

RESEARCH ARTICLE

Flood-stimulated herbivory drives range retraction of a plant ecosystem

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Abstract

1. Climate change is generating extreme climate events, affecting ecosystem integrity and function directly through increases in abiotic stress and disturbance and indirectly through changes in the strength of biotic interactions. As consumers play an essential role in ecosystem functioning and have been shown to be highly sensitive to climate conditions, improved understanding of their role under changing environmental conditions is necessary to accurately anticipate climate change impacts on ecosystem integrity.
2. We evaluated if prolonged periods of extreme rain, a climatic event increasing in severity in many places around the world, and coincident increases in coastal flooding duration intensify consumer control of foundational salt marsh grass structure and quantify the consequences of flooding–consumer interactions on salt marsh range extent. To achieve this, we analysed: historic trends in crab grazing; crab numbers and activity in and out of rainy years on the low marsh edge; vegetation retreat from the low marsh edge at a plot scale in a manipulative enclosure experiment; vegetation retreat at a landscape-scale from drone image analyses; and the vertical erosion in the lowest edge of an Argentinean salt marsh.
3. During flooded periods, crabs congregated in the low marsh, resulting in localized overgrazing of salt marsh grass and the rapid horizontal retreat of the marsh edge (98.5 cm on average). Salt marsh edge retreat resulted in a loss of ~4.5% of the total marsh area at the landscape scale. Inside crab exclusion plots, although grass cover declined slightly during the study period, the marsh edge did not retreat.
4. *Synthesis.* This study provides experimental evidence that an extreme climate event can destabilize a local consumer–prey interaction, indirectly triggering the range contraction of a critical coastal habitat. This work contributes to a growing body of research demonstrating that consumers can be unleashed, rather than suppressed, by extreme climatic events. Moreover, in cases where consumer fronts form during such events, the result can be not only local (along habitat edges) but also landscape-scale extinction of foundation species and the habitats they biogenically create. Together, this supports the general idea that models of future climate scenarios integrate the indirect effects on ecosystem-regulating food web interactions.

KEYWORDS

climate change, climate–plant–herbivore interaction, ecosystem functioning, extreme climate events, global change ecology, herbivore pressure, *Neohelice granulata*, salt marsh

1 | INTRODUCTION

Among the impacts of global change drivers on ecosystems, there is overwhelming evidence that climate change is increasing the frequency and severity of extreme climate events worldwide (Diffenbaugh et al., 2017), leading to the decline of ecosystem service provisioning (Mooney et al., 2009; Runting et al., 2017), and driving seasonal/local to persistent state shifts of entire ecosystems (Simenstad et al., 1978). While most models and theory suggest that the detrimental effects of climate change on ecosystems are direct (i.e. increased physical stress), emerging evidence and theory suggest that the major effects can be indirect, caused by altered biotic interactions (e.g., plant–herbivore interactions, O'Connor, 2009; mutualisms, Angelini et al., 2016). In the latter case, modifications of grazer and/or predator activity triggered by extreme climate events or anthropogenic disturbances are being increasingly recognized as particularly common processes that can lead to ecosystem decline across diverse ecosystems. For example, drought can provoke the runaway consumption of foundational grass in salt marshes (He et al., 2017; Silliman et al., 2005) and trigger massive locust swarms (Peng et al., 2020), eutrophication can stimulate the aggregation of crown-of-thorns sea stars and their decimation of their coral prey (Brodie et al., 2005; Fabricius et al., 2010), and warming ocean waters has been shown to trigger microbial disease outbreaks that drive massive declines of reef-defining corals (Maynard et al., 2015; Williams & Miller, 2005). Thus, deeper mechanistic understanding of the indirect consequences of climate change is urgently needed to anticipate the scale and nature of its impacts.

One powerful, emergent food web effect that has the potential to interact with extreme climate events is that which is generated by consumer fronts—that is, the concentration of large numbers of mobile consumers (grazers or predators) that locally overwhelm the carrying and/or renewal capacity of their prey resources (Silliman et al., 2013). Theoretical models and empirical examples suggest that whether consumer fronts result in ephemeral or persistent impacts on ecosystem structure and function depends on the spatial extent of the area impacted, as well as the functional role and recovery potential of the prey resource that has been consumed (Silliman et al., 2013). Recent evidence of consumer fronts across diverse ecosystems suggests that increasing physical stressors caused by different aspects of global change can amplify consumer stress, generating stronger and longer lasting effects of consumer fronts (i.e. gypsy moth: Elkinton & Liebhold, 1990; Australian plague locust: Hunter, 2004; marsh periwinkle: Silliman et al., 2005; wildebeest: Sinclair, 2003; Sinclair et al., 2007; crabs: Crotty et al., 2020). Thus, it remains essential to disentangle how consumer fronts will respond to changing baseline environmental conditions and evaluate their consequences for ecosystem structure and stability.

Salt marshes are particularly and increasingly threatened by climate change not only because of sea-level rise (Dangendorf et al., 2019; Nicholls & Cazenave, 2010) but also because changes in precipitation regimes that can modify freshwater inputs, driving either extreme droughts (Silliman et al., 2005) or longer inundations (depending on the region, see Alberti, Montemayor, et al., 2007; Karl & Trenberth, 2003). In both cases, climate change is having strong, direct effects on the physiology of salt marsh plants (Charles & Dukes, 2009). During floods, marsh plants can suffer from oxygen stress in waterlogged soils (Caudle & Maricle, 2012), while during droughts, plants suffer from osmotic and metal toxicity effects in soils (Brown et al., 2006; Derksen-Hooijberg et al., 2019; Portnoy & Valiela, 1997). In addition to these direct effects, drought can also modify salt marsh grazers' activity, potentially affecting salt marsh plants (He et al., 2017; Silliman et al., 2013). Consumer fronts and enhanced grazing activity in salt marshes have the potential to devastate foundational plants, driving vegetation die-off patches and zones (He et al., 2017) with the consequent loss of biodiversity, as well as the decline of the key ecosystem services they provide (Crotty et al., 2020). Whether prolonged flooding events modify consumer activity (as drought can do) and indirectly affect salt marsh vegetation and ecosystem service provisioning is still unknown.

Salt marshes along the Southwestern Atlantic coast (between southern Brazil, 32°S, and northern Patagonia, 42°S) are characterized by the presence of salt-tolerant grasses of the genus *Spartina* (*S. densiflora* and *S. alterniflora*) that grow year-round, forming dense monospecific stands across the entire intertidal zone (see Bortolus, 2006; Isacch et al., 2006). Within these marshes, burrowing crabs of the species *Neohelice granulata* commonly occur at high densities (often >60 crabs/m²; e.g. Iribarne et al., 1997). These crabs are herbivores and can exert strong top-down control of salt marsh plant production (Bortolus & Iribarne, 1999; Daleo et al., 2011, 2014) and expansion (Alberti, Méndez Casariego, et al., 2010). Interestingly, these crabs are more active under water and move between mudflats and salt marshes following the tidal cycle (Luppi et al., 2013), aggregating during high tides in the lowest salt marsh edges. As a consequence, in almost all salt marshes inhabited by these crabs, plants on the lower edge of these coastal wetlands are more heavily grazed than plants located in the marsh interior (Alberti, Escapa, et al., 2007). Many of these crab-grazed salt marshes are located within the Pampas region of Argentina, whose mean annual rainfall and the frequency of very rainy episodes have both increased over the last 50 years (Berbery et al., 2006). Climate projections indicate that both trends are expected to accelerate under global warming scenarios (Morales et al., 2020). As a consequence, Argentinean salt marshes associated with freshwater discharges (i.e. coastal lagoons and river mouths, Isacch et al., 2006) are suffering more frequent and longer lasting inundations (see Alberti, Montemayor, et al., 2007;

Canepuccia et al., 2007). Indeed, Alberti, Montemayor, et al. (2007) found that prolonged flooding increases crab grazing and coincident grass tiller mortality, and suggested that changes in rainfall patterns could affect the location of the lowest salt marsh edge through biotic interactions. However, no studies have resolved whether crab herbivory can actually change local plant community structure and lead to wholesale loss of grasses along the lower margins of these intertidal wetlands and coincidence collapse of the marsh edge—that is, ecosystem retreat.

During a recent extreme rainfall event in the Pampas region, we observed that the lower edge of the salt marsh began to retract. Given that increased flooding leads to more active crabs at the marsh edge (Méndez Casariego et al., 2011) and that crabs eat plants when submerged (Alberti, Montemayor, et al., 2007), we hypothesized that enhanced flooding due to high rainfall events induces crab consumer fronts, thereby enhancing consumer pressure and driving the collapse of lower intertidal salt marsh plant communities. To address this hypothesis, we evaluated (a) historic trends in crab grazing, as well as (b) crab numbers and activity in and out of rainy years in the low marsh, (c) the vegetation retreat at a plot scale from a manipulative enclosure experiment, (d) the vegetation retreat at a landscape scale from drone imagery analyses, and finally (e) the vertical erosion of the marsh edge after vegetation retreat.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was carried out in the Mar Chiquita coastal lagoon (Buenos Aires, Argentina; 37°32'S, 57°19'W), a brackish lagoon (salinity 0.5–34‰) that is an UNESCO World Biosphere Reserve. The lagoon is located in the southern limit of the floodplain Pampas region and is affected by semidiurnal microtides (<1 m; Isla, 1997). The main habitats around the lagoon are mudflats and large, irregularly flooded plains dominated by the cordgrass *Spartina densiflora* in the lower and higher intertidal respectively (Isacch et al., 2006). In particular, the entire study was carried out in a salt marsh located in a channel near the mouth of the lagoon along 250 m of coastline. In the low marsh, mean crab density is nearly 60 crabs/m² (Iribarne et al., 1997). In this region, the mean annual precipitation is 935 mm; however, during the 2016–2017 period (the first 2 years of our experiment), the mean annual precipitation was, on average, ~38% higher (i.e. 2016: 1,162.1 mm; 2017: 1,420.5 mm annually), but fell back to 921.5 mm in 2018, a level close to the long-term mean.

To evaluate whether this 2016–2017 extreme climate event could indirectly shrink vegetation zonation by enhancing crab consumer pressure, we implemented studies to address the following questions: (1) Are extreme rainfall events that cause longer lasting flooding becoming more frequent?, (2) Can these extreme events induce crab consumer front formation?, (3) What are the separate and combined effects of extreme precipitation and crabs on vegetation biomass?, (4) Can crabs cause the retreat of the lower salt

marsh edge and, hence, salt marsh range contraction? and (5) How do changes in vegetation due to precipitation–crab interactions modify vertical erosion?

2.2 | Are extreme events that cause longer lasting flooding becoming more frequent?

In this region, heavy rains in short time periods cause coastal wetlands to flood (Berbery et al., 2006). Mar Chiquita coastal lagoon, in particular, has an irregular flooding regime that depends more on winds and rain than on tides (Isacch et al., 2006; Reta et al., 2001). Previous works from our group have shown that extreme rainfall events can lead to persistent salt marsh flooding and that up to 10%–20% of the total salt marsh area can remain in a flooded stage for weeks at a time during months that experienced double the average rainfall (Alberti, Montemayor, et al., 2007; Canepuccia et al., 2007). Moreover, there is also evidence showing that salt marsh flooding is associated with increased crab activity and herbivory pressure (Alberti, Montemayor, et al., 2007; Méndez Casariego et al., 2011). To evaluate historical and contemporary patterns of extreme rainfall events (and their potential association with crab grazing), we obtained daily precipitation values from the Argentinean National Weather Service (Servicio Meteorológico Nacional Argentino) for the Mar del Plata station (37°56'S; 57°35'W), located 25 km south of our study site. We analysed monthly total extreme precipitation (mm) for a 16-year period (between November 2002 and December 2018), for which we have crab herbivory data (see next section). For this analysis, we only summed the days with more than 50 mm of rain (extreme precipitation) in the monthly extreme precipitation totals.

2.3 | Can these extreme rainfall events induce crab consumer front formation?

Crab feeding activity was estimated during two consecutive years, one with typical rainfall events (2013: 815 mm annually) and another after a very rainy event (2014: 1,255.2 mm annually). The observation area comprised five 5 m² (0.5 m × 10 m) plots in the salt marsh edge and five plots of the same size in the mudflat perpendicular to the shore that were staked on the corners. Observations of surface crab activity were carried out with binoculars (Bushnell 10 × 50 at a 10 m distance) every 40 min along the tidal cycle (from low tide to high tide). This methodology was repeated for 5 consecutive days in early September each year. Total sampling effort (time spent on surveys) was the same for each plot and day. During these surveys, we recorded the total number of crab individuals feeding on the surface per hour in each habitat.

We supplemented the crab grazing observation surveys with surveys of crab herbivory by summarizing the percentage of live *Spartina densiflora* leaves with signs of herbivory (i.e. lacking their tips and/or with missing tissue along leaf edges; see Alberti, Cebrian, et al., 2011) per tiller during 2002–2005, 2012, 2017 and 2018 from

historical datasets collected by members of our research group and others at this study site. Given that tillers of this plant species turn over at least once per year and that leaves are shed several times per year, this assay of grazing intensity summarizes the plant's cumulative exposure to grazing over short to moderate time periods (a week to a few months; González Trilla et al., 2010; Vera et al., 2009). Since leaf production and crab herbivory are seasonally variable (Alberti, Cebrian, et al., 2011; J. Alberti unpubl. Data), we compared 3 years for which we had herbivory data for the same period (August–September) and that annual precipitation was remarkably different (2003: 1,077.7 mm, 15% above the mean; 2004: 739.7 mm, 21% below the mean; 2017: 1,420.5 mm, 52% above the mean). We used these data to evaluate if there were differences in crab herbivory in the lowest edge of the salt marsh between years with contrasting annual rainfall.

2.4 | What is the separate and combined effect of extreme precipitation and crabs on vegetation biomass?

In May 2016, we initiated a crab exclusion experiment that lasted 2 years (until June 2018). Twenty 0.25 m² areas, standardized for plant cover, composition and density, located in the lowest edge of the salt marsh and randomly assigned each to one of the following two treatments: (a) control, which were unmanipulated areas delimited with wooden stakes in two opposite corners and (b) crab exclusion, that consisted in enclosure plots delimited with plastic mesh fences (50 cm × 50 cm × 40 cm, 1 cm² opening; *N* = 10 replicates per treatment). Similar exclusions have been widely used in this system, demonstrating that crab density diminishes inside the cages, and the use of cage controls has consistently shown that there are no artefacts associated with cage use (Alberti, Méndez Casariego, et al., 2010; Daleo et al., 2007, 2009). In June 2018, we harvested all the aerial plant biomass, separated it into live and dead material, oven-dried and weighed it.

2.5 | Can crabs cause the retreat of the lowest salt marsh edge and, hence, marsh range contraction?

Given that the impact of crab herbivory was unexpectedly high (see Section 3), we also estimated if it was intense enough to cause a retreat of the marsh edge at a plot scale. Thus, we measured the distance of the straight line perpendicular to the shore that connected the location of the salt marsh edge at the beginning of the experiment and at the end, for each enclosure plot given that remained as islands of live plants in a matrix of short dead tillers (along 57 m of the marsh; see Figure S1). The salt marsh edge can easily be defined by an abrupt change in vegetation cover (from >40% to 0%). Positive values indicate salt marsh plant expansion into the mudflat, while negative values would denote a retreat of the salt marsh edge.

Given that the edge showed a clear retraction (see Section 3), and that the line where the vegetation was at the beginning of the experiment was easily identified due to the exposed rhizomes or short dead tillers, we used an RTK drone flying at 35 m height to obtain high-resolution images of the salt marsh edge (1.5 cm/pixel, see Figure S2) in May 2019. With the resulting orthomosaic (i.e. combination of high-resolution images into a single one spanning a much longer spatial extent), we measured marsh edge retraction and estimated relative elevation where the vegetation was at the beginning and where it was after the extreme rainfall event on 50 points along 250 m of the marsh edge (i.e. at a 'landscape-scale'). To evaluate if salt marsh retreat was related to edge elevation (e.g. if lower elevation areas are inundated more and, hence, more exposed to crab herbivory), we analysed whether edge movement was related to the initial relative intertidal elevation of the vegetation edge (i.e. before the extreme rainfall event). We obtained the relative difference in intertidal elevation before and after the extreme rainfall event from the drone images.

2.6 | How do changes in vegetation due to precipitation–crab interactions modify vertical erosion?

As die-off driven by flooding and crab herbivory involved the loss of above-ground biomass but left easily identifiable dead below-ground structures, one year after the end of the experiment (June 2019), we estimated the vertical erosion in different points of our experimental area. We quantified the vertical distance between sediment surface and rhizomes in zones formerly covered by *S. densiflora* using a ruler. We sampled two different conditions: Areas where vegetation was lost, and areas where vegetation remained as isolated patches (see Figure 1 for zones without vegetation). We repeated this measurement in a more erosive zone, adjacent to our experimental area, where we expected higher vertical erosion after vegetation loss (see Figure S4). Positive values (i.e. rhizomes exposed above the sediment surface) indicate vertical erosion, while negative values denote that the rhizomes were still covered by surficial sediments and thus below-ground. Although there are more accurate methods to measure vertical erosion, this method is suitable for evaluating vertical changes in the soil surface elevation (and thus, vertical erosion) for the purpose of this study given that the study area was covered by vegetation and all rhizomes were below the sediment surface prior to the start of the flooded period that was the focus of this work.

2.7 | Statistical analyses

To evaluate the effect of an atypically rainy event in crab activity, we first performed a *t* test for unequal variances comparing total feeding activity (mudflat + salt marsh) during a typical (2013) and a rainy year (2014). In addition, to see if the feeding activity was similar

FIGURE 1 (a) Study site just before crab enclosure experiment finished (June 2018). (b) Retreat of the lowest salt marsh edge. (c) Effect of crab enclosure (0.5 m \times 0.5 m, compare vegetation in enclosure and control plots—delimited by two wooden stakes). (d) Photograph of *Neohelice granulata*



between mudflat and salt marsh, we used a t test for equal variances (2013), and a t test against zero (2014; since there was no activity at all in the mudflat). All of these analyses allowed us to determine whether there were changes in total activity and/or changes in where crab feeding was concentrated. To evaluate if there was a relationship between extreme annual rainfall and crab herbivory (as the proportion of non-eaten leaves), we performed a zero-inflated linear model with year as a fixed factor, using `GLMMTMB` package (Magnusson et al., 2017) for R. This model type was selected due to the large number of zeros in our crab herbivory surveys. The significance of each fixed term was evaluated using the likelihood ratio test (consistent with the AIC criterion; Zuur et al., 2009). For multiple comparisons, we used the function `glht` from the `MULTCOMP` package (Hothorn et al., 2008). To test the significance and effect size of crab exclusion on plant above-ground biomass, we performed a t test for unequal variances for biomass data collected at the end of the experiment. To evaluate if the salt marsh edge retreated, we performed a t test against zero (if edge did not retreat, edge movement will be equal to zero) for plot scale and landscape scale. To evaluate if there was a relationship between relative initial intertidal elevation and the salt marsh edge retreat, we performed a linear regression. To evaluate if the vegetation had an effect on vertical erosion at plot scale (estimated as the position of the rhizomes—assuming that less buried or more exposed rhizomes denoted more erosion), we performed a t test between areas with and without *S. densiflora* cover. We transformed data using \log_{10} for *S. densiflora*

biomass, and squared values for initial intertidal elevation to meet the assumptions of normality or homoscedasticity to perform this analysis. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality after transformations. All analyses were performed using R (R Core Team, 2016).

3 | RESULTS

During the 16-year period in which we evaluated intense precipitation events, four of the five rainiest months occurred during the last 4 years, with the most extreme occurring during April 2017 (170 mm in 48 hr, ~30% higher than the second highest event). This 2017 event produced several months of flooding and overlapped with particularly high herbivory levels (i.e. 81.1% of partially consumed *S. densiflora* leaves, while during 2004, there were no extreme rainy events and ~37.7% of *S. densiflora* leaves were consumed; Figure 2a). Moreover, another atypically high rainy event occurred during March 2014 (i.e. 124 mm in 48 hr). Following this extreme event, crabs exclusively fed in the salt marsh ($t = 10.7$, $df = 4$, $p < 0.001$, Figure 2b), as opposed to the preceding year (with average precipitations) when the number of crabs feeding in the salt marsh was 35.2% lower than in the mudflat ($t = 3.68$, $df = 8$, $p = 0.006$). The total number of crabs feeding was similar between years ($t = 0.68$, $df = 9.7$, $p = 0.5$), indicating that flooding shifted where a similar number of crabs were feeding in the landscape.

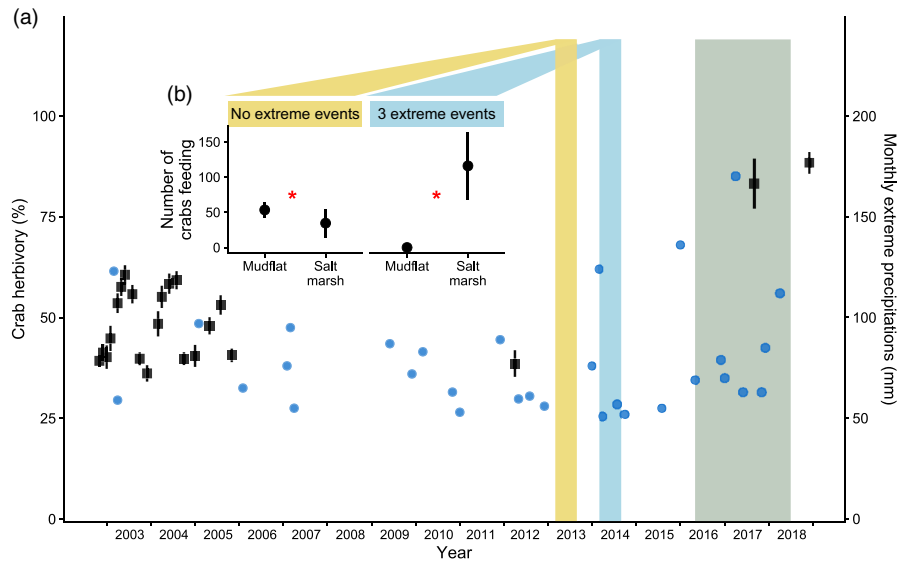


FIGURE 2 (a) Crab herbivory and precipitation. Dark grey squares represent mean crab herbivory, and vertical bars denote the standard error (%; left y-axis), while sky blue circles represent the amount of precipitation occurred during extreme (more than 50 mm of rain in 24 hr) precipitation events in a given month, which usually lead to flooding (mm, right y-axis). Months without extreme precipitation events, thus, accumulate 0 mm in extreme events, even if experienced precipitation during non-extreme events (i.e. <50 mm of rain in 24 hr) and are not shown. Yellow shaded area encompasses a 6-month period previous to the 2013 crab activity survey (March–August 2013; no events with more than 50 mm of rain in one day) and blue shaded area encompasses a 6-month period previous to the 2014 crab activity survey (March–August 2014; 3 months with more than 50 mm of rain in 1 day). Grey shaded area highlights the experimental period. (b) Crab feeding activity (number of crabs feeding in each 5 m² plot per 40 min) during September 2013 (no extreme rainfall events) and September 2014 (after three extreme events between March and August) in the mudflat and the salt marsh. Black dots represent the data mean, and vertical bars denote the standard error. Red asterisks denote significant differences between mudflat and salt marsh for a given year

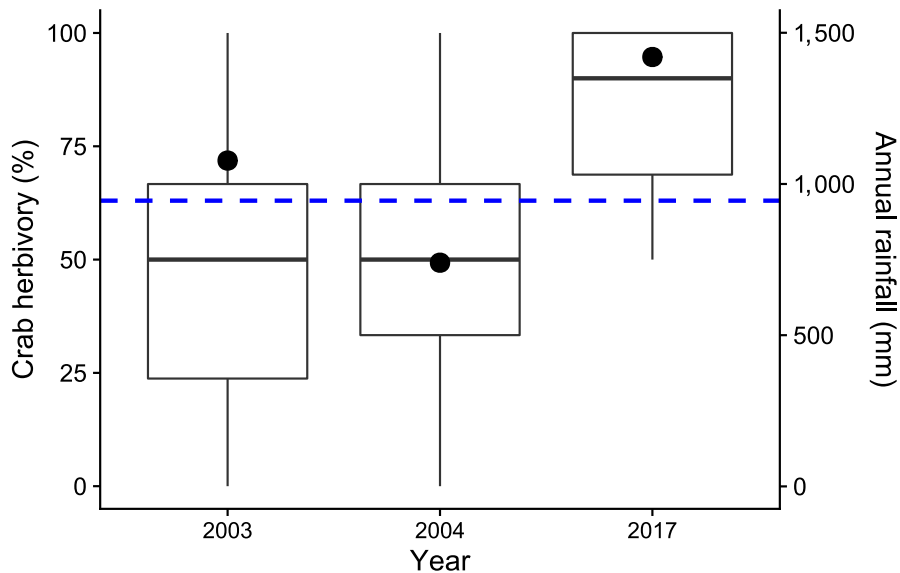


FIGURE 3 Precipitations and crab herbivory for 2003 (a year with precipitations slightly above mean annual rainfall), 2004 (a year with precipitations below mean annual rainfall) and 2017 (a year with precipitations ~50% above mean annual rainfall). Circles represent annual rainfall (mm, right y-axis), while boxes represent crab herbivory estimated as percentage of live *Spartina densiflora* leaves with signs of herbivory (%; left y-axis). Dashed line denotes mean annual precipitation (945 mm). Note that for statistical analysis, healthy leaves (%; i.e. 100 – crab herbivory) was used as the response variable. Here and in the following figure, horizontal bars denote median values, boxes include 50% of the data and vertical bars encompass the lowest and the highest values

Complementary to these findings, we found that crab herbivory in the rainiest year (~50% above the mean, i.e. 2017) was 77% higher than that reported during more commonly drier conditions (i.e. 2003 and 2004; $\chi^2 = 16.691$, $df = 2$, $p < 0.001$, Figure 3). As a consequence of increased crab herbivory pressure, plant biomass (and vegetation cover as well, Figure 4a; and see Figure S3) fell in control plots exposed to these herbivores, with control plots supporting 62.1% less

aerial biomass than crab exclusion plots at the end of the experiment ($t = 4.17$, $df = 12.48$, $p = 0.001$).

Enhanced crab herbivory translated into a significant retreat of the marsh edge at the end of the experiment at the plot scale ($98.5 \text{ cm} \pm 62.73 \text{ cm SD}$; $t = 4.96$, $df = 9$, $p < 0.001$; Figure 4b,c). Vegetation retreat was extensive enough that exclusion plots became isolated patches with live plants surrounded by mudflats (see

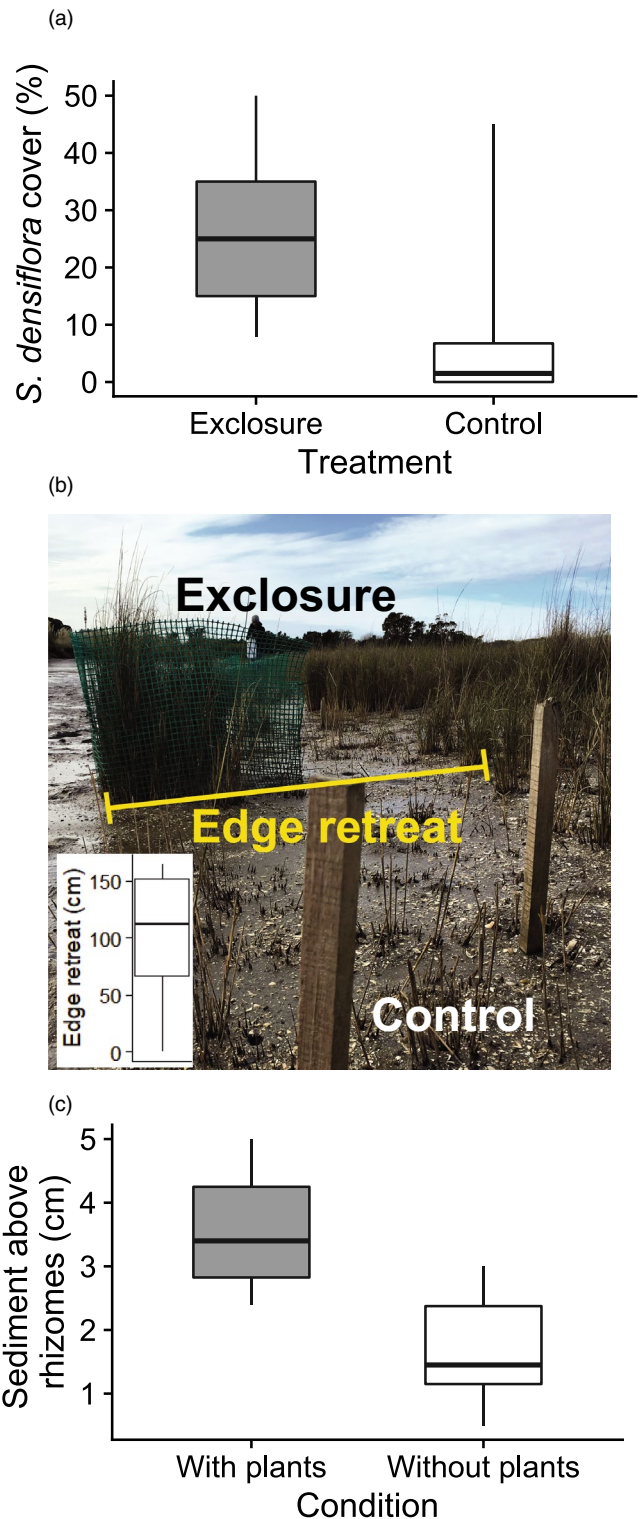


FIGURE 4 (a) *Spartina densiflora* cover (%) in exclusion and in control plots, at the end of the experiment (December 2018). Data are presented prior to transformations. (b) Edge retreat at the end of the experiment. It was estimated as the connecting line between the low edge of the vegetation within exclusions and the new line of vegetation at the end of the experiment (photograph). Given that edge retreat exceeded exclusion dimensions (box-plot), we quantified the retreat only in exclusions (that remained as islands of live plants in a matrix of short dead tillers). (c) Distance between the surface and the rhizomes (cm) for two conditions: with plants (i.e. similar to exclusions) and without plants (i.e. similar to control plots)

Figure 1). At the landscape scale, using drone images, we further discovered that the edge retraction represents a 4.5% of the salt marsh extent (0.89 m of roughly 20 m of salt marsh width; see Figure S2a). Nevertheless, this retreat was not homogeneous along the shoreline, with vegetation retreat being considerably higher at relatively lower than higher intertidal elevations ($F = 6.2$, $df = 1, 46$, $p = 0.01$; see Figure S2b). The loss of above-ground vegetation, in turn, led to enhanced vertical erosion; in die-off zones devoid of live plants, rhizomes were 1.66 cm (± 0.84 cm *SD*) below the surface, while in zones still maintaining live plants, rhizomes were 3.56 cm (± 0.9 cm *SD*) below-ground ($t = 4.42$, $df = 18$, $p < 0.001$; Figure 4d). In fact, in the more erosive zone adjacent to our study area, rhizomes were 2.9 cm exposed above-ground (± 0.68 cm; see Figure S4).

4 | DISCUSSION

Our field survey results showed that, after prolonged flooding events caused by unusually high periods of rainfall, crabs congregate in the low marsh to feed, in effect forming a temporary consumer front. Field experiments revealed that increased consumption by crabs in this consumer front locally eliminates plants and then propagates landward to cause low marsh edge retreat. Importantly, drone images showed that this impact was not limited to our experimental plots but occurred at a larger, landscape spatial scale. Finally, this retreat of the lower salt marsh edge led to a vertical soil erosion, and decreased potential for recovery. Combined, these results show that extreme climate events trigger enhanced crab herbivory in the lowest edge of the marsh, driving foundational plant and marsh surface elevation loss and ecosystem edge retreat. This study reveals for the first time that extreme rainfall events can redefine salt marsh edge by inducing ephemeral, but intense, consumer fronts, pinpointing the alteration of biotic interactions as the main mechanism behind the effect of extreme climate events on salt marsh erosion.

It is now well known that salt marshes are regulated by both abiotic and biotic factors (Bakker et al., 2015; Gough & Grace, 1998). However, for years it was considered that principally abiotic factors modulated salt marsh structure and function (Kiehl et al., 1997). In the last decades, small vertebrate and invertebrate herbivores have been increasingly recognized as fundamental and determining factors in the functioning of salt marshes and other coastal wetlands (Crain, 2008; Silliman & Bortolus, 2003). In fact, we now know that herbivores can strongly control salt marsh primary production (Angelini et al., 2018; Kuijper & Bakker, 2005), change plant species composition (Alberti, Canepuccia, et al., 2011; Carson & Root, 2000) and regulate succession dynamics (Bromberg Gedan et al., 2009; Daleo et al., 2014). Moreover, as both abiotic and biotic factors act simultaneously (Suzuki et al., 2014), environmental conditions can act as modulators of herbivore impacts on salt marshes (see Silliman et al., 2005).

Although crab herbivory in Argentinean salt marshes was already recognized as a primary determinant of plant standing

biomass (~23.7% less biomass) and tiller mortality (Alberti, Cebrian, et al., 2011; Alberti, Escapa, et al., 2007), similar crab enclosure experiments performed in the past, during less rainy periods, did not show massive changes in vegetation biomass (contrasting starkly with the present study with ~100% less biomass), and no effects in the movement of the marsh edge were previously observed (Alberti, Méndez Casariego, et al., 2010; see Figure S5). Nevertheless, and in accordance with previous findings showing that flooding can increase crab herbivory pressure (Alberti, Montemayor, et al., 2007; Méndez Casariego et al., 2011), our experiment that overlapped with a highly rainy period revealed that inundations following extreme events result in a concentration of crabs feeding at the salt marsh edge, promoting low-marsh vegetation collapse and redefining the low salt marsh zonation and geomorphic structure of marshlands in our study system. Our results show that, during an extremely rainy period, crab herbivory was intense enough to not only to decrease plant standing biomass but also to cause a retreat of salt marsh edge, redefining the geospatial structure and spatial extent of the salt marsh at a landscape scale.

In salt marshes worldwide, it has been demonstrated that consumers can regulate the resilience of the ecosystem. Die-off vegetation zones induced by drought-consumer interactions in Chinese (He et al., 2017) and US salt marshes (Angelini et al., 2018; Silliman et al., 2005) have persisted with no signs of recovery for many years, even decades, due to grazing after the consumer front vanishes; while after extreme rainy events, crabs can suppress the recovery of degraded Chinese salt marshes (He et al., 2019). Particularly, in Argentinean salt marshes, it has been demonstrated that even under normal climate conditions, crab herbivory is strong enough to delay for years or even prevent the recovery of disturbed patches (Alberti, Escapa, et al., 2010; Alberti, Méndez Casariego, et al., 2010; Daleo et al., 2011; Kaminsky et al., 2015). Indeed, given the usually strong grazing pressure, neither sexual nor asexual reproduction seems to be sufficient to enable vegetation to establish into bare areas (including vegetation expansion towards the mudflat). In a broader context, all of this evidence suggests that even after the consumer front vanishes, its impacts have the potential to remain for much longer periods, potentially leading to an alternate stable state (Silliman et al., 2012).

Recent studies have revealed different ways in which climate change factors can affect salt marshes through altered biotic interactions. Sea-level rise can amplify the function of salt marsh Sesamid crabs, transforming these once-inconspicuous grazers into a keystone species (Crotty et al., 2020). Specifically, in southeastern US salt marshes, crab-grazed creek heads, through the removal of vegetation, enhance the vulnerability of macrobenthic invertebrates to predation and strongly reduce secondary production across adjacent marsh platforms (Crotty et al., 2020). Moreover, extreme droughts can enhance vegetation control by snails (Silliman et al., 2005) and crabs (He et al., 2017), while extreme rainfall can aggregate gypsy moth individuals into a consumer front (Elkinton & Liebhold, 1990). These consumer fronts have been shown to provoke the formation of vegetation die-off patches in other salt marsh ecosystems,

but they have not shown ecosystem range retractions as revealed in this study. Combined, this evidence reveals that climate change can induce significant and persistent losses of salt marsh vegetation through enhanced grazer activity.

This environmentally enhanced herbivory pressure may not be limited to salt marshes but may be widespread, as both theoretical (e.g. O'Connor, 2009) and empirical evidence show that environmental conditions affected by global change can influence herbivory in several systems (Bale et al., 2002; e.g. temperature and rainfall in terrestrial systems Holmgren et al., 2001; Lima et al., 2002; temperature and eutrophication in marine systems, Martinetto et al., 2010; O'Connor, 2009; Vergés et al., 2014; Wernberg et al., 2011). There are a wide variety of known mechanisms behind the increase in herbivore pressure due to changes in environmental conditions, including the generation of suitable conditions for consumer population growth via improvements in vegetation quality (Cornelissen, 2011; Rosenblatt & Schmitz, 2016), reduced plant tolerances to grazing due to increased physical stressors for plants (Silliman et al., 2005), changes in the behaviour and/or physiology of herbivores, such as the increase of metabolic rates (Chalifour et al., 2019; Rosenblatt & Schmitz, 2016) or changes in diet preference (Gutbrodt et al., 2011). Moreover, climate change alters not only species distribution (i.e. zonation patterns, see Harley et al., 2006; Thomas et al., 2006; and with it, the strength and sign of interspecific interactions, see Leonard, 2000) but also the time that they interact (i.e. community dynamics; Hawkins et al., 2009). For example, in marine systems, warming can increase the overlap between the foraging range of the dominant predator and the habitable zone of its prey, ultimately affecting zonation patterns (Harley, 2011). In terrestrial systems, a recent study revealed that warming can also affect the encounter between predators (spiders) and preys (grasshoppers) with noticeable consequences even for plants (Barton & Schmitz, 2018). Analogously, we show that extreme rain can temporarily increase encounters between crabs and plants. Whatever the causes are behind the altered consumer impacts under varying environmental conditions, it is clear that we expect analogous plant–consumer interaction shifts to occur worldwide (i.e. altered consumer impacts following climate changes).

As vegetation biomass is strongly associated with salt marsh sediment stabilization, and thus with prevention of shoreline erosion (Möller et al., 2014; Shepard et al., 2011; Silliman et al., 2016), vegetation loss can accelerate sediment loss, reducing the potential for system recovery, with the consequent decline of many ecosystem services, such as carbon sequestration (Coverdale et al., 2014), pollutant filtration and coastal protection (Silliman et al., 2019). However, although we documented the vegetation loss due to crab herbivory, we cannot confidently conclude that this is the ultimate mechanism behind the loss of sediment, as there can be other mechanisms involved. For example, previous studies showed that invertebrates can also promote marsh erosion via accelerated creek expansion (due to the softened sediment associated with invertebrates bioturbation) in marsh channels (Escapa

et al., 2007; Talley et al., 2001; Vu et al., 2016). Moreover, in our study site, floods enhance crab activity and their burrow maintenance activities (Méndez Casariego et al., 2011), which may amplify sediment removal by tides (Gutiérrez et al., 2006). Furthermore, wave action due to dominant winds can be another important cause of sediment erosion. In Patos Lagoon (southern Brazil), it has been demonstrated that when estuarine water level increases due to heavy rains, the erosive action of waves generated by wind can be maximum (Marangoni & Costa, 2009; Ortega et al., 2021). Nevertheless, in Mar Chiquita coastal lagoon, some physical features, such as water energy, erosive power and tidal amplitude, are higher in the mouth and decrease towards the inner lagoon (Isla, 1997; Marcovecchio et al., 2019). Particularly, our study site (a channel that flows into the lagoon) is a low energy body of water (Marcovecchio et al., 2019; Reta et al., 2001) compared to other open water system. Thus, we believe that our results suggest that at least great part of observed erosion can be attributed to the interaction between enhanced erosive power, due to increased water levels during flooding events and crab-induced vegetation loss. However, further studies would be needed to determine the relative importance of these non-exclusive mechanisms of salt marsh erosion triggered by crabs and climate change. Nonetheless, we think that the loss of vegetation due to crab herbivory is the most likely mechanism, as crabs and their burrows were highly abundant in the low marsh, while sediment loss was maximum where vegetation was lost (and where crab grazing was higher). The observed magnitude of marsh retraction can look anecdotal, but if we put together our results, that is, mean shoreline retraction was 89.7 cm (range 0–289 cm), mean vertical loss of sediment was 1.92 cm (range 0–4 cm), with the available estimates of soil density (mean: 0.95 g/cm³, range: 0.68–1.18 g/cm³; P. Martinetto et al., unpubl. data) and %C (mean: 0.52%, range: 0%–1.046%; P. Martinetto et al., unpubl. data) for the 5-cm top sediment of this salt marsh, it is suggested that 85.3 kg C per km of shoreline was lost due to the interaction between crab herbivory and this likely climate change-associated high rainfall event. Therefore, extreme changes in weather conditions can affect the stability and recovery of salt marshes as well as their delivery of ecosystem services.

Given that most climate change model predictions are based on physiological characteristics, and do not take into account biotic interactions (He et al., 2017; Pearson & Dawson, 2003), our results suggest that ecosystem resilience can be overestimated. Indeed, our results uniquely show a cascade of biotic and abiotic events triggered by extreme climate events that affected the delivery of an ecosystem service (i.e. C accumulation, Figure 5). Analogously, consumer fronts triggered by extreme climate events can have the potential to affect the functioning of many different systems from terrestrial to marine, and from wetlands to arid systems (Silliman & He, 2018; Silliman et al., 2013). The intensification of these conditions may magnify/promote more frequent, destructive and longer lasting consumer fronts (Silliman et al., 2013), accelerating the next steps of the cascade. Taking together this study and the broader literature on these topics, it seems nearly certain that increases in

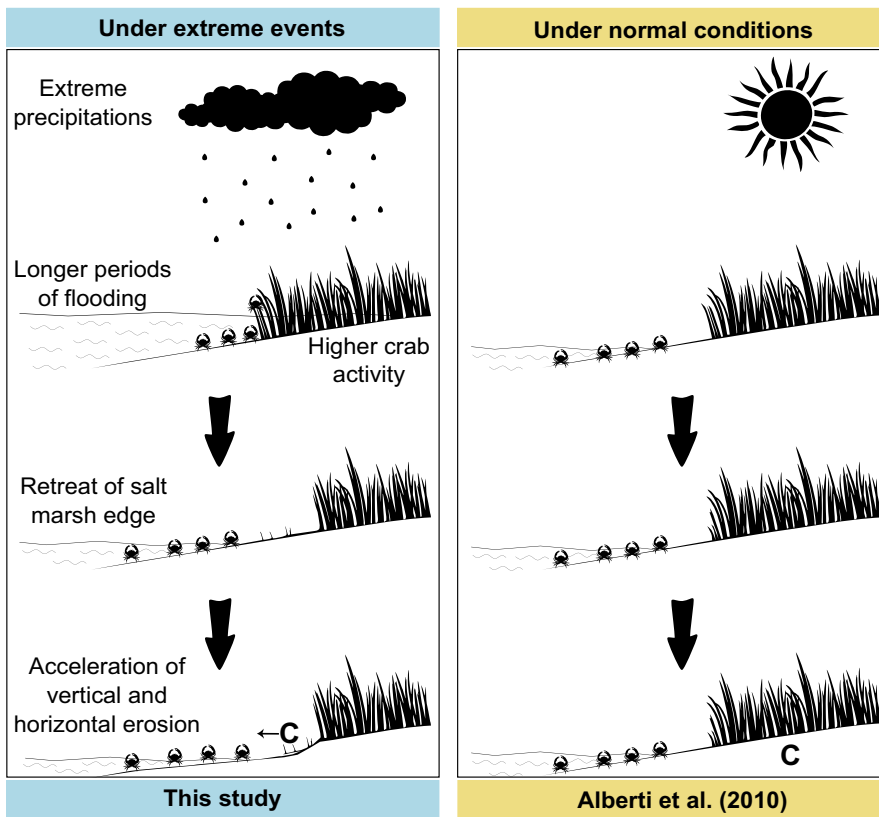


FIGURE 5 Conceptual model of the cascade triggered by extreme climate events in salt marshes. Extremely atypical rainfall promotes longer flooding periods in salt marshes. This concentrates crab feeding activity in the low salt marsh edge, and propagates upwards, leading to die-off vegetation zones and the retreat of the lower edge of salt marsh vegetation. Vegetation loss potentially accelerates shoreline vertical erosion, ultimately affecting the delivery of ecosystem services (i.e. shoreline protection and C accumulation). Under normal conditions, herbivores do not generate salt marsh vegetation die-off; hence, the lower salt marsh edge remains unchanged

extreme weather conditions will affect the delivery of ecosystem services through biotic drivers. Our results suggest that if climatic events act additively or synergistically with biotic stressors, then the resistance point of plants to the climatic stressors predicted by physiological models that do not take into account biotic interactions is going to overestimate ecosystem resilience. In this context, it is highly relevant to not only include the direct effects of climate change on ecosystems but instead to also include indirect biotic drivers triggered by climate change for models of future scenarios.

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CONFLICT OF INTEREST

Brian Silliman and Christine Angelini are Associate Editors of Journal of Ecology, but took no part in the peer review and decision-making processes for this paper. All other authors declare no conflict of interest.

AUTHORS' CONTRIBUTION

C.R., P.D., J.A. and O.I. conceived the idea and designed methodology; C.R., P.D., J.A. and J.N. collected the data; C.R., P.D. and J.A.

analysed the data; O.I., B.R.S. and C.A. revised critically for important intellectual content. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13735>.

DATA AVAILABILITY STATEMENT

All data used for the presented results are provided as CSV files and can be downloaded from Dryad Digital Repository <https://doi.org/10.5061/dryad.8sf7m0cnm> (Rocca et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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