reported changes in biomass driven by crabs in *S. alterniflora* (herbivory and fungus infection: Daleo et al., 2009) and *S. densiflora* (senescence, Alberti et al., 2011; consumption, Alberti et al., 2010a; AMF, Daleo et al., 2007) salt marshes. AB, above ground; BG, below ground; AMF, arbuscular mycorrhizal fungi.

Spartina leaves and their detritus and the damaged leaves suffer from more fungal infection and consequently less production and increased senescence. Crab burrows increase soil oxygenation promoting aerobic decomposition of the OM in the sediment and affecting also the architecture and the production of roots (Daleo and Iribarne, 2009). The increment of O₂ in the sediment promotes AMF association which in turn increases the productivity of the salt marsh. Plants growing in soils with a greater number of burrows have better quality and are preferred by herbivores. Burrowing activity positively affects detrital burial by increasing the trapping of detritus inside burrows as well as by covering fallen detritus with sediment. However, burrowing also negatively affects C burial by removing, mixing and disrupting the structure of the sediment, and exposing the buried C to degradation and erosion.

Most of these crab effects, however, are context dependent, with clear differences in the key pathways between the two dominant *Spartina* species. While *S. alterniflora* is more sensitive to herbivory (Figure 3A, Table 2), indirect effects related to bioturbation are more significant in *S. densiflora* salt marshes (Figure 3B, Table 2). In particular, the facilitation of AMF associations allows *S. densiflora* to increase its biomass by 35% and delineates the zonation when both species coexist. These differences may result in different C stock gains and losses; thus, the resulting scenarios for both types of salt marshes may be different.

The present review is focused on the effects of *N. granulata* on C stocks and sequestration but of course no single factor can explain the variability in salt marsh C sequestration. There are, for instance, large scale external factors that can modify crab effects (Alberti et al., 2007b). Marangoni and Costa (2012) found a similar inhibition of *S. densiflora* growth and invasion and displacement by *S. alterniflora* tillers by increasing the flooding frequency of the intertidal area, which occurs under moderate-strong El Niño (ENSO) events, as a result of excessive rainfall and subsequent high fluvial discharge in the microtidal estuaries located along the southern Brazilian and NE Argentinean coasts. This response may or may not be related to AMF sensitivity to flood-induced anaerobic conditions. Previously, other studies had pointed out important effects of ENSO events on the productivity and C accumulation of microtidal SWA marshes. Cunha et al. (2005) observed significantly higher biomass production (aerial and belowground biomass) during a strong ENSO (1992-93) than a non ENSO period (1993-1994), and they associate this result to a 2.8°C higher average air temperature during ENSO. Significantly increased night time temperatures occur during strong ENSO events in southern Brazil (Marengo, 2007), and this may explain why biomass production by the C₄ *S. alterniflora* was more affected by temperature, than solar radiation or salinity in a study by Cunha et al. (2005). On the other hand, low salinity due to excessive rainfall and high discharge of rivers in SWA estuaries during ENSO events can stimulate the spreading and herbivory pressure by rodents, such as *Myocastor coypus* (Costa et al., 2004), *Cavia aperea* (Canepuccia et al., 2010), and *Akodon azarae* (Pascual et al., 2015) into estuaries, which strongly affect the standing biomass of *Spartina* species.

CONCLUSION

South American salt marshes are highly productive systems year round (Montemayor et al., 2015) resulting in large stocks of C stored in above and below ground biomass. Herbivory by crabs has a greater incidence on *S. alterniflora* than on *S. densiflora*. Thus, top-down mediated processes will probably have a stronger impact in the C transformation path in *S. alterniflora* salt marshes. There is a gap in information related to C content in salt marsh sediments. However, several mechanisms mediated by bioturbation suggest that crabs may increase degradation as well as increase retention of detritus, especially in *S. densiflora* salt marshes where detritus production and dead biomass is high. Although, we are presenting here a hypothetical model that requires evaluation, it is based on strong scientific evidence. Overall, these results show a potential context dependency of C accumulation in salt marshes, reinforcing the need to be very careful if extrapolations from other systems are going to be used in order to accurately estimate the value of ecosystem services.

In this sense, context dependency should be seen as a scientific challenge rather than an obstacle redirecting the effort to increase the geographic scale. A recent review on the ecological functioning of South American salt marshes highlights the difficulties to establish global generalization when paradigms are built on partial information (Alberti et al., 2015). For South American salt marshes there are no CBRs reported yet; however, the extensive research on the ecological functioning of these ecosystems that has been undertaken over the last two decades (Alberti et al., 2015) provides the basis to generate hypotheses on the functioning of salt marshes in terms of C sequestration and storage. Testing these hypotheses will improve our knowledge on the factors that drive salt marsh C sequestration variability.

The notion that one single species can be responsible for the major functioning of an ecosystem has been stressed in ecological studies in the second half of the XX century. Even concepts as “key-stone species” (Paine, 1969) and “ecosystem engineers” (Jones et al., 1994) have been developed to account for the paramount role of certain species within an ecosystem. By the end of the XX century the focus changed to consider the importance of species in terms of biodiversity and its relationship with ecosystem stability maintenance (Kareiva and Levin, 2003). Thus, ecological studies have moved from detailed study of plants, animals and their interactions to more qualitative and experimental approaches (helped by methodological advances) where, in many cases, energy flows are the focus. Beside the framework in which ecologists have settled their studies, it is undeniable that in some cases a single species can control the functioning of an ecosystem (e.g., dominant plant species, bivalve beds, beavers). To maintain a historical perspective will improve our ability to reconsider the importance of older approaches in order to foresee productive new research directions.

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All authors listed, have made substantial, direct and intellectual contribution to the work, and approved it for publication.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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