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Crab Burrowing Limits Surface Litter Accumulation in a Temperate Salt Marsh: Implications for Ecosystem Functioning and Connectivity

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ABSTRACT

Burial of aboveground plant litter by animals reduces the amount available for surface transport and places it into a different environment, affecting decomposition rates and fluxes of organic matter to adjacent ecosystems. Here we show that in a Southwestern Atlantic salt marsh the burrowing crab *Neohelice granulata* buries aboveground plant litter at rates (0.5–8 g m^{-2} day^{-1}) comparable to those of litter production (3 g m^{-2} day^{-1}). Buried litter has a low probability (0.6%) of returning to the marsh surface. The formation of burrow excavation mounds on the marsh surface is responsible for most litter burial, whereas litter trapped in burrows was an order of magnitude lower than rates of burial under excavation mounds. Crab exclusion markedly increased surface litter accumulation (3.5-fold in just 21 days). Tides with the potential to transport significant amounts of surface litter are infrequent; hence, most litter is buried before it can be transported elsewhere or decomposes on the surface. Crab litter burial can account for the observed low levels of surface litter accumulation in this ecosystem and likely drives organic matter transformation and export. The impacts of ecosystem engineering by this crab species are therefore substantial and comparable in magnitude to the large effects found for tropical crabs and other litter-burying organisms, such as anecic earthworms.

Key words: burrow excavation; litter burial; *Neohelice granulata*; ecosystem engineering; ecosystem export; internal ecosystem functioning.

Authors contributions All authors contributed to study conception, study design, interpretation of findings, and commenting on manuscript drafts. JLG performed the field research. JLG, CGJ, and PDR were primarily responsible for data analysis. JLG and CGJ wrote and edited the drafts of the manuscript.

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INTRODUCTION

Surface plant litter is a major component of terrestrial and wetland ecosystems that has habitat and biogeochemical significance (Brinson and others 1981; Facelli and Pickett 1991; Batzer and Wissinger 1996). Aboveground plant litter can accrue in situ, decompose on the surface, be transported by wind or water (for example, Welbourn

and others 1981; Conners and Naiman 1984; Findlay and others 1990; Twilley and others 1997), be buried in situ by geomorphic forces (upheaval, landslip, sedimentation; for example, Metzler and Smock 1990; Walker and Shiels 2008), or as is quite common, be locally buried by animals (for example, Foster and Stubbendieck 1980; Anderson 1988; Zacheis and others 2002). Because litter burial reduces the potential for surface transport and changes the decomposition environment, it can alter the amount of organic matter exported to adjacent ecosystems and the quality of organic matter that is exported or retained. Hence, the burial of litter by animals has the potential to be an important biological control on material fluxes across ecosystem boundaries (compare material subsidies caused by animal movement among ecosystems, Polis and others 1997) as well as the internal functioning of ecosystems. Understanding how physical ecosystem engineers (sensu Jones and others 1994), including litter-redistributing animals, can influence connectivity and interdependence among ecosystems is increasingly recognized as relevant to ecosystem-based management and protected area design (Gillis and others 2014; van de Koppel and others 2015).

Burrowing crabs are major agents of litter relocation in coastal tropical ecosystems. Gecarcinid land crabs in coastal forests take surface litter into their burrows for food or lining burrows (for example, O'Dowd and Lake 1989; Green and others 1999; Sherman 2003). Many mangrove crabs (primarily sesarmids) carry detached mangrove leaves into burrows where they are cached, macerated, and conditioned, then eaten (see review in Kristensen 2008). Litter burial by these crab species frequently reduces surface litter accumulation (for example, Robertson 1986; O'Dowd and Lake 1989; Twilley and others 1997; Green and others 1999; Sherman 2003) and increases litter decomposition rates (for example, Green and others 1999; Middleton and McKee 2001; Kristensen 2008). Litter burial by mangrove crabs often substantially reduces tidal export of litter to adjacent coastal waters (for example, Robertson 1986; Twilley and others 1997).

Burrowing crabs can occur at remarkably high densities in temperate coastal ecosystems, most notably in salt marshes (50–200 individuals m^{-2}; for example, Bertness and Miller 1984; Taylor and Allanson 1993; Breitfuss and others 2004; Wang and others 2010). The extent to which their effects may be comparable to those found for tropical crabs with respect to surface litter accumulation, ecosystem export, and internal functioning is largely unknown. However, their effects are likely significant (Botto and others 2006; Wang and others 2010), and there is indirect supporting evidence showing high rates of sediment turnover, altered vertical litter distributions and changes in biogeochemistry associated with crabs in temperate coastal ecosystems (Takeda and Kurihara 1987; Iribarne and others 1997, 2000; Gutiérrez and others 2006; Wang and others 2010).

Surface litter accumulation in lower elevations of many Southwestern Atlantic salt marshes is remarkably low relative to primary production (for example, Cunha and others 2005; Montemayor and others 2011; Online Appendix 1). Counterintuitively, low levels of surface litter accumulation are particularly notable in many micro-tidal salt marsh estuaries where low tidal amplitudes and intermittent flooding should create reduced potential for net export of surface litter. These lower marsh areas are, however, densely populated by the burrowing crab Neohelice granulata (often > 60 burrows m^{-2}; Bortolus and Iribarne 1999; Gutiérrez and others 2006). In contrast to leaf-burying crabs in the coastal tropics, individuals do not carry litter into their burrows for lining, maceration, conditioning and subsequent consumption. These crabs are not routinely observed consuming litter on the marsh surface (compare extensive field evidence of herbivory; for example, Bortolus and Iribarne 1999; Alberti and others 2007, 2011). Nevertheless, since their burrows are remarkably large (up to 7 cm diameter, 1 l volume, and 1 m depth; Iribarne and others 1997), burrows could passively trap a significant fraction of litter that might otherwise be transported by tides (Iribarne and others 2000; Botto and others 2006). Furthermore, a single crab can excavate up to 90 g DW sediment day^{-1} forming sediment mounds on the marsh surface while burrowing (Gutiérrez and others 2006). These mounds could potentially bury a large fraction of surface litter.

Given the high density of N. granulata, its numerous burrows, and its capacity to excavate sediment at high rates, we predicted that litter burial by this species could account for observed low surface litter accumulation at lower marsh elevations, with concomitant influence on net litter export and internal ecosystem functioning. Here we quantified rates of litter deposition into crab burrows and burial under sediments excavated by crabs and tested whether litter burial by crabs results in long-term litter incorporation into marsh sediments. We evaluated the net effect of crabs on litter accumulation via a crab exclusion experiment. We show that tides with the potential for

exporting litter are infrequent in the study area, and therefore unlikely to account for observed low levels of surface litter accumulation. We provide evidence that largely rules out other possible causes of observed surface litter dynamics. We briefly discuss potential implications of crab litter burial for material connections among adjacent ecosystems and internal ecosystem functioning. Finally, we draw some parallels and distinctions with other animals that bury litter.

METHODS

Study Area

Research was conducted at Mar Chiquita coastal lagoon, Argentina, a 46-km^2 body of brackish water with semi-diurnal low amplitude tides (< 1 m; Fasano and others [1982]). The lagoon is surrounded by almost monospecific stands of cordgrass, *Spartina densiflora* (Isacch and others [2006]), interspersed with numerous tidal creeks. The marshes are located above mean high tide level and therefore only intermittently flooded by tides.

All field studies were conducted from January 2003 to February 2006 in a marsh area at the eastern margin of Cangrejito creek (37°44'S, 57°26'W)—a small tidal creek draining a basin (ca. 1500 ha) that flows into the lagoon ca. 1 km from its inlet. Studies were distributed over a ca. 3-ha area located at lower marsh elevations ca. 0–40 m from the marsh/lagoon interface comprising 30–40% of the marsh elevation range. These lower elevations support high crab densities (nearly 70 burrows m^{-2}, Gutiérrez and others [2006]) and flood when tides measured at the nearby port of Mar del Plata (38°02'S, 57°32'W) exceed 1.89 m (see Online Appendix 2), or when major rainfall and overland runoff events occur.

Mean surface-level and buried stocks (20 cm depth) of aboveground *S. densiflora* litter—defined as detached, senescent stems or leaves greater than 1 cm length—are less than 48 and 39 g DW m^{-2}, respectively (see Online Appendix 1) and represent 4.6 and 3.6% of annual litter production, respectively (1054–1223 g DW m^{-2} year^{-1}; Vera and others [2009]).

Litter Deposition into Crab Burrows

Daily rates of litter deposition into crab burrows (DEPOSITED) were estimated using bottom-capped PVC pipes buried in sediment with the opening flush to the sediment surface. PVC pipes are reasonable burrow mimics of similar size and shape as natural burrows, and are used by crabs at the same frequency as natural burrows (Gutiérrez and others [2006]). *N. granulata* burrows in salt marshes approximate vertical cylinders of variable opening diameter (up to 7 cm) and depth (30–100 cm; Iribarne and others [1997]). We used pipes of different diameters (1, 2, 3, 4, 5, and 6 cm) to span the range of observed natural burrow openings. Although the depth of *N. granulata* burrows is variable, we used a constant pipe depth of 40 cm that was the average burrow depth observed in the low marsh (that is, 30–50 cm; J. Gutiérrez personal observation). Direct measures of litter deposition into crab burrows were not possible because the amount of previously deposited litter could not be ascertained without destroying or altering burrows.

Crabs had free access to burrow mimics in order to include any effects of crab movement in and out of mimics on litter trapping. Six mimics of each diameter ($n = 36$ total) were deployed. The amount of litter collected during 24 h was sampled on 12 dates of marsh flooding by spring tides (January 22, 23, and 24, 2003; January 14, 23 and 24, and December 13, 14, 15, 16, 17, and 18, 2004), and 9 dates where tides were insufficient to flood the marsh (January 29 and 30, 2003; January 15, 16 and 17 and December 9, 10, 11, and 12, 2004). Material deposited in burrow mimics was sampled after two tidal cycles (ca. 24 h) and sieved through a 1-mm mesh, and the litter (defined in Study Area above) was thoroughly washed, dried (48 h at 50°C), and weighed ($\pm$ 0.001 g).

Mean rates of DEPOSITED (g DW litter^{-1} m^{-2} day^{-1}) on each sampling date were separately estimated using randomization and re-sampling (Manly [1998]; 10,000 iterations) by combining data on: (1) the amount of litter deposited in burrow mimics of different size classes (that is, 1, 2, 3, 4, 5, and 6 cm entrance diameter) and (2) the density of burrows of each size class found in the field. Burrow density in each size class was obtained from burrow counts and diameter measures ($\pm$ 1 mm) in 36 random plots (0.35 × 0.35 m) sampled during the same time period as measures of DEPOSITED (January 27, 2003; January 22, 2004; and December 14, 2004).

Litter Burial under Excavated Sediments

New litter from the canopy and extant surface litter, including litter locally transported by tides, can be buried under freshly excavated sediment mounds formed during crab burrow construction and maintenance. These same sediment mounds

can also contain previously buried litter. To estimate rates of new litter burial, we measured: (a) total litter (TOTAL) in freshly formed mounds and (b) the amount of previously buried litter (PREVIOUS) in freshly formed mounds when new litter inputs were prevented. Estimates for TOTAL and PREVIOUS were determined separately but concurrently as follows. To estimate TOTAL, we randomly selected six naturally formed burrows in each of six entrance diameter classes (1–1.9, 2–2.9, 3–3.9, 4–4.9, 5–5.9, and 6–6.9 cm). Prior to each of twenty 24-h sampling periods (12 dates when marsh flooding occurred: January 22–24, 2003; February 5–7, 2004; and December 13–18, 2004. Eight dates when flooding did not occur: January 29, 30, 2003; January 28–30, 2004; and December 9–12, 2004), we removed and discarded preexisting sediment mounds associated with each burrow down to the level of the surrounding, unmodified sediment surface. We then recorded the proportion of burrows in each size class showing sediment excavation during the sampling period and collected each fresh sediment mound. To estimate PREVIOUS, we used the same basic design (6 × 6 size classes of randomly selected burrows). Prior to each of sixteen 24-h sampling periods coincident with the estimation of TOTAL (9 dates when marsh flooding occurred: February 5–7, 2004; December 13–18, 2004. Seven dates when flooding did not occur: January 28–30, 2004; December 9–12, 2004), a 0.2 × 0.2 m area around each burrow was cleared of surface litter and sediment mounds, and new litter inputs were prevented by covering the area with a small wire cage with sides and a top (1 mm mesh; 15 × 15 × 15 cm). The proportion of burrows showing excavation during the sampling interval was recorded, and each fresh sediment mound was collected. Mounds from both protocols were sieved (1 mm mesh) and the litter treated as above (see Litter Deposition in Crab Burrows).

Mean rates of TOTAL and PREVIOUS litter burial (g DW litter^{-1} m^{-2} day^{-1}) on each sampling date were separately estimated using randomization and re-sampling (Manly 1998; 10,000 iterations) in a manner similar to estimation of DEPOSITED. Here we combined data on: (1) litter in sediment from un-caged (TOTAL) or caged samples (PREVIOUS); (2) observed densities of natural burrows in each size class; and (3) the proportion of burrows in a size class with fresh excavation. As with estimates of DEPOSITED, burrow density in each size class was obtained from burrow counts and diameter measures (± 1 mm) in 36 random plots (0.35 × 0.35 m) sampled on January 27, 2003; January 22, 2004; and December 14, 2004 (that is,

during the same time period as measures of TOTAL and PREVIOUS). T tests (Zar 1984) were used to evaluate whether the proportion of burrows showing new sediment excavation differed between dates with and without tidal flooding.

Long-Term Probabilities of Litter Burial and Exhumation

The probability that litter remained buried under excavated sediments or remained on the marsh surface over longer time periods was evaluated using a litter-tethering experiment. Although tethering limits the tidal transport of surface litter, it nevertheless can be used to estimate the probability of burial of any litter that remains within the low marsh over the longer term. Given prevailing tidal conditions at the site (that is, no flooding or limited potential for tidal export in the majority of dates; see ''Results''), most pieces of litter would be expected to undergo limited or no transport before they are buried.

Pieces of *S. densiflora* (10–15 cm length) detached from standing-dead shoots were individually tied to a nylon thread (0.3 ml, 0.3 mm dia.) attached to a wire stake anchored in sediment. On January 23, 2004, tethered litter pieces were deployed in the field either on the sediment surface or at a depth of 1–2 cm into different sediment mounds ($n = 60$ in each case). The status of litter pieces was monitored after 1, 5, 12, 19, 26, 33, 50, 65, 84, and 115 d and categorized as: (1) buried if litter tether ends were located belowground; or (2) not buried if litter tether ends were found on the surface with litter attached, or without litter attached (that is, conservatively assumed to be no longer buried). Transition probabilities (that is, the probability of occurrence for a status class given previous status) are calculated as:

$$p_{ij} = s_{ij} \bigg/ \sum_{j=1}^{2} s_{ij}$$

where p_{ij} is defined as the transition probability from status i to status j and s_{ij} is the number of time intervals in which status i was followed by status j.

Effect of Crab Exclusion on Surface Litter Accumulation

A crab exclusion experiment was conducted to test whether litter can accumulate on the sediment surface in the absence of crabs and tidal transport. Sixteen 0.3 × 0.3 m plots separated by 5 m were distributed along a transect parallel to and 10 m from the lower marsh edge. Crab exclusion and

controls ($n = 8$ each) were systematically assigned to ensure even dispersion. Each plot was surrounded by 1-mm mesh walls buried 10 cm into sediments with 0.5 m emergent height. Controls had two 5×5 cm holes cut in the base of the wall on each side to allow free access by crabs, while the outside top of the mesh walls of crab exclusion plots had a downward projecting strip of transparent plastic film (10 cm width) to reduce the likelihood of crabs climbing in. At the start of the experiment, all plots were cleared of detached litter, and crabs found in exclosures were removed by hand (January 31, 2005). Exclosure plots were visited every 1–2 days until the end of the experiment (February 21, 2005) to remove any crabs that had managed to climb in or burrow underneath. The null hypothesis (no difference in litter accumulation between treatments) was evaluated using a two-tailed t test adjusted for inequality of variances (Welch's approximate t; Zar 1984). This test was chosen because it is robust to the heterogeneity of variances observed in the data after F tests (Zar 1984) and to non-normality (Zar 1984).

Frequency of Potential Litter Export by Tides

Litter flotation and movement by tides—litter transport—is a prerequisite for export from the lower marsh to the estuary or higher marsh. Transported litter can be exported, locally redistributed, or even imported from elsewhere to varying degrees. Directly measuring export, redistribution and import with reasonable precision at appropriate spatial and temporal scales was not technically feasible. Nevertheless, the amount of litter transported by tides can be used to estimate the maximum amount of litter that could be exported from the lower marsh—maximum potential export (hereafter MPE; that is, the amount of material exported when retention and internal redistribution are null). MPE was estimated from field measures of tidal litter transport over a range of observed variation in marsh flooding depth using litter mark-recapture.

Dried pieces of surface litter 5–20 cm length were lightly coated with fluorescent aerosol paint. Painting increased dry weight by 8–14%, which offset weight loss from drying (9–12%). Painted and unpainted fresh litter floated the same way in a brackish water trial ($n = 50$ pieces of each type). In nine experiments (May 8–10, 2004; January 26–28, 2005; and February 1–3, 2006), each conducted in a different approximately 10×10 m location, and 2–3 g DW of painted litter (equivalent to 22–33 g DW m^{-2} and within the range of surface litter stocks observed in the marsh; see Online Appendix 1) was added to each of five 0.3×0.3 m plots where crabs had been removed by hand and their burrows filled with sediment. After two tidal cycles (that is, ca. 24 h), all painted litter found in the area was collected, washed, oven-dried, and weighed as above. Since plots were open, some were re-colonized by crabs during the period. Plots with newly excavated crab sediment mounds at the time of litter recapture were excluded from analyses to eliminate bias due to litter burial, resulting in 1–4 plot-level estimates for each experiment. Litter recovered from plots with no crab burrowing were pooled for each experimental date to generate a single data point per date. Data were expressed as percent original painted litter mass added to all plots that subsequently remained on the surface.

To relate litter transport to tidal flooding regimes, maximum flooding depth was measured at each location on each date. An iron stake (2 m h) with 30 plastic cups (2 cm opening dia., 5 cm depth) vertically attached at 5-cm intervals using duct tape was anchored 0.5 m into sediment. An additional cup was buried in sediment with the top 1 cm above the marsh surface to record flood levels greater than 1 cm and less than 5 cm. The uppermost plastic cup that was completely filled with water after 24 h was considered to be the marsh flooding depth. Since co-occurring rain never completely filled cups (< 5 cm depth), the maximum height of completely filled cups below the highest incompletely filled or empty cup was considered the maximum tidal height. Zero or negligible flooding that would have no influence on litter transport was considered to have occurred when the cup at the sediment surface was not completely full (that is, < 1 cm water depth).

Beta regression (Ferrari and Cribari-Neto 2004) was used to evaluate the relationship between percent litter transport and maximum flooding depth. The beta regression model was fit as a generalized linear model (McCullagh and Nelder 1989) using a logit link function. The goodness of fit of the model was evaluated with a Wald test (Wasserman 2004) and McFadden's pseudo-R^2 (Long 1997). All analyses were carried out in R (R Development Core Team 2017) using the ''betareg'' package (Cribari-Neto and Zeileis 2010). Daily MPE values at the marsh from October 1, 2004, to October 30, 2005, were calculated based on the maximum tide gauge level recorded at the nearby port of Mar del Plata on each of those dates (data provided by Servicio de Hidrografía Naval, Ministerio de Defensa, Argentina). A maximum tide re-

cord gauge height of 1.89 m was determined to be the threshold for flooding in the lower marsh (see Online Appendix 2).

RESULTS

Litter Deposition into Crab Burrows

Mean rates of litter collected in burrow mimics—that is, DEPOSITED (see ''Methods'')—ranged from 0.14 to 0.50 g m^{-2} day^{-1} on dates with tidal flooding, and 0.02 to 0.09 g m^{-2} day^{-1} on dates without tidal flooding (Figure 1). Rates were at least an order of magnitude lower than rates of litter burial (see below) and at least half an order of magnitude lower than rates of surface litter production (see Study Area and Online Appendix 1).

Litter Burial under Excavated Sediments

The percentage of burrows showing fresh sediment excavation was higher on dates with tidal flooding than on dates without tidal flooding (t test: $t = 6.45$, $df = 19$, $P < 0.01$; Figure 2C). Mean amounts of litter found in freshly formed mounds (that is, TOTAL; see ''Methods'') ranged from 4.01 to 8.46 g DW m^{-2} day^{-1} on dates with flooding and 0.46 to 1.53 g DW m^{-2} day^{-1} on dates without flooding (Figure 2A). Amounts of previously buried litter found in freshly excavated mounds when new litter inputs were prevented by caging (that is, PREVIOUS; see ''Methods'') were at least an order of magnitude lower than the above TOTAL values, ranging from 0.01 to 0.16 and 0 to 0.02 g DW m^{-}

^{2} day^{-1} on dates with and without flooding, respectively. TOTAL minus PREVIOUS values for litter were ca. 0.5–8 g DW m^{-2} day^{-1} (Figure 2A, B) with previously buried litter representing approximately 4% of total litter. These results indicate that most litter previously buried by crabs was not returned to the surface but remained relatively deeply incorporated in marsh sediments and/or had decomposed to a size less than 1 cm (Figure 2B); that most litter found in freshly excavated mounds was therefore new surface litter; and that this new surface litter was being buried at a daily rate equivalent to 15–270% of the daily-averaged rate of aboveground litter production in the marsh (ca. 3 g DW m^{-2} day^{-1}; see Vera and others 2009).

Long-Term Probabilities of Litter Burial and Exhumation

All tethered pieces of litter initially placed on the marsh surface were found to be buried by the end of the experiment (that is, 115 days; 98.3% buried by day 33), whereas 96.7% of tethered litter initially buried under mounds remained buried by that date (Figure 3). Litter tethered on the marsh surface had a 29.9% probability of being buried by the next sampling date (5–20 days). In contrast, tethered litter buried under mounds had only a 0.6% probability of returning to the marsh surface during the same intervals.

Effects of Crab Exclusion on Surface Litter Accumulation

Surface litter accumulation was ca. 3.5-fold greater in the crab exclusion treatment compared to controls after 21 days (t test adjusted for inequality of variances: $t = -4.99$, $df = 8$, $P < 0.01$; Figure 4). Mean litter accumulation in exclusion plots reached 70 g DW m^{-2} by this time, substantially exceeding mean observed surface litter stocks (< 48 g DW m^{-2}, see Study Area and Online Appendix 1).

Frequency of Potential Litter Export by Tides

We observed from 2 to more than 80% litter transport out of plots following tidal inundation in litter mark-recapture experiments. The relationship between litter transport (T) and maximum flooding depth (MFD) is satisfactorily described by a beta regression model where

$$T = e^{-2.67 - 0.07\text{MFD}} / \left(1 + e^{-2.67 - 0.07\text{MFD}}\right)$$
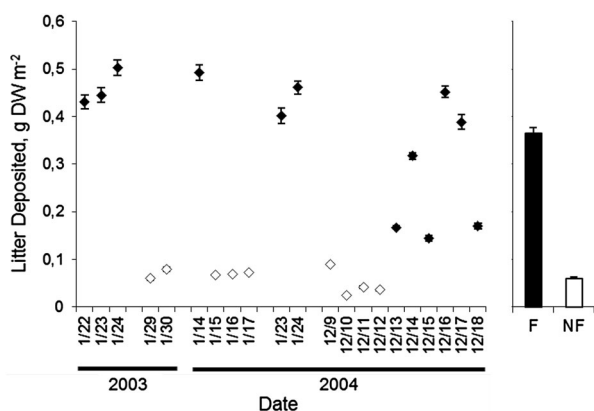

Figure 1. Mean ± SE, g DW m^{-2} litter deposited into crab burrow mimics (that is, DEPOSITED, see text) over 24-h periods on 21 sampling days (left panel) and grand mean ± SE under flooding (F) and non-flooding (NF) conditions (right panel). Filled and open symbols or bars indicate dates with and without tidal flooding, respectively.
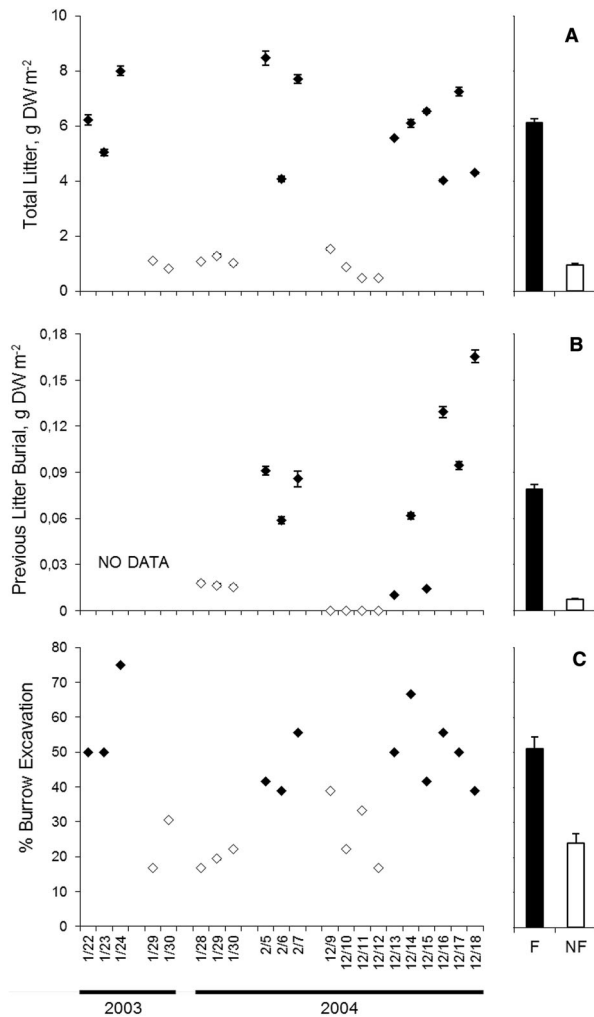
Figure 2. **A** Mean ± SE, g DW m^{-2} total litter buried in fresh sediment mounds excavated by crabs (that is TO-TAL, see text) over 24-h periods on 21 sampling days (left panel) and grand mean ± SE under flooding (F) and non-flooding (NF) conditions (right panel). **B** Mean ± SE, g DW m^{-2} previously buried litter found in fresh sediment mounds excavated by crabs (that is, PREVIOUS; see text) over the same periods as (**A**) (left panel) and grand mean ± SE under flooding (F) and non-flooding (NF) conditions (right panel). Note the different y-axis values range compared to (**A**). **C** Daily percentage of crab burrows with fresh sediment excavation for 36 burrows sampled in the same period as (**A**) and (**B**) above (left panel) and mean ± SE across flooding (F) and non-flooding (NF) dates (right panel). Filled and open symbols or bars are dates with and without tidal flooding, respectively.

(Wald test: $F = 24.15$, $df = 1, 6$, $P < 0.01$; pseudo-$R^2 = 0.84$; $SE_1 = 0.47$, $SE_2 = 0.01$). Litter transport remained low (less than 20%) when maximum

flooding depths were less than 20 cm but increased to more than 50% when maximum flooding depths were in excess of 40 cm (Figure 5). The model also predicted that 99% of litter would be transported at a flooding depth of 98 cm (that is, tide gauge heights in excess of 2.87 m at Mar del Plata port based on a 1.89-m tidal height threshold for marsh flooding, see Online Appendix 2).

Analysis of tidal gauge records indicated that marsh flooding would have occurred on 155 of the 395 days (39% of days) from October 1, 2004, to October 30, 2005 (again using a 1.89-m tidal height threshold for marsh flooding; see Online Appendix 2). Maximum potential export (MPE) was estimated to be less than 20% on 89 of these 155 flooding dates (Figure 6A using daily MPE estimates based on tidal records and the above beta regression model). The mean and maximum intervals between dates with MPE estimates in excess of 20% were 5 and 32 days, respectively (Figure 6B). The analyses showed a relatively low frequency of marsh flooding and a low frequency of flooding events sufficient to potentially export litter.

DISCUSSION

Crab Burrowing as the Cause of Low Surface Litter Accumulation

Our findings show that crabs bury substantial amounts of surface litter under their excavation mounds on a daily basis. Only a very small fraction of previously buried litter (ca. 4%) has a probability of returning to the surface. Passive trapping of litter by burrows does occur but is an order of magnitude lower than rates of burial under excavation mounds (see Figure 1). Both crab burrowing and litter burial increase when marsh flooding occurs (see Figures 1, 2). The observed increase in burrowing frequency following flooding is commensurate with greater crab foraging and burrow maintenance activities that are known to occur following tidal inundation (see Méndez-Casariego and others 2011; Luppi and others 2013; Bas and others 2014).

Several lines of evidence indicated that crab burrowing can account for the low levels of observed surface litter accumulation. As noted above, daily rates of litter burial by crabs were equivalent to 15–270% of the daily-averaged rate of aboveground litter production in the marsh (ca. 3 g DW m^{-2} day^{-1}; see Vera and others 2009). In addition, litter had a very low probability of being exhumed after burial (0.6%) and thus tended to remain
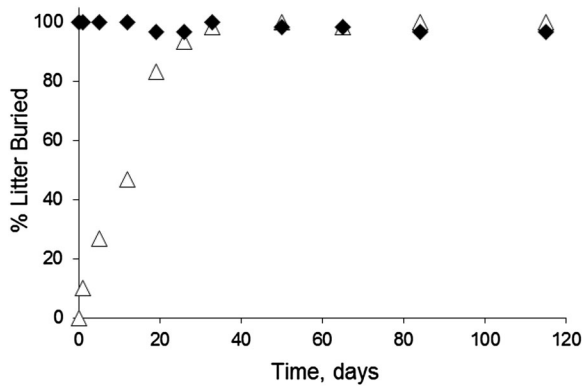
Figure 3. Percentage of litter buried by crabs over the course of the litter-tethering experiment. Tethered litter was initially placed on the sediment surface (open triangles; $n = 60$) or inserted into sediment mounds excavated by crabs (filled diamonds; $n = 60$).
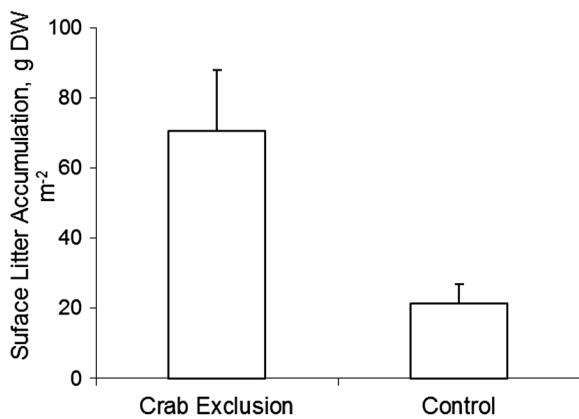

Figure 4. Total surface litter accumulated (g DW m^{-2}) in crab exclusion and control plots by the end of the 21-day experiment. $P < 0.01$ (t test adjusted for inequality of variance).

buried over the long term (that is, weeks to months, see Figure 3). Moreover, crab exclusion experiments resulted in a 3.5-fold increase in marsh surface litter in just 21 days, reaching levels (70 g DW m^{-2}; see Figure 4) that exceeded the maximum surface litter stocks recorded in the study area (48 g DW m^{-2}; see Study Area and Online Appendix 1).

In contrast to burial, tidal export appears to be a relatively minor source of surface litter loss. Despite daily tides, mean and maximum marsh flooding recurrence intervals during the study period were less frequent—3 and 12 days, respectively (see Figure 6B). Yet even on flooding dates, estimates of maximum potential export (MPE) for many of those dates were low (for example, MPE < 20% in ca. 60% flooding dates; see Figure 6A). It is also

worth noting that much of the transport estimated by MPE might well be local litter redistribution rather than oceanward or landward cross-boundary transport (see MPE definition and measurement in ''Methods''). This implies that the period between actual export events could be even longer than estimated from MPE estimates. Given that potential litter export by tides is, at best, intermittent and often likely of minor magnitude (see frequency distribution of MPE values, Figure 6A), daily litter burial by crabs is expected to substantially exceed daily litter export under most circumstances. In addition, cumulative burial by crabs at the observed rates (that is, similar to litter production) would deplete marsh surface litter stocks by the time that tides with substantial potential for export would occur. Such a conclusion does not, of course, preclude the effects of episodic storms that could remove sediments and buried litter, although that is beyond the scope of this study.

Litter burial due to sedimentation is likely negligible in comparison with rates of litter burial by crabs. Sedimentation in salt marshes is generally less than 1.5 cm year^{-1} (Mitsch and Gosselink 1993). It usually ranges from zero to a few millimeters per year in intermittently flooded marsh zones (for example, Warren and Niering 1993; Leendertse and others 1997), and the lower elevation marsh of our study site is only intermittently flooded (see above). In contrast, burrowing crabs at this site excavate an average of ca. 550 g DW sediment m^{-2} day^{-1} (Gutiérrez and others 2006). Based on a sediment bulk density of 1.7 g DW cm^{-3} (Fanjul and others 2007), this would result in an equivalent surface deposition rate by crabs of
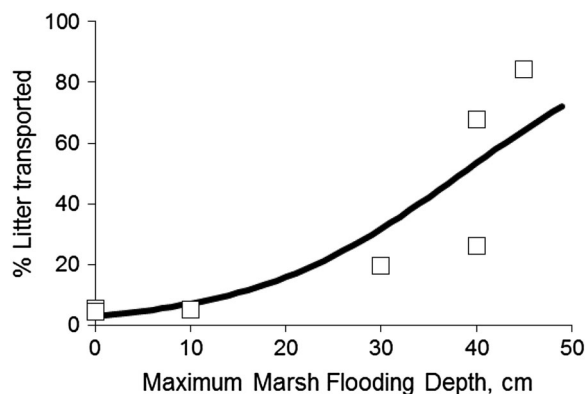

Figure 5. Beta regression model relating maximum marsh flooding depth (cm) over two consecutive tidal cycles (ca. 24 h) to the percent of marked litter transported out of 0.09 m^{-2} plots during the same period (that is, equivalent to maximum potential export, MPE, see text).
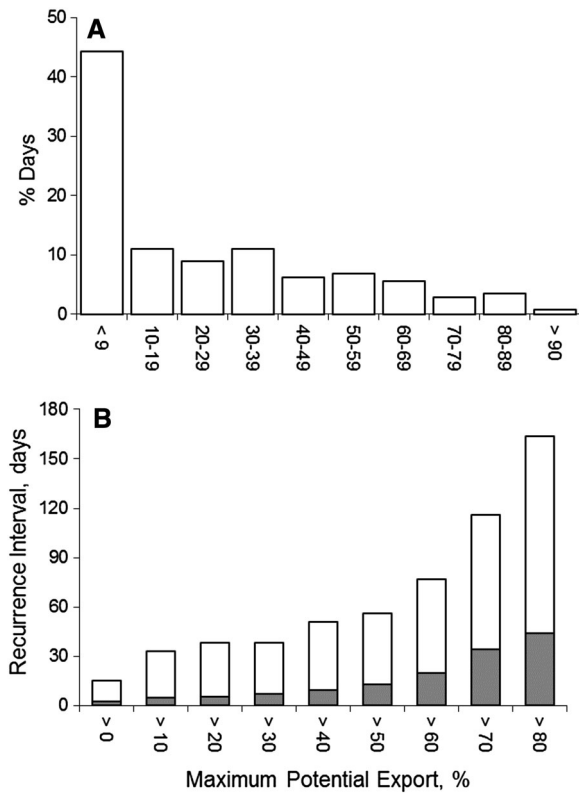
Figure 6. **A** Frequency distribution of percent of days by percent maximum potential export range (MPE, see text) predicted from tidal records for the period October 1, 2004, to October 30, 2005. **B** Mean (gray bars) and maximum recurrence (full bars) intervals at varying levels of maximum potential export, MPE (see text) predicted for the same period.

approximately 11 cm year^{-1} (extrapolated from ca. 0.03 cm day^{-1}), substantially greater than rates of other sedimentary processes.

Surface litter losses from sources other than crab burial and tidal export are also likely to be minor. Surface decomposition rates for *Spartina densiflora* litter are remarkably slow (just 37% weight loss after 410 days and less than 3% loss within the first month; Montemayor and others 2011) relative to the short time that litter remains on the marsh surface before being buried by crabs (that is, a month or less; see Figure 3). Losses due to surface decomposition in the period between litter detachment and burial are therefore likely to be inconsequential. Significant physical comminution of smaller pieces of surface litter down to a size class below our definitional threshold (that is, > 1 cm length, see "Methods") also seems unlikely given the low tidal amplitudes, the attenuation of wave energy by marsh vegetation (for example, Bouma and others 2005), and the short time interval before crab burial. We are also not aware of any species (including *N. granulata*) that could potentially comminute litter to this extent over comparable time periods. Consumption of litter pieces as defined in this study by this crab species appears to be a negligible source of litter disappearance in our marsh; it was never observed during our study, nor was litter ever observed to be collected and carried into burrows. Plant material is commonly found in the gut of crabs inhabiting salt marshes, including this species. It may derive from litter consumption or from processing sediment rich in microbially conditioned detritus (see D'Incao and others 1990; Iribarne and others 1997; Barutot and others 2011; Bas and others 2014). Some studies indicate potential for litter consumption (for example, Barutot and others 2011; Bas and others 2014), although this has not been confirmed, and as noted above, was never observed in our study.

In summation, our findings indicate that litter burial by crabs is an important source of surface litter loss at our study site. Although most of our field measurements and experiments were conducted during the austral summer, crabs are active all year round (that is, no seasonal dormancy; see Méndez-Casariego and others 2011; Luppi and others 2013; Bas and others 2014). Litter burial would therefore be expected to occur all year round, albeit at rates that will vary with fluctuations in crab activity and litter production. The fact that surface litter stocks remain low relative to production at other times of the year (see Online Appendix 1) supports this argument; that is, even at temporally variable levels of crab activity, burial is still sufficient to reduce surface litter stocks.

Potential Implications for Ecosystem Functioning

It follows from the above that via the burial of surface litter, crabs are a fundamental driver of a pathway that connects aboveground primary production back to marsh sediments following shoot senescence. We expect this to have the following potential implications for the functioning of these salt marshes:

1. *Decreased particulate organic matter export and increased in situ processing* Daily litter burial by crabs is expected to reduce the amount of litter exposed to tides by the time that tides with the potential to export litter actually occur. This means that crabs should reduce the magnitude of litter exported to adjacent seaward ecosystems or the landward higher marsh relative to

comparable ecosystems without these crabs (see Gallagher and others 1980; Jackson and others 1986; Bouchard and Lefeuvre 2000). Mass balance considerations also imply that crab burial increases the amount of surface marsh litter being processed in situ to a degree equivalent to reduced litter export, with most of this material being processed below the sediment surface due to crab burial.

2. *Accelerated litter decomposition* Senesced marsh plant shoots can show higher rates of decomposition when buried (Sun and others 2015; Sun and Mou 2016). In contrast to surface litter, buried litter enters into more prolonged and direct contact with water and dissolved mineral nitrogen, both of which are expected to favor microbial colonization and decomposition (see Valiela and others 1985; Halupa and Howes 1995; Liao and others 2008). Furthermore, the decomposition of buried litter is unlikely be inhibited by hypoxia because crab burrowing markedly increases subsurface oxygen concentrations (from threefold to more than 20-fold depending on depth; see Daleo and others 2007). By translocating litter to a milieu more conducive to higher decomposition rates, crabs should be accelerating overall aboveground plant matter decomposition within the ecosystem, thereby increasing net nutrient mineralization and respiration rates (see also Zacheis and others 2002; Suárez and others 2006).

3. *Increased dissolved organic matter and inorganic nutrient export and/or uptake by plants* Buried aboveground litter appears to be a significant addition to belowground detritus production. Indeed, annual rates of litter burial by crabs (183–2920 DW m^{-2} $year^{-1}$ by extrapolation from 0.5 to 8 g DW m^{-2} day^{-1}) are substantial relative to annual estimates of belowground production in *Spartina* spp. marshes (300–7000 g m^{-2} $year^{-1}$; Hemminga and others 1996). Increased organic matter availability within marsh sediments, together with accelerated decomposition in the belowground milieu (see above), are expected to contribute to a net increase in pore water concentrations of dissolved organic matter and inorganic nutrients. This could translate into increased nutrients available to plants and/or entering surface or subsurface hydrologic transport (see Fanjul and others 2008, 2015).

Qualitatively, crab impacts in these marshes are comparable to plowing of crop residues in agroecosystems, which generally increase decomposition rates, plant nutrient uptake, and nutrient losses via leaching relative to no-till agriculture (see Hendrix and others 1986; Holland and Coleman 1987). Nevertheless, crab litter burial operates jointly with other crab influences on ecosystem functioning that do not necessarily have analogues in agroecosystems. Known effects include burrowing and sediment mixing (which reduces anoxia, thus favoring decomposition and plant mycorrhizal colonization and nutrient uptake; see Daleo and others 2007; Fanjul and others 2007, 2015); grazing (which reduces tiller survival, thus increasing tiller production; Alberti and others 2011); and defecation into burrows (which likely represents a considerable input of labile carbon and nutrients to subsurface sediments; for example, Gutiérrez and others 2006, Fanjul and others 2008). It is notable that all these crab influences are likely to act in synergy with litter burial to further reduce particulate organic matter export while enhancing in situ decomposition and dissolved nutrient fluxes.

Although these crabs do not appear to directly consume litter or transport it to their burrows (their burrows primarily serve as protection from predators and against desiccation; Luppi and others 2013), how crab litter burial and the other above-noted crab influences ultimately affect crab food availability via the above kinds of ecosystem effects is an unanswered question that may have important longer-term dynamic consequences (that is, ecosystem engineering feedbacks; Jones and others 2010).

Concluding Remarks

Our findings align *Neohelice granulata* with tropical counterparts such as land and mangrove crabs, as well as unrelated animals such as anecic earthworms (Suárez and others 2006) and geese (Zacheis and others 2002), all of which can bury a substantial fraction of aboveground plant litter production, thereby re-directing organic matter fluxes and transformations. Certainly, burial mechanisms vary among these organisms. Although tropical crabs and anecic earthworms actively move litter into their burrows (Brown and others 2000; Sherman 2003; Kristensen 2008), *N. granulata* and geese bury litter incidentally as a consequence of burrow excavation and trampling, respectively (Zacheis and others 2002; this study). Furthermore, litter burial (litter caching) by tropical crabs and earthworms subsequently involves maceration and conditioning, then consumption to varying degrees (see Brown and others 2000; Sherman 2003; Kristensen 2008). Hence, the net

contribution to organic matter processing by these species results from the interplay of litter translocation and consumption. In contrast, incidental litter burial by *N. granulata* and geese does not involve litter consumption. Nevertheless, some impacts of litter burial expected with *N. granulata* are likely general across disparate litter-burying organisms and their ecosystems (for example, increased litter decomposition rates, sediment respiration, nutrient mineralization, and dissolved nutrient fluxes; see O'Dowd and Lake 1989; Green and others 1999; Zacheis and others 2002; Bohlen and others 2004; Suárez and others 2006; Kristensen 2008).

Finally, our findings add to recently growing understanding of and interest in the role of physical ecosystem engineers on connectivity among and functioning across ecosystem boundaries (see Gillis and others 2014; van de Koppel and others 2015). Although recent developments on this topic have emphasized effects on transport and connectivity caused by the physical structures of the engineers themselves (that is, effects of autogenic engineered structures on wave energy and sediment trapping by corals, oyster reefs, mangrove forests, seagrass meadows, and mussel beds; see Gillis and others 2014; van de Koppel and others 2015), earlier studies on mangrove crabs (for example, Robertson 1986; Twilley and others 1997) and our results suggest that engineers that locally redistribute materials can also have significant cross-ecosystem impacts. Given that burrowing crabs occur in salt marshes across five continents (for example, Bertness and Miller 1984; Takeda and Kurihara 1987; Wolfrath 1993; Taylor and Allanson 1993; Breitfuss and others 2004) and that their densities and sediment excavation rates are often comparable to, or even larger than, those of *N. granulata* (for example, Taylor and Allanson 1993; Wang and others 2010), we might expect crab burrowing to cause substantive litter burial in salt marshes throughout the world with concomitant local and cross-ecosystem consequences.

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