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ORIGINAL PAPER

Exploitation of a marine subsidy by a terrestrial invader

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Abstract Intertidal environments receive energy from marine ecosystems in the form of marine wrack, which makes up the base of a food web that includes both intertidal and terrestrial consumers. Consumption of wrack by terrestrial consumers can elevate their abundance and alter how they interact with organisms in adjacent terrestrial environments. Although rarely documented, terrestrial invaders may exploit marine wrack subsides and potentially disrupt intertidal and terrestrial food webs. Here, we examine consumption of marine wrack resources by the introduced Argentine ant (*Linepithema humile*), which occurs commonly on beaches in southern California. In controlled trials the Argentine ant readily scavenged arthropod detritivores (amphipods and flies) abundant in wrack. In spite of obvious risks (e.g., exposure to tides, desiccation, thermal stress) associated with intertidal foraging, Argentine ant activity on beaches was comparable to that in spatially-paired, scrub environments. Foraging on beaches allowed ants to access higher densities of arthropod prey and carrion compared to those found in scrub environments. Stable isotope analyses provide evidence for extensive assimilation of marine-derived resources. Values of δ^{15}N and δ^{13}C for the Argentine ant were higher at beach sites than at scrub sites, and Argentine ant δ^{15}N values broadly overlapped those of intertidal consumers at beach sites. Although ants are known to forage in intertidal environments, this study provides a novel example of an introduced ant species exploiting a cross-boundary subsidy.

Keywords Invasion · *Linepithema humile* · Resource subsidy · Scavenging · Stable isotope analysis

Introduction

Predicting how introduced species impact ecosystems remains a central challenge in the field of invasion biology (Ricciardi et al. 2013). Introduced species experience abiotic and biotic factors that qualitatively and quantitatively differ from those in their native range, and these disparities can both limit and enhance invasion success. Host shifts and novel partnerships (Ricciardi et al. 2013; Bezemer et al. 2014; Traveset and Richardson 2014), for example, represent novel extensions of niche space that contribute to invasion success in ways that can be difficult to anticipate. Introduced species may also expand into habitats not found in their native range; such shifts in foraging behavior can increase invasion success when they enhance reproductive success or survival.

Behaviorally dominant, introduced ants disrupt ecosystems (Holway et al. 2002; Lach and

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Hooper-Bui 2010; Cameron et al. 2016). Ant invasions are a growing concern in that most species with a history of invasion continue to spread into new regions while other species are emerging as potential invaders (Wong et al. 2023). Given that ants broadly interact with other organisms, it is perhaps unsurprising that novel species interactions contribute to the success of ant invasions (Helms and Vinson 2002; O'Dowd et al. 2003; Wilder et al. 2011). Invasion success may also increase when introduced ants expand into novel habitats (i.e., habitats not present in the native range), but such cases are less well studied.

In this study we consider intertidal foraging by the introduced Argentine ant (*Linepithema humile*). This niche axis may be unique to introduced populations of this species, and access to marine-derived resources could enhance invasion success. Intertidal foraging by ants is not without precedent (Yensen et al. 1980; Nielsen 1997; Garcia et al. 2011; Piovia-Scott et al. 2011; Loken and Oliver 2016), but exploitation of marine-derived resources by introduced ants remains surprisingly underappreciated despite reports of potential impacts (Allen et al. 2001; Wetterer & Lombard 2010). Moreover, intertidal foraging by native ant species can elevate colony size (Garcia et al. 2011) and alter food web interactions in adjacent terrestrial environments (Piovia-Scott et al. 2011). Exploitation of marine-derived resources by introduced ant species could thus magnify invasion impacts, and an improved understanding of this phenomenon seems warranted.

Here, we examine the Argentine ant's exploitation of resources from marine wrack, which consists of organic matter of marine origin (e.g., algae, surf grass, and driftwood). Wrack supports a food web that includes both intertidal and terrestrial consumers (Spiller et al. 2010; Piovia-Scott et al. 2011). We first performed a cafeteria experiment to determine what components of marine wrack are recognized as food by the Argentine ant. Second, we compared spatially-paired coastal (beach) and inland (scrub) sites with respect to Argentine ant activity and arthropod biomass. Lastly, we used stable isotope analyses to assess the extent to which the Argentine ant assimilates marine resources by comparing the δ^{15}N and δ^{13}C values between Argentine ant workers collected at coastal versus inland sites and among other organisms at each type of site. This study revealed that an abundant and disruptive terrestrial invader readily forages in intertidal environments (Fig. 1) where it exploits and likely benefits from a cross-boundary, resource subsidy.

Methods

Cafeteria experiments

We performed cafeteria experiments (Houadria et al. 2016; Tsang et al. 2020) to determine what components of marine wrack were recognized as food by the Argentine ant. In July 2021 we collected common wrack organisms (Dugan et al. 2003; Wooldridge et al. 2016) from the sandy beach at the Scripps Coastal Reserve (32.876018, -117.251247), San Diego Co., CA: giant kelp (*Macrocystis pyrifera* (Laminariaceae)), surf grass (*Phyllospadix* sp. (Zosteraceae)), seaweed flies (*Fucellia* sp. (Diptera: Anthomyiidae)), and sandhoppers (*Megalorchestia* sp. (Amphipoda: Talitridae)). After collection these

Fig. 1 Argentine ant workers on coralline algae in intertidal marine wrack at Tourmaline Beach, San Diego County, California. Photo by Craig Chaddock

organisms were immediately stored in a cooler with ice packs and then transferred to a freezer at 0 °C in the laboratory within 4 h of collection. We tested the attractiveness of each type of organism to naïve, free-living colonies of the Argentine ant at Rose Canyon Open Space Park (32.850822, -117.231166), which is c. 3 km from the coast. We established a linear transect of 20 bait stations in riparian vegetation and parallel to Rose Creek; bait stations were at least 10 m apart.

We conducted two different cafeteria experiments. First, we measured the amount of each resource (kelp, surf grass, amphipods, or seaweed flies) removed from open centrifuge tubes placed on level ground after 60 min. Each bait station received one resource type on a given day and all four types over the course of four, consecutive days in a randomly determined order. Individual baits consisted of five seaweed flies, five sand hoppers, ten pieces (3 × 3 mm) of kelp, or ten pieces (1 × 5 mm) of surf grass. In the second experiment, we compared the time it took ants to remove either five seaweed flies or five sand hoppers from centrifuge tubes. In this trial individual bait stations received each bait type over the course of two days with the order determined at random. Both experiments used dead amphipods and flies. Talitrid amphipods and adult flies can easily evade capture by ants while alive, and these resources are thus presumably obtained by scavenging rather than predation (Holway and Cameron 2021). Ants may prey on fly larvae and pupae as well as other wrack arthropods with limited mobility.

Ant activity and arthropod biomass

We used pitfall traps to compare Argentine ant activity and arthropod biomass (potential prey and carrion) at eight pairs of coastal (beach) and inland (scrub) sites distributed along a c. 30-km stretch of coastal San Diego Co., CA (Table 1). All beach sites were ungroomed, and marine wrack is present all year (Wooldridge et al. 2016). Scrub sites were 1–3 km from the coast and supported native perennial vegetation, primarily California sagebrush (*Artemisia californica*), California buckwheat (*Eriogonum fasciculatum*), chamise (*Adenostoma fasciculatum*), laurel sumac (*Malosma laurina*), and lemonade berry (*Rhus integrifolia*). We sampled sites in spring (April–May 2023), summer (July–August 2022), and fall (October–November 2022). For statistical comparisons, data were pooled across the three sampling rounds at each site.

At each site and season, we deployed five traps in a linear transect with traps separated by at least 10 m. Beach transects were oriented parallel with the ocean at about the high-tide line. Each trap consisted of a 50-ml centrifuge tube containing 30 ml of salty, soapy water (as in Hanna et al. 2015a, b). Traps were buried in the sand (beach sites) or soil (scrub sites) with the rim of each tube level with the substrate surface. We left traps in the ground for 8–14 h between dusk and dawn. After traps were retrieved, contents were double strained through two sieves to collect all invertebrates present. Invertebrates were then desiccated in a drying oven for a minimum of 2 d at 55–60˚C until completely dry. Non-ant arthropod biomass (ants excluded) was weighed; Argentine ant workers were counted. At each site biomass and activity measures were converted to mg / trap / h and workers / trap / h, respectively. Arthropod biomass represents potential energy available as prey and carrion (as in Spiller

Table 1 Names and locations of spatially-paired beach and scrub sites where we estimated arthropod biomass and ant activity and collected samples for stable isotope analysis. Spatial pairs are on the same row

Beach sites	Scrub sites
Tourmaline Beach (32.80534, -117.26253)	Kate Sessions Park (32.81233, -117.23829)
Windansea Beach (32.82625, -117.27970)	La Jolla Natural Park (32.84320, -117.2628)
Scripps Pier (32.86625, -117.25416)	Skeleton Canyon (32.86630, -117.24739)
Scripps Coastal Reserve (32.87689, -117.25133)	UC San Diego (32.88665, -117.23607)
Torrey Pines State Beach (32.94804, -117.26471)	Crest Canyon (32.95250, -117.25459)
Fletcher Cove (32.99115, -117.27439)	San Dieguito Park (32.99911, -117.23510)
Swami's Beach (33.03468, -117.29246)	Manchester Res. (33.03030, -117.24547)
Moonlight Beach (33.04838, -117.29831)	Oak Crest Park (33.04511, -117.26619)

et al. 2010), whereas the number of ants captured provides a measure of ground foraging activity.

Stable-isotope analysis

To estimate the extent to which the Argentine ant assimilates marine-derived resources in intertidal environments, we used stable-isotope analyses (Spiller et al. 2010). Values of $\delta^{15}N$ and $\delta^{13}C$ are typically higher in marine systems compared to terrestrial systems and can be used to assess assimilation of marine-derived resources by terrestrial consumers (Hobson 1999; Stapp & Polis 2003; Paetzold et al. 2008). Samples were collected at the same pairs of beach and scrub sites used in *Ant activity and arthropod biomass* (Table 1). At beach sites we collected giant kelp (*Macrocystis pyrifera*) (Laminariaceae)), surf grass (*Phyllospadix* sp. (Zosteraceae)), seaweed flies (*Fucellia* sp. (Diptera: Anthomyiidae), sandhoppers (*Megalorchestia* sp. (Amphipoda: Talitridae)), and beetles (Coleoptera). At scrub sites we collected California buckwheat (*Eriogonum fasciculatum*), lemonade berry (*Rhus integrifolia*), laurel sumac (*Malosma laurina*), isopods (*Armadillidium vulgare*), spiders (Araneae), silverfish (Thysanura), and darkling beetles (*Eleodes* spp. (Coleoptera: Tenebrionidae)). At all sites we collected a minimum of 40 Argentine ant workers during each sampling round. Specimens were collected either by hand, aspirator, or net and immediately stored in a cooler with ice packs and transferred to a freezer at 0 °C in the laboratory within 4 h of collection. We collected samples for stable isotope analysis during two seasons: summer (July–August 2022) and fall (October–November 2022). In preparation for stable isotope analysis, we removed gasters from ant workers (Tillberg et al. 2006). All samples were then desiccated in a drying oven for a minimum of 2 d at 55–60˚C until completely dry. A homogenized mass of 0.6–1.1 mg of each arthropod sample or 2.6–3.3 mg of each plant or algal sample was packed into 5 × 9 mm tin capsules and sent to the University of California Santa Cruz Stable Isotope Facility (https://isotope.ucsc.edu/sil). This facility uses a CE Instruments NC2500 elemental analyzer coupled to a Thermo Scientific DELTAplus XP isotope ratio mass spectrometer via a Thermo-Scientific Conflo III. For statistical comparisons, we calculated means for each organism at each site across the two sampling rounds and used these time-averaged, site means as data points in all analyses.

Statistical analysis

We performed all statistical analyses and prepared all figures in R (R Core Team 2021).

Results

Cafeteria experiments

The Argentine ant readily scavenged dead arthropods abundant in wrack but did not remove pieces of giant kelp or surf grass. In the first cafeteria experiment the mean (± SE) proportion of each type of marine resource that remained in bait stations after 60 min was as follows: 0.00 ± 0.00 (talitrid amphipod), 0.05 ± 0.05 (seaweed fly), 0.99 ± 0.05 (sea grass), and 1.00 ± 0.00 (giant kelp). In the second cafeteria experiment the Argentine ant removed talitrid amphipods from bait stations more quickly (13.8 ± 1.7 min) than seaweed flies (20.4 ± 2.2 min; paired *t*-test: $t_9 = 3.061$, $P = 0.014$). Although we did not systematically monitor resources after ants removed them from centrifuge tubes, amphipods, and flies were carried away from bait stations and presumably transported to nearby nests.

Ant activity and arthropod biomass

The number of Argentine ant workers captured in pitfall traps did not differ between beach and scrub sites (Fig. 2A; paired *t*-test: $t_7 = 0.074$, $P = 0.94$). Non-ant arthropod biomass was higher at beach sites compared to scrub sites (Fig. 2B; paired *t*-test: $t_7 = 5.35$, $P = 0.001$). This difference was driven by talitrid amphipods, which were the most abundant arthropod taxon present (89.5% (2136/2386) of all individuals) in pitfall trap samples from beach sites.

Stable-isotope analysis: Organisms collected at beach and scrub sites formed distinct clusters with respect to variation in values of $\delta^{15}N$ versus $\delta^{13}C$ (Fig. 3). The Argentine ant was a member of either group depending on which type of site it was collected. At beach sites, the Argentine ant overlapped broadly with intertidal consumers with respect to its $\delta^{15}N$ values (Fig. 3). Values of $\delta^{15}N$ and $\delta^{13}C$ for

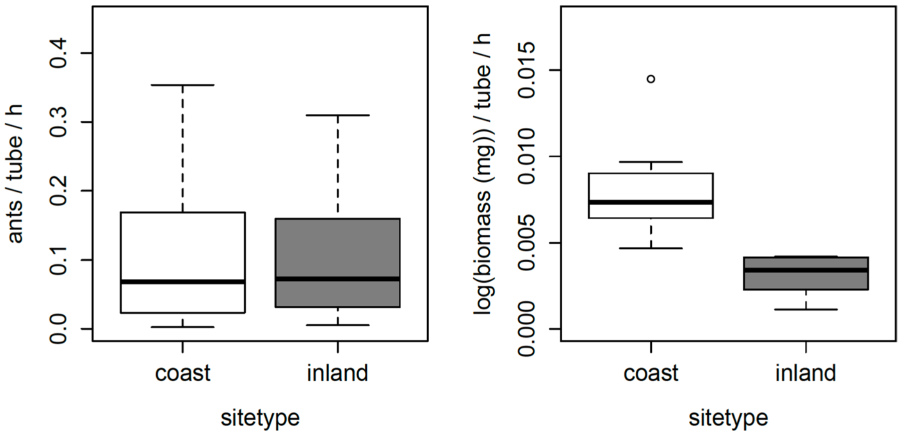

Fig. 2 **A** Argentine ant activity and **B** arthropod biomass at eight spatially-paired coastal (beach) and inland (scrub) sites. Box plots show median (bold line), first and third quartiles, and minimum and maximum; unfilled circles represent outliers

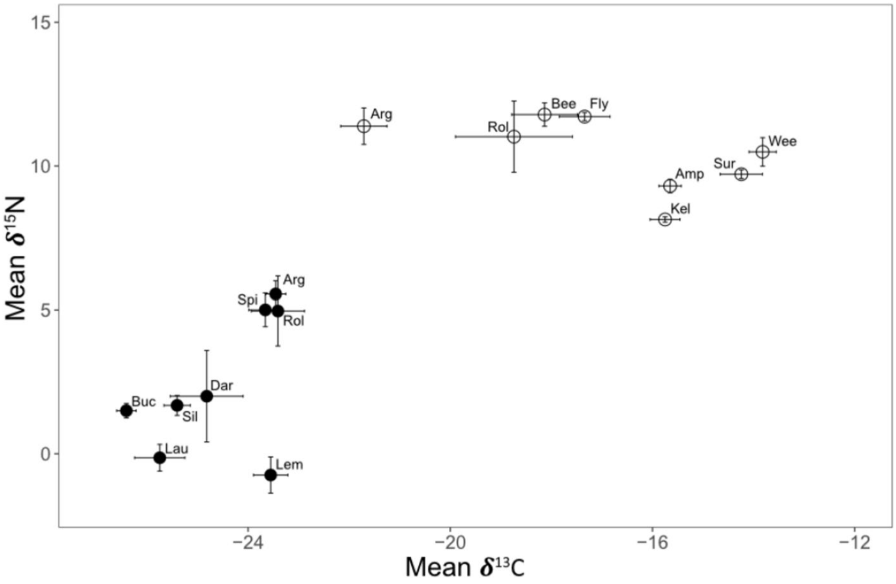

Fig. 3 Natural values of δ^{13}C and δ^{15}N of plants, algae, and arthropods collected at eight pairs of coastal (beach; open symbols) and inland (scrub; closed symbols) sites (Table 1). For each organism at each type of site, δ^{13}C and δ^{15}N values are averaged across summer and fall sampling periods. Central points indicate joint means; lines show standard errors. Code names are as follows: Buc = California buckwheat (*Eriogonum fasciculatum*), Lau = laurel sumac (*Malosma laurina*), Lem = lemonade berry (*Rhus integrifolia*), Sil = silverfish (Thysanura), Dar = darkling beetles (*Eleodes* spp.), Rol = isopods (*Armadillidium vulgare*), Spi = spiders (Araneae), Arg = Argentine ant (*Linepithema humile*), Wee = weevils (Coleoptera), Fly = seaweed flies (*Fucellia* sp.), Amp = sandhoppers (*Megalorchestia* sp.), Kel = giant kelp (*Macrocystis pyrifera*), Sur = surf grass (*Phyllospadix* sp.)

the Argentine ant were higher at coastal sites compared to at inland sites: δ^{15}N (paired *t*-test: $t_7 = 6.39$, $P = 0.00037$; Fig. 4A) and δ^{13}C (paired *t*-test: $t_7 = = 3.83$, $P = 0.0065$; Fig. 4B).

Discussion

The Argentine ant, a widespread invader of terrestrial ecosystems in coastal southern California (Hanna et al. 2015a; Naughton et al. 2021; Menke and Holway 2020; Achury et al. 2021), commonly forages in intertidal beach environments. Two lines

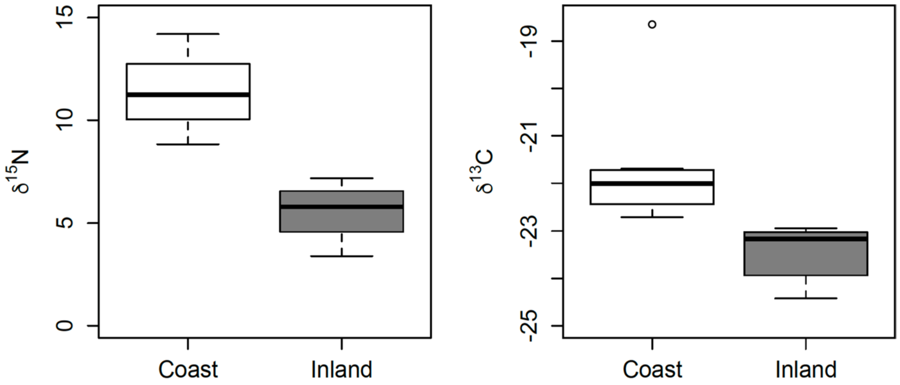

Fig. 4 Natural values of (A) δ^{15}N and (B) δ^{13}C for the Argentine ant at coastal (beach) and inland (scrub) sites. Box plots show median (bold line), first and third quartiles, and minimum and maximum; unfilled circles represent outliers

of evidence support the idea that this invader extensively assimilates marine-derived resources. First, the Argentine ant readily scavenged talitrid amphipods and seaweed flies, which are abundant in marine wrack (Dugan et al. 2003). Second, Argentine ant δ^{15}N values broadly overlapped those of marine consumers at beach sites. Despite obvious risks associated with intertidal foraging, Argentine ant activity in beach and scrub habitats did not differ. Presumed costs of beach foraging may be outweighed by access to high densities of arthropod carrion and prey available in these intertidal environments.

Although previous studies of invertebrates in marine wrack on southern California beaches do not mention the Argentine ant (Dugan et al. 2003; Wooldridge et al. 2016), our study found that the Argentine ant can be common in such habitats (Fig. 1). This apparent discrepancy likely resulted from our selection of sites based in part on Argentine ant occurrence and the lack of winter sampling (when the Argentine ant may be less abundant on beaches) in the present study. Most of our coastal sites were on narrow beaches below coastal bluffs. These environments concentrate wrack and provide ants with nest sites above the high tide line that are situated in proximity to wrack resources. Although the Argentine ant nests above the high tide line, they readily forage in the intertidal portions of beaches (see also Garcia et al. 2011; Piovia-Scott et al. 2011). In this region the Argentine ant appears largely absent from more gradually sloping beaches where marine wrack resources are dispersed across expanses of sand. Large areas of sand are unsuitable for this species given that physiological limitations preclude them from invading dry, well-drained soils (Menke and Holway 2006). Additional surveys of beach environments could clarify factors that encourage invasion by ants.

Cafeteria experiments and stable isotope analyses provide evidence that the Argentine ant exploited and assimilated resources from marine wrack. Unlike other wrack organisms, which are largely restricted to the intertidal, Argentine ant colonies simultaneously forage in the intertidal and in adjacent upland environments. Presumed inputs of terrestrial resources to ant colonies thus complicate interpretation of stable isotope comparisons between the Argentine ant and other wrack feeding organisms. The Argentine ant's values of δ^{13}C, in particular, may be influenced by nectar and honeydew obtained from adjacent terrestrial environments; marine wrack is presumably deficient in nutritionally-accessible carbohydrates (e.g., sugars).

The exploitation of marine-derived resources by the Argentine ant raises questions about ecological effects that might result from this phenomenon. Intertidal foraging by the Argentine ant could affect food web interactions in adjacent terrestrial environments. Piovia-Scott et al. (2011), for example, found that when native carpenter ants fed on intertidal wrack arthropods, herbivory increased on plants in adjacent terrestrial environments because ants shifted their foraging away from plants. In the present system marine-derived resources could increase colony size (Garcia et al. 2011) and carbohydrate demand (Vidal et al. 2018). These responses might in turn increase floral visitation (to obtain nectar) by ants and disrupt plant-pollinator interactions (LeVan et al. 2014, Hanna et al. 2015a, b) in terrestrial environments adjacent to beaches. Intertidal foraging by ants may also result in the transport of marine-derived nutrients inland (Paetzold et al. 2008). Although the spatial scale of such nutrient transfer might be modest compared to that generated by more mobile consumers, introduced populations of the Argentine ant exhibit seminomadic behavior (Markin 1970) and form expansive supercolonies (Thomas et al. 2006). The Argentine ant might thus transfer marine-derived resources farther inland compared to native ants.

While the colonization of novel environments is an inherent part of the invasion process, this study provides a potential example of an introduced species occupying a novel type of habitat. Intertidal foraging by the Argentine ant has not been reported from its native range, which mostly lies inland (Wild 2004). In its native Argentina, however, this species does commonly forage along riverbanks that provide access to resources of aquatic origin but that are unsuitable for nesting (Le Brun et al. 2007). Riverbank foraging also occurs in other ant species (Paetzhold et al. 2006), and intertidal foraging on beaches provides another example of this type of behavioral plasticity. Given the tendency for behaviorally dominant, introduced ants to attain high densities and to exhibit omnivory (Holway et al. 2002; Lach and Hooper-Bui 2010), intertidal foraging by introduced ants could be common and seems worthy of further investigation.

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Data availability The datasets generated used in this study will be uploaded to Dryad following confirmation that this manuscript has been accepted for publication.

Declarations

Competing interest The authors have not disclosed any competing interests.

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