

Crab regulation of cross-ecosystem resource transfer by marine foraging fire ants

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Abstract Permeability of boundaries in biological systems is regulated by biotic and/or abiotic factors. Despite this knowledge, the role of biotic factors in regulating resource transfer across ecosystem boundaries has received little study. Additionally, little is known about how cross-ecosystem resource transfer affects source populations. We used experiments, observations and stable isotopes, to evaluate: (1) the proportion of intertidal-foraging black fire ant (*Solenopsis richteri*) diet derived from marine sources, (2) how black fire ant cross-ecosystem resource transfer is altered by the dominant bioengineer in the intertidal, a burrowing crab (*Neohelice granulata*), (3) the top-

down impact of these terrestrial ants on a marine resource, and (4) the effect of marine resources on recipient black fire ants. We found that more than 85% of the black fire ant diet is derived from marine sources, the number of intertidal foraging ants doubles in the absence of crab burrows, and that ants cause a 50% reduction in intertidal polychaetes. Also, ant mound density is three times greater adjacent to marine systems. This study reveals that cross-ecosystem foraging terrestrial ants can clearly have strong impacts on marine resources. Furthermore, ecosystem engineers that modify and occupy habitat in these ecosystem boundaries can strongly regulate the degree of cross-ecosystem resource transfer and resultant top down impacts.

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Introduction

Ecosystem boundaries, like semi-permeable membranes, regulate the transfer of resources and organisms between adjacent ecosystems (Naiman et al. 1988), and an understanding of ecosystem boundary features that alter permeability is needed to predict these transfers and their effects in recipient communities (Cadenasso et al. 2003; Laurance et al. 2001). It was recently hypothesized that variability of subsidy effects (i.e., resource transfers) across ecosystems can be driven by biological factors, i.e., predation, competition and ecosystem engineering at boundaries (Marczak et al. 2007b). Little data, however, are available to test this hypothesis. In addition, more is known about how resource flow across ecosystem boundaries influences recipient communities (e.g., Carlton and Hodder 2003; Nakano and

Murakami 2001; Paetzold et al. 2005; Sanzone et al. 2003) than source communities (but see Paetzold and Tockner 2005).

When cross-ecosystem resource transfers occur passively (i.e., are donor-controlled) these are termed subsidies and a distinction is often made between these subsidies and the active transfer of resources via mobile consumers foraging cross-ecosystem (Richardson et al. 2010). This distinction may be an arbitrary one because higher densities of active cross-ecosystem foragers in their “home” ecosystem may be supported by resources from the adjacent ecosystem and thus be subsidized. There are many examples of this for a variety of vertebrate and invertebrate terrestrial consumers that forage in the marine intertidal zone, e.g., omnivorous mice (Stapp and Polis 2003), 45 species of mammals (Carlton and Hodder 2003), and various arthropods (Polis and Hurd 1996). These studies found that intertidal/marine subsidies lead to increases in terrestrial consumer populations and that marine-derived resources contributed to adjacent terrestrial food webs (Polis and Hurd 1996). Furthermore, populations and/or supply of the cross-ecosystem resources that are being actively foraged may still be “donor-controlled” particularly in coastal communities where many populations are governed by “supply-side” ecology (Gaines and Roughgarden 1985; Gaines and Bertness 1992).

As many shoreline communities are steep in gradient, short in width and are home to or adjacent to the home of many cross-ecosystem foragers, it is not surprising that the land–water interface has been the focus of many studies of resource transfer across boundaries (Gratton et al. 2008; Polis et al. 1997). The direct effects of the boundary-zone, landscape attributes of shorelines (e.g., perimeter/area ratio), biological (e.g., productivity) and physical processes (e.g., flow, tides and weather), have been shown to regulate the transfer of resources and organisms across ecosystem boundaries (Marczak et al. 2007b; Witman et al. 2004 and references therein). None of these studies, however, have experimentally examined the effects of ecosystem engineers on mobile consumers foraging cross-ecosystem, although these effects are likely to be important given the abundance and widespread distribution of ecosystem engineers on shorelines (Crain and Bertness 2009; Iribarne et al. 1997; Jones et al. 1997; Kristensen 2008).

Salt marshes are dynamic land–water boundaries where resources cross the boundary in both directions (marine ↔ terrestrial) daily (Nixon 1980; Valiela et al. 1978). These environments are also commonly inhabited by ecosystem engineers that alter community processes and structure (Bertness 1985; Gutiérrez et al. 2006; Paramor and Hughes 2004). An observational study in Argentinean marshes suggested that terrestrial black fire ants (*Solenopsis richteri* Forel) that forage on marine polychaetes in intertidal mud-

flats may be limited by the burrowing activities of the crab (*Neohelice granulata* Dana) (Palomo et al. 2003b). This crab is the most abundant macroinvertebrate in Argentinean marshes, reaching densities of up to 75 m⁻² (Botto et al. 2006). It is also a dominant ecosystem engineer and its burrowing activities regulate ecosystem structure, plant growth, plant zonation, mycorrhizal symbioses, nutrient loading, and infaunal zonation and abundance (Alberti et al. 2010; Botto and Iribarne 1999; Botto et al. 2005; Daleo et al. 2007; Escapa et al. 2004; Fanjul et al. 2008; Gutiérrez et al. 2006). The overlap in habitat use between this cross-ecosystem foraging ant, this key ecosystem engineer, and the lack of direct interactions between the two (i.e., predation, competition; E.A. Garcia, personal observation), suggest indirect effects caused by crab bioturbation (for example, burrows trapping water from the high tides thus increasing the moisture content of the surrounding area creating unsuitable conditions for foraging ants, and/or altering the zonation and abundance of potential infaunal ant prey items) may regulate cross-ecosystem transfer in this system.

Here, we used a multi-pronged approach to address the hypotheses that marine prey sources are important to black fire ants, ant predation greatly impacts marine source populations, and terrestrial ant foraging in the intertidal is moderated by the presence of bioturbation caused by the ecosystem engineering activities of burrowing crabs. Additionally, we hypothesized that foraging on and access to marine prey sources has a positive impact on ants. To examine these hypotheses, we (1) analyzed stable isotopes of ants and other invertebrates along the terrestrial–marine interface to elucidate the importance of marine resources for ants, (2) experimentally excluded ants from foraging in the marine zone to examine their top-down effect on the abundance of marine resources, (3) experimentally excluded crabs from intertidal areas to investigate how the presence of crabs and bioturbation in the boundary zone affected cross-ecosystem, biotic transfer of resources by ants, and (4) surveyed the number and dimensions of ant mounds near and far from marine resources while also comparing these results to published data on black fire ant mounds far from marine sources to assess if ants benefited from access to foraging on marine resources.

Materials and methods

Study site

The study was conducted in the Mar Chiquita coastal lagoon (38°00'S, 57°30'W) in central Argentina during the summer months (December–March; temperature range 12–27°C) on unvegetated intertidal mudflats adjacent to

pampas grassland, dominated by the pampas grass *Cortaderia selloana* (Schult. & Schult. f., Asch. & Graebn). Black fire ant (*S. richteri*) mounds are common in this pampas grass habitat. *S. richteri*, native to southeastern Brazil and central-eastern Argentina, is a generalist consumer with an optimal foraging temperature between 21–29°C. A small ledge (approximately 60 cm high) forms the distinct boundary between our intertidal mudflat study site and the grassland habitat. Our study site was also adjacent to a 5-km estuarine channel that connects the lagoon to the sea. The ledge is not present throughout the entire area adjacent to the estuarine channel; instead there are areas of ~100-m-width salt marsh (dominated by the cordgrass *Spartina densiflora* Brongn) separating the grassland from the mudflat. The salt marsh and mudflat areas are also the habitat of the herbivorous–detritivorous burrowing crab, *N. granulata* which produces extensive bioturbated areas where our experimental work was conducted.

Stable isotopes survey

To examine the importance of marine resources to *S. richteri*, we measured the natural abundance of C and N stable isotope values of invertebrates from the three habitat types (terrestrial, salt marsh and intertidal mudflat). Invertebrates in the salt marsh and terrestrial habitats were collected using a handheld blower (with a vacuum kit and 0.5-mm-mesh bag within the end of the blower tube, STIHL® BG 55, USA) over a 1-m² area for 2 min of sampling effort ($n = 3$ samples in each habitat). The intertidal mudflat was selectively sampled for dominant consumers [a total of 10 snails (*Heleobia australis* d'Orbigny), 10 polychaetes (*Laeonereis acuta* Treadwell) and 4 crab (*N. granulata*) claws] which were hand-collected from three random locations within the study area. Finally, 20–30 *S. richteri* were collected per mound from 10 randomly chosen ant mounds in the terrestrial zone (ranging 2–50 m distance from mudflat) of the study site that were ≥ 10 m from each other, in an effort to sample mounds that may be a part of different colonies.

Terrestrial and salt marsh invertebrates were sorted to family, all others collected were sorted to species, and snails and crabs were pulled from their shells. We did not acidify the snail and crab samples to remove inorganic carbonates; instead, all invertebrates collected were rinsed with DI water prior to freezing the samples. All *S. richteri* (whole bodies) collected from an individual mound were pooled and mound samples were analyzed separately. For all other invertebrates except *N. granulata* claws which were analyzed individually, individuals were pooled into family or species groups by habitat type to have enough mass to run the isotope sample. Samples were then frozen, dried at 60°C and homogenized using a mortar and pestle.

All samples were analyzed for $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ at Colorado Plateau Stable Isotope Laboratory of Northern Arizona University, Flagstaff, AZ, USA. Isotopes are reported in the standard notation relative to international standards V-Pee Dee Belemnite for C and atmospheric N₂ for N, where $\delta X(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$ and R is the molar ratio of ^{heavy}X : ^{light}X (Lajtha and Michener 2007).

Ant exclusion experiment

To quantify the top-down impact of black fire ants on polychaetes, three treatments were established on the intertidal mudflat during low tide on 31 January 2008. Treatments ($n = 10$) were: (1) ant exclusion (plastic plate perimeter covered with Tanglefoot®, Contech Enterprises, Canada, secured by U-stakes), (2) exclusion control (plate perimeter without Tanglefoot®), and (3) control (no plastic plate perimeter). Plate perimeters were 26 cm in diameter and were placed on level with the surface of the mudflat. All treatments were randomly placed within the zone just above the low tide water level, where density of polychaete burrows was high and ant predation was concentrated. The experiment ended after 72 h because exclusion treatments became less effective as they got covered by sand and other debris with tidal inundation. One 10 × 10 cm (diameter × depth) PVC core sample was collected from each treatment at the end of the experiment and all samples were sieved through a 0.5-mm sieve. All polychaetes found were counted and identified to species.

Crab exclusion experiment

To examine whether ant foraging and thus the biotic transfer of nutrients across ecosystems was affected by the presence of crabs and/or bioturbation, four treatments were established on the intertidal mudflat on 5 January 2008. Treatments were 1 × 2 m and consisted of: (1) crab exclusion cage without bioturbation, (2) exclusion control (half an exclusion cage consisting of only two sides, a 1- and 2-m side connected at a corner), (3) crab exclusion with bioturbation (exclusion cage with eight artificial burrows), and (4) uncaged control. The purpose of the crab exclusion treatments with and without bioturbation was to separate out the effect of crab presence from the effect of bioturbation on ant foraging because we hypothesize that it is the presence of burrows (i.e., bioturbation) that deters the ants from foraging in those areas and not just the presence of crabs. All treatment plots were in the intertidal mudflat at the base of the pampas grass zone with the long axis perpendicular to the shore. As the study site included a mix of large patches with crab burrows interspersed with smaller patches without burrows; the four treatments were placed as a block within areas with crab burrows because the

intention of this experiment was to examine how the presence of crabs affected ant foraging on marine resources. Individual treatments were ≥ 1 m apart within each block and location of treatments within a block was randomly chosen. Each block, consisting of one replicate of each treatment, was ≥ 10 m apart ($n = 6$ blocks). For caging treatments, plastic caging (1 cm mesh) was buried 10 cm deep by 30 cm tall and was supported by thin rebar stakes with clear plastic sheeting covering the top 10 cm of both the inner and outer part of the cage. The plastic sheeting prevented crabs from being able to climb over the top and the bottom mesh was left alone to allow the natural tidal regime into the cages. Any burrows present in the crab exclusion with and without bioturbation treatments were plugged up with mud from outside the treatment. Then 2 days later in the crab exclusion with bioturbation treatments, artificial burrows were excavated using a soil corer (5 × 10 cm, diameter × depth) with the density and diameter of artificial burrows within the natural range previously recorded for this study site (density range 0–75 m⁻², diameter mean ± SD 5.3 ± 1.8 cm; Botto et al. 2006; Iribarne et al. 1997). The 2-day time period was to allow multiple high tides to pass over the treatment area in order to help homogenize the surface before the artificial burrows were dug. On occasion, crabs were able to burrow into exclusion treatments and any crabs found within exclusions, on our daily visit to the site, were removed and the burrow entrances were plugged up with mud from outside the treatment area. We did not quantify the number and frequency of crabs getting into exclusions as this occurred infrequently. Also, artificial burrows were maintained every 2 days throughout the experiment because high tides would sometimes deposit sediment in the burrows and we wanted to mimic *N. granulata* burrows where the entrances always remain open. To quantify whether ant foraging varied through the summer and/or due to the presence of crabs and/or bioturbated areas, we conducted counts every 4–6 days ($n = 5$) of foraging *S. richteri* in each treatment. Counts were conducted during low tide because *S. richteri* was only observed foraging in the intertidal during sunny (non-rainy) days at low tide. Each count lasted 90-s, which was enough time to scan the entire treatment area and count all ants present. The experiment ran for a total of 27 days not including an initial 2-week period for plots to recover from establishment. At the end of the experiment (day 27), one sediment core sample (5 × 8 cm diameter × depth) was collected from a randomly chosen location within each treatment to measure sediment salinity. The core samples were weighed, dried to constant weight, mixed with a known volume of distilled water, measured by refractometry after 48 h, and then corrected to reflect the original concentration of salt.

Ant mound survey

We surveyed the number of ant mounds “near” (≤ 10 m) and “far” ($10 < x \leq 20$ m) from the estuarine channel to assess whether closer proximity to marine resources was related to more mounds. We choose the 10-m distance as the difference between “near” and “far” mounds based on studies of other *Solenopsis* sp. which found maximum foraging distances of 5 m for one species and 13.3 ± 3.2 m for another (we could not find any published information on maximum foraging distances for *S. richteri* specifically) (Perfecto 1994; Showler et al. 1990). We used 50 × 2 m transects ($n = 10$ per area) during January–February 2007, and recorded the number and dimensions of all *S. richteri* mounds found along each transect. These dimensions were then used to calculate mean “near” and “far” mound volume according to Tschinkel (1993) and overall mound basal area and volume according to Porter et al. (1997).

Statistical analyses

We examined the effect of crabs and crab burrows on foraging ants through time using repeated-measures ANOVA. Ant count data were $\log_{10}(n + 1)$ transformed to meet assumptions. We analyzed salinity at the end of the crab exclusion experiment using a one-way ANOVA. We used Tukey HSD tests for all post hoc pairwise comparisons. Differences in the abundance of polychaetes in ant exclusion treatments were analyzed using a one-way ANOVA. We examined “near” (≤ 10 m) and “far” ($10 < x \leq 20$ m) from the intertidal mudflat *S. richteri* mound abundance and volume differences using a *t* test. All analyses were performed using STATISTICA 8.0 (StatSoft, Tulsa, OK, USA). To quantify the relative proportions of the two main prey source groups (1: terrestrial invertebrates; and 2: intertidal invertebrates) in the diets of *S. richteri*, we used the 2 source, 1 isotope (e.g., $\delta^{13}\text{C}$) IsoError model (for detailed methodology of running the IsoError model, see Phillips et al. 2005; Phillips and Gregg 2001). We used mean ($\pm 1\text{SE}$) $\delta^{13}\text{C}$ for *S. richteri* that were adjusted for diet–tissue fractionation of 0.4‰ for C (Post 2002). Only those invertebrates collected in the stable isotope survey that over the course of the study were observed to be prey of *S. richteri* were used in the IsoError model. The terrestrial invertebrate prey source was the mean (± 1 SE) $\delta^{13}\text{C}$ value of all Hemiptera, Diptera, Coleoptera, and Isopoda collected in the terrestrial habitat. The intertidal invertebrate prey source was the mean (± 1 SE) $\delta^{13}\text{C}$ for all Hemiptera, Diptera, Coleoptera, Isopoda, Amphipoda, and *L. acuta* collected in the intertidal.

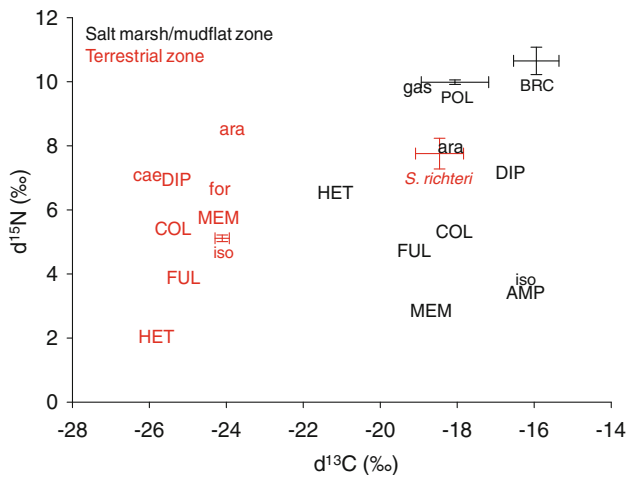


Fig. 1 A dual isotope plot of natural $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for invertebrates collected in the terrestrial zone, and invertebrates collected in the salt marsh and mudflat zones. Abbreviations in all capital letters are the invertebrates that were included as *S. richteri* prey items in the IsoError model. for Formicidae (excluding *S. richteri*), AMP Amphipoda, ara Araneae, COL Coleoptera, DIP Diptera, cae Caelifera, HET Heteroptera, iso Isopoda, FUL Fulgoroidea, POL *L. acuta*, gas *H. australis*, BRC *N. granulata* and MEM Membracidae. For Heteroptera, Fulgoroidea, Membracidae, Araneae, Diptera, Coleoptera, Caelifera, marine Isopoda, Amphipoda, and *H. australis* values shown are a composite of multiple individuals combined in order to have enough mass to run the sample and therefore have no error bars. Multiple composite samples of terrestrial Isopoda (*iso*), *L. acuta* (*POL*), *S. richteri* (mean \pm 1 SE, $n = 2, 2$ and 10 , respectively) and individual *N. granulata* claws (*BRC*) were analyzed (mean \pm 1 SE, $n = 4$)

Results

Stable isotopes survey

$\delta^{13}\text{C}$ isotope values of invertebrates formed two distinct clusters in isotope bi-plot space (Fig. 1). Hemiptera (including Heteroptera, Fulgoroidea and Membracidae), Araneae, Caelifera, Diptera, Coleoptera, Isopoda, and Formicidae (except *S. richteri*) collected in the terrestrial zone had much lower $\delta^{13}\text{C}$ values (mean \pm SE, -24.9 ± 0.3) compared to Hemiptera (including Heteroptera, Fulgoroidea and Membracidae), Araneae, Diptera, Coleoptera, Isopoda, Amphipoda, *H. australis*, *L. acuta*, and *N. granulata* that were collected in the salt marsh and intertidal mudflat zones (mean \pm SE, -18.0 ± 0.5). $\delta^{13}\text{C}$ isotope values of *S. richteri* (mean \pm SE, -18.4 ± 0.4) were within the range of $\delta^{13}\text{C}$ isotope values for invertebrates collected in the marine zones.

The IsoError mixture model was run on the two prey source groups: (1) terrestrial invertebrates ($\delta^{13}\text{C} = -24.9 \pm 0.3$), and (2) intertidal invertebrates ($\delta^{13}\text{C} = -18.0 \pm 0.5$). The model yielded the following prey source proportions for *S. richteri*: (1) terrestrial invertebrates: $11.9 \pm 10.3\%$, and (2) intertidal invertebrates: $88.2 \pm 10.3\%$.

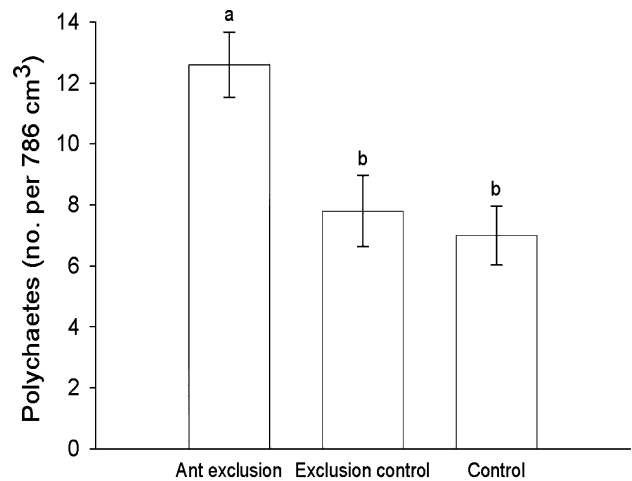


Fig. 2 Number of polychaetes in 786 cm^3 (mean \pm 1 SE, $n = 10$) in the ant exclusion, exclusion control, and control treatments. Different letters above bars indicate significant differences according to Tukey's post hoc test, $p < 0.02$

Ant exclusion experiment

Ant exclusion had a significant effect on mean number of polychaetes found in treatment areas ($F_{2,27} = 8.04$, $p = 0.002$), with almost twice the number of polychaetes where ants were excluded compared to the controls (Fig. 2; Tukey, $p < 0.02$).

Crab exclusion experiment

Overall, there was a significantly greater mean number of *S. richteri* observed foraging within the 2-m^2 crab exclusion without artificial burrow treatment areas during 90-s scans (treatment effect: $F_{3,20} = 17.53$, $p < 0.001$), compared to crab exclusion with artificial burrows and control treatments (Fig. 3; all Tukey's, $p < 0.02$). Additionally, the mean number of foraging ants found in all treatments significantly decreased through time (Fig. 3; time effect: $F_{4,80} = 11.34$, G-G adj. $p < 0.001$) and there was no interaction between time and treatment (time \times treatment effect $F_{12,80} = 1.06$, $p = 0.4$). Finally, sediment salinity (mean \pm SE $67.0 \pm 3.55\text{‰}$) was not significantly different ($F_{3,20} = 0.47$, $p > 0.7$) between treatments at the end of the experiment.

Ant mound survey

The abundance of "near" ($n = 47$) the intertidal mudflat (i.e., marine resources) *S. richteri* mounds was three times greater than "far" mounds ($n = 15$) ($t_{1,18} = 2.43$, $p = 0.03$). Mean mound volume (L) "near" the intertidal mudflat was greater than those found "far" from the channel

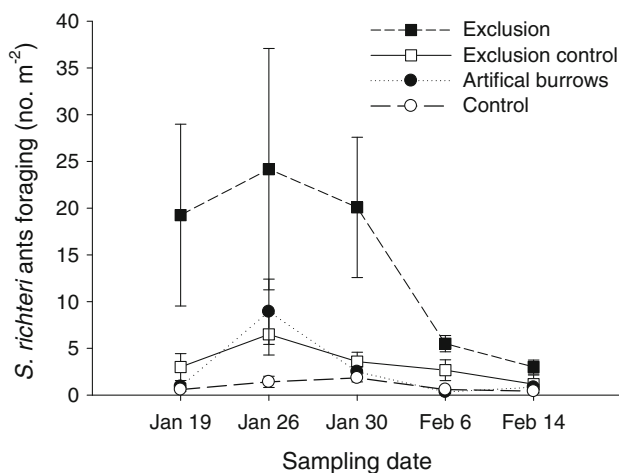


Fig. 3 Black fire ants (*Solenopsis richteri*) observed foraging (number per m² ± 1SE, $n = 6$) during 90-s scans of the four treatments during January and February 2008. Treatments are exclusion (solid squares), exclusion control (open squares), exclusion with artificial burrows (solid circles) and control (open circles). There were significantly more ants foraging in the exclusion treatment at all times compared to all other treatments according to Tukey's post-hoc test, $p < 0.02$. Additionally, the mean number of ants foraging decreased through time ($p < 0.001$)

(mean ± SE, 40.8 ± 5.6 and 29.9 ± 5.7 ; respectively), but this was not significantly different ($t_{1,28} = 1.36$, $p = 0.18$). Finally, the summary overall mean (±SE) dimensions of mounds surveyed were: height (cm) = 26.8 ± 1.37 , width (cm) = 33.8 ± 1.55 , basal area (cm²) = $1,011 \pm 101$ and volume (L) = 19.1 ± 2.25 .

Discussion

Previous work has suggested that mobile organisms that forage cross-ecosystem act as important vectors of resource transfer across ecosystem boundaries increasing habitat permeability (Witman et al. 2004). This study demonstrates that ecosystem engineering by burrowing crabs in the boundary zone affected the intensity of cross-ecosystem foraging and thus biotic transfer of nutrients by reducing the number of cross-ecosystem ant foragers. Furthermore, our stable isotope mixing models revealed that marine prey sources made up a significant proportion of cross-ecosystem foraging ant assimilated diet and our results are the first experimental evidence that these transfers, in turn, reduce the density of a prey source population, as ants had strong negative impacts on intertidal polychaetes.

Additionally, we found that the number of recipient *S. richteri* mounds was greater adjacent to marine resources compared to the number of mounds found farther away potentially indicating a positive effect on recipient ant communities. Tschinkel (1993) found *S. invicta* mound volume to be closely related to colony size. If we assume this to be

true for *S. richteri*, then ant colony size “near” marine food sources was greater, as the number of mounds was greater and there was a similar trend in mean mound volume. Moreover, comparing our results to Porter et al.'s (1997) roadside mound survey, overall mean mound sizes (i.e., height, width, basal area and volume) at our sites were greater than those found at their South American sites and similar to or greater than those at their North American sites where fire ants are introduced, free from their natural predators, and exhibit higher population densities. The increase in the number of mounds near the intertidal could also be due to more competitors or predators in the terrestrial system, better building material, and/or a better thermal environment. We cannot rule out these possibilities but the mound survey data does reveal an interesting pattern that could support the idea that access to, and predation on, marine sources likely benefits *S. richteri*. This is a topic that needs further investigation as it has important management implications such that colonies benefiting from access to marine resources may be the best targets for pesticide or biocontrol given that this species and the closely related *S. invicta* are causing major environmental and economic impacts in countries where they have been introduced, and are often found near intertidal areas (Morrison et al. 2004).

Most studies examining marine/terrestrial cross-ecosystem transfer of resources have focused on identifying which terrestrial organisms forage in the intertidal and how this impacts recipient populations. None of these studies have experimentally investigated potential impacts on source populations (but see Paetzold and Tockner 2005). Here, we used exclusion experiments to show that terrestrial ants reduced polychaete densities by half. A possible alternate hypothesis for these results is that ant presence caused the polychaetes to burrow deeper. However, previous work on this species of polychaete at this site found that of the over 2,400 polychaete burrows surveyed, ~92% of burrows were located within the top 10 cm of the surface (Palomo and Iribarne 2000). Thus, our 10-cm core samples were representative of polychaete density in those areas and, therefore, predation by ants is the most likely explanation of our results. We also found further evidence supporting that the change in polychaete density in the experiment was due to predation versus a change in polychaete behavior as we witnessed 30 *S. richteri* predation events over the course of our observations of ant foraging in the crab exclusion experiment: 20 on polychaetes and 10 on various intertidal invertebrates (e.g., dead crabs and amphipods). Furthermore, Palomo et al. (2003b) observed a 66% attack rate of black fire ants on polychaetes in their study located at the same study site. This reduction of a source population (polychaetes) by half (whether through predation or change in behavior) observed after only 72 h suggests intertidal foraging ants may also have a huge impact on the intertidal

community over longer time periods. This high predation rate likely has important consequences for the system since (1) polychaetes are also an important food source for fishes (Martinetto et al. 2005) and migratory birds (Palomo et al. 2003a) and (2), as a result of their feeding activities, they promote sediment stability (Palomo and Iribarne 2000). These experimental and observational results are in line with the isotope mixing model which included polychaete stable isotope values as part of the marine prey source category that was found to make up the majority proportion of *S. richteri* assimilated diet. This compares starkly with published inland isotope values ($\delta^{13}\text{C} \sim -23$; LeBrun et al. 2007) that show *Solenopsis* sp. ants derive resources from terrestrial sources.

While evidence of strong cross-ecosystem linkages initiated by biotic agents is not uncommon (e.g., Marczak et al. 2007b; Polis et al. 1997; Polis and Hurd 1996; Stapp and Polis 2003), studies of boundary attributes regulating these fluxes are rare (but see Greenwood and McIntosh 2008; Marczak et al. 2007a). Ecosystem engineers affect a variety of ecosystem processes (e.g., sediment processing, Flecker 1996; nutrient export, Moore et al. 2007) that often indirectly result in positive and/or negative effects on other species (Jones et al. 1994, 1997). The intertidal boundary zone in our study is the dominant habitat for the burrowing crab *N. granulata*, a well-documented ecosystem engineer (Botto et al. 2005; Fanjul et al. 2008; Gutiérrez et al. 2006). Palomo et al. (2003b) found that *S. richteri* distributions never overlapped with that of the burrowing crab. Our experimental results go further to show that crab burrowing activities negatively affected ant foraging in the intertidal. *N. granulata* burrows strongly affect sediment chemistry (i.e., salinity, redox potential, dissolved inorganic nitrogen), and their impact increases with depth, but sediment surface is typically oxic whether burrows are present or not (Fanjul et al. 2007). Coupling this information with the fact that ants walk on the sediment surface (most of the time) or dig superficial tunnels, the impact of crabs on ants does not seem to be mediated by altered sediment chemistry. Burrow openings might also affect ants by reducing the available surface area to walk, but given the very small size of ants and not extremely high burrow densities, this does not seem a likely mechanism. Crabs can also affect polychaetes (and thus, ants) and, indeed, it has been reported that more polychaetes are commonly found within crab beds than outside (Botto and Iribarne 1999). However, based on that pattern, we would expect increased ant activity when burrows are present, which is the exact opposite pattern to what we found in this study. The most likely mechanism by which crabs exclude ants may be related to the fact that burrows retain water from previous high tides and thus create large areas that remain moist/humid well after receding tides—environmental conditions that are unsuitable for ant forag-

ing. Evidence supporting this proposed mechanism is provided by the observation that ants were only ever observed foraging in the intertidal during low tides on sunny, hot days which dried out the sediment surface layer of the mudflat. Furthermore, previous studies have found higher water content (Botto and Iribarne 2000; Escapa et al. 2004) and lower permeability (Botto and Iribarne 2000) within *N. granulata* beds compared to outside crab beds at the same location as this current study. Additional experimentation could better explicitly test this mechanism by experimentally altering the moisture content of the mudflat and observing resultant impacts on ant foraging.

To our knowledge, there is no other evidence of ecosystem engineers mediating the transfer of resources between ecosystems by another species. However, this is probably an overlooked rather than a rare phenomenon, as the same patterns have been observed in other SW Atlantic estuaries (Bahía Samborombón, 36°18'31''S, 56°45'56''W; Bahía Anegada, 40°32'38''S, 62°17'46''W; J. Alberti, personal observation). There is a lot of potential opportunity to further examine this phenomenon especially considering the fact that biotic agents commonly promote the flux of resources between land and water (Gratton et al. 2008; Polis et al. 1997), and that ecosystem engineers are commonly found on shorelines (Crain and Bertness 2009; Iribarne et al. 1997; Kristensen 2008).

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