Boring crustaceans shape the land–sea interface in brackish Caribbean mangroves

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Citation: Davidson, T. M., G. M. Ruiz, and M. E. Torchin. 2016. Boring crustaceans shape the land–sea interface in brackish Caribbean mangroves. Ecosphere 7(8):e01430. 10.1002/ecs2.1430

Abstract. Consumer effects on the structure and extent of habitat-forming foundation species such as trees and coral reefs are well known, but the role of non-consumer interactions is less studied. Red mangroves are major foundation species at the land–sea interface, creating critical habitat in the tropics and subtropics. The complex aerial roots of mangroves (Rhizophora mangle) provide structural support to the tree and support diverse marine biota including boring isopods (Sphaeroma terebrans). These isopods frequently bore into root tips of mangroves causing atrophy, which can alter the structure and extent of mangrove habitat. We conducted a large-scale isopod exclusion experiment across 18° of latitude at eight locations from Panama to Florida to test how isopods affect mangrove root structure and anchorage across a broad geographic range. We hypothesized that excluding isopods would increase root growth rates, morphological complexity, and anchorage compared to roots exposed to isopods. After one year, mangrove roots protected from boring isopods with cages increased growth by 2.5–19 times and exhibited a more complex morphology compared to uncaged controls. Further, 15% of caged roots became anchored in the sediment compared to none of the uncaged isopod-inhabited roots. This suggests that these isopods, which are native to the Indo-Pacific, are a major, widespread structuring agent of mangrove root habitat in the Caribbean and Florida, potentially limiting mangrove encroachment into estuarine waters.

Key words: boring isopod; ecosystem engineering; ecotone; habitat edge; introduced species; land–sea interface; marginal habitat; non-consumer interactions; non-herbivorous interactions; plant–animal interactions; Rhizophora mangle; Sphaeroma terebrans.

INTRODUCTION

Biotic interactions can play a major role in altering the structure and extent of habitat-forming foundation species (Décamps and Naiman 1990, Silliman et al. 2013, Sarneel et al. 2014). Consumer interactions, in particular, strongly influence foundation species (Silliman et al. 2013) and are widespread, occurring in diverse environments across different taxa. For example, elephants maintain the extent of woodlands and savannahs (Laws 1970, Dublin et al. 1990), aquatic herbivores limit the expansion of riparian vegetation into open water (Sarneel et al. 2014), and pocket gopher root herbivory inhibits the encroachment of Aspen forests in meadows (Cantor and Whitham 1989). Such effects are particularly apparent in intertidal marine habitats where the lower limit of some marine foundation species is often set by consumers that create
defined intertidal zonation (Paine 1966, Harley 2003, He et al. 2015). However, the role of non-consumptive processes in structuring marine habitat-forming species has received far less attention.

Mangroves form a critical habitat between land and sea along sheltered tropical and subtropical shorelines. Mangroves are highly productive and provide myriad ecosystem services (including coastal protection and stabilization, sewage treatment, and nursery for fisheries species) and products (Rönnbäck 1999, Saenger 2002). Red mangroves (*Rhizophora* spp.) are especially common at the land–sea margin where they form a complex habitat composed of dense thickets of rapidly growing aerial roots (up to 9 mm a day; Gill and Tomlinson 1971). The dense thickets of roots grow out from the mangroves on the banks or down from overhanging branches and often create a complex habitat. Red mangrove root systems provide an important hard substratum that is colonized by diverse communities of root epibionts (Sutherland 1980, Ellison and Farnsworth 1992) and mobile epifauna such as fish and crustaceans (Thayer et al. 1987, Primavera 1998, Nagelkerken et al. 2008), including commercially fished species.

The biota that inhabit mangroves can greatly affect mangrove growth, architecture, and zonation (Smith 1987, Perry 1988, Feller 2002, Cannicci et al. 2008). For example, herbivory by wood-boring insects alters tree architecture and the distribution of canopy gaps (Feller 2002), leaf-eating insects can change canopy structure through mass defoliation (Anderson and Lee 1995), and crab herbivory may limit the distribution of mangrove propagules (Smith 1987, but see Sousa and Mitchell 1999). Boring sphaeromatid isopods are particularly important in structuring the root habitat of the seaward brackish mangroves. Sphaeromatid isopods burrow into mangrove root tips where they live and filter feed. They do not feed on plant tissue, but the boring damage reduces root growth (Perry 1988, Brooks and Bell 2002) and eventually causes root atrophy and breakage (Rehm and Humm 1973). However, isopod boring can also promote the creation of new root tips (Simberloff et al. 1978, Brooks and Bell 2002). Some studies suggest that the effects of boring by sphaeromatid isopods may scale up to cause the toppling of trees (Rehm and Humm 1973), alter tree-level morphology (Davidson et al. 2014), or modify tree and root architecture (Simberloff et al. 1978, Brooks and Bell 2002).

The boring isopod *Sphaeroma terebrans* occurs in high abundances in brackish mangroves from Brazil to Florida (Kensley and Schotte 1989) but is considered to be introduced from the Indo-Pacific (Carlton and Ruckelshaus 1997). Despite being widespread, thus far, studies have only descriptively (or correlatively) measured the effects of *S. terebrans* (Rehm and Humm 1973, Simberloff et al. 1978, Santhakumari 1991, Davidson et al. 2014). Since isopod boring truncates roots and may prevent root anchorage in sediment (Rehm and Humm 1973), *S. terebrans* could alter mangrove root habitat for marine species and potentially limit the seaward extent of brackish Caribbean and Florida mangroves. However, no studies have examined the ecological effects of *S. terebrans* in mangroves from the Caribbean or experimentally excluded isopods to determine whether isopods can prevent root anchorage and thus limit the lower extent of mangroves.

To determine how boring isopods affect mangrove root growth, morphology, and ability to anchor into sediment, we conducted an isopod exclusion experiment at eight sites across 18° of latitude. We hypothesized that roots protected from isopods would (1) grow faster, (2) develop more complex morphology (longer maximum root lengths, more root tips, longer root tip lengths, more root spreading nodes), and (3) anchor into the sediment more frequently compared to roots exposed to isopods. We conducted a series of standardized experiments across latitude to examine the variation in response to boring throughout the large geographic range of the introduced isopod. Combined, the results from this experiment reveal how non-consumer interactions of a small but widespread introduced marine invertebrate can alter the structure and extent of critical mangrove habitat from Florida to Central America.

**Methods**

**Site characteristics**

We conducted a broad-scale experiment replicated across 2000 km to evaluate the effects of boring isopods (*S. terebrans*) on the growth and
Fig. 1. Map of mangrove study sites (A) in Florida (3 sites), Belize (2), and Panama (3). The abbreviations for each site are included in parentheses adjacent to each site name. (B) A photograph of a typical brackish red mangrove site (BC, Panama). The seaward edge of this creek is lined with overhanging roots. The creek is approximately 10 m wide. (C) A section of root bored by isopods (~40 cm long), close-up of an isopod-bored root tip, and the isopod borer, *Sphaeroma terebrans* (~8 mm long).
morphology of red mangrove (*Rhizophora mangle*) aerial root systems in the Caribbean (Panama and Belize) and Florida (Fig. 1). Experiments were conducted in the free-hanging aerial roots along the seaward edge of brackish mangrove creeks and channels (mean ± SD salinity: 25.8 ± 3.1, range: 21.5–32). Experimental sites were defined as 100–300 m stretches of red mangrove shoreline separated from other sites by many kilometers (except for two sites in Belize that were separated by 1.6 km). The locations of these sites were selected based on accessibility by boat or kayak, presence of brackish salinities, and presence of populations of boring isopods (*S. terebrans*). The shoreline was dominated by red mangroves; only the occasional black mangrove (*Avicennia germinans*) or white mangrove (*Laguncularia racemosa*) was observed. The tidal range at the sites varied from 1.06 m in Florida to 0.19 m in Belize. Additional details on the physical characteristics of the sites are included in Appendix S1: Table S1.

**Study species**

*Sphaeroma terebrans* is broadly distributed throughout brackish waters along the Atlantic coast of the Americas from Brazil to Virginia (USA), West and East Africa, India, and in the western Pacific from Australia to Taiwan (Harrison and Holdich 1984, Kensley and Schotte 1989, Davidson et al. 2014). *Sphaeroma terebrans* is thought to be introduced to the Caribbean and Florida from the Indo-Pacific (Carlton and Ruckelshaus 1997), but other authors consider the species cosmopolitan (Baratti et al. 2011). Correlative studies from its native range suggest *S. terebrans* can be damaging to mangroves (Santhakumari 1991, Davidson et al. 2014), but most studies document the species boring into dead wood or marine structures (Pillai 1955, Harrison and Holdich 1984). However, studies from Florida mostly document *S. terebrans* inhabiting the soft aerial root tips of red mangroves (*Rhizophora* spp.) where they have considerable effects (see Introduction).

**Isopod exclusion experiment**

At each site, we selected 20 free-hanging aerial roots along the seaward edge of the mangroves for experimentation (30 roots in the initial BC site). We selected roots haphazardly based on the availability of new unbranched roots that recently entered the water (35.2 ± 0.75 cm below the high tide mark, mean ± SE) and were within 2 m of the bank. Because isopods can colonize roots in less than a day (Brooks and Bell 2002), few roots touching the water were not already colonized. Thus, when necessary, we used roots that had been minimally colonized by isopods (1–3 borings in the first few centimeters of a root tip) and removed the colonized portion of the tip to provide a fresh substratum. Clipping the roots did not substantially affect annual growth (mean clipped roots vs. unclipped roots: 77 ± 19 cm and 97 ± 31 cm, \( t = 0.58, P = 0.57 \)), and any potential effect was distributed equally across both treatments. Further, there was no difference in the treatment response between clipped and non-clipped roots when analyzed separately (Appendix S3). Each root was then randomly assigned to one of two treatments, being either caged or left uncaged to serve as a control. The cages were constructed of 1-mm fiberglass mesh sewn into long sleeves with one open end (120 cm in length × 25 cm in circumference). We placed the cages around individual mangrove roots and closed the open end using cable ties affixed at 30 cm from the tip of the root, thus leaving ample room for root growth. Cable ties were also affixed to each control root at 30 cm from the tip to serve as a fixed reference point; this distance was chosen to avoid the zone of elongation/growth of the aerial root, which extends up to 23 cm from the root tip (Gill and Tomlinson 1971). Previous experiments indicate that similar cages do not affect mangrove root growth (Perry 1988; T. M. Davidson, unpublished manuscript). Further, we suspect that any potential cage effect, if present, would reduce root growth and our ability to detect a treatment effect and thus run counter to our hypothesis. We returned to each site after one year to measure the differences in root growth and morphology between caged roots and control roots. Fouling organisms were rarely observed on the cages; only five cages in the Alcove site in Belize were fouled (~5–20% cover) by the end of the experiment.

For each root, we measured the change in root growth (total length in cm) in the initial root tip (hereafter: primary root tip), numbers of newly grown root tips (hereafter: root tips), the mean
lengths of newly grown root tips, the maximum depth of the root in the water, and the number of root spreading events (hereafter: damage nodes; Fig. 2). Damage nodes indicate a location that was damaged sufficiently enough to elicit the growth of new root tip(s). We calculated the total amount of root growth by summing the total lengths of the primary root tip and all new root tips (not including the 30 cm original primary root length) and noted whether the root was anchored in the sediment. When caged roots became firmly anchored, we measured the root length from the cable tie to the surface of the sediment; thus, values for some caged roots are conservative. Maximum root depth was measured in addition to total growth because it reflects how far a root is vertically submerged in the water (likely an important aspect of root habitat provided by mangroves, Fig. 2); total root length, however, reflects both the vertical growth of the primary root but also the lengths of newly grown root tips. In addition, we recorded the numbers of borings created by isopods and examined roots for the presence of other borers (shipworms, limnoriids, insects). We excluded roots from the experiment analyses if their cages had large tears and extensive isopod colonization or if there was evidence that insects killed a root (dead root with insect borings and frass). Some roots were unable to be located due to insect damage that caused the collapse of roots or entire branches, loss of tags marking the location of roots, or vandalism. Thus, the respective sample size for exclusion and control roots in each site was Galeta (9, 9), BC (15, 14), BDD (7, 7), Alcove (9, 9), Maya (10, 10), Bear (3, 9), Env (5, 9), and Brad (8, 9). *Sphaeroma terebrans* was the only borer found in the included roots.

**Data analysis**

We used two-way ANOVA with treatment as a fixed factor (cage or no cage) and site as a random factor to test the effects of isopods on the root growth, number of root tips, number of damage nodes, mean root tip length, and root depth at each site. Pairwise analyses were conducted using *t* tests specific to each site. We corrected for possible multiple testing issues using false discovery rate (FDR)-corrected *P* values specific to each family of tests (Appendix S2: Table S1). For all tests, we evaluated the statistical assumptions using frequency histograms, qqplots, scatterplots, and boxplots and used square-root-, cube-root-, or log-transformations, when necessary, to improve normality, equalize the variance between treatment groups, and reduce the influence of outliers. We examined whether the proportion of roots that became anchored in the mud differed between treatments using a Fisher’s exact test. The duration of the experiment varied due to logistical constraints (Appendix S1: Table S1) so all numerical measurements (total growth, mean root tip length, maximum depth of the root) were standardized based on one year of growth (values divided by experimental duration in days × 365 d). Values are presented as means ± SE throughout.

**Results**

Mangrove root growth was 2.5–19 times greater in the caged treatments that excluded isopods than the control roots open to isopod colonization (*P* < 0.001, *F*<sub>1,7</sub> = 194.25, Fig. 3; site × treatment interaction: *P* = 0.70, *F*<sub>7,126</sub> = 0.67, cube-root-transformed). The differences in root growth between treatments were consistent in all locations except at one site in Florida after the FDR correction (see Appendix S2: Table S1 for raw and FDR-corrected *P* values). The cages at
that site (Bear Creek) were heavily torn, perhaps due to the presence of oysters and barnacles that interacted with water flow. The remaining three intact cages apparently still failed to completely exclude isopods for an unknown reason. Other locations in Florida also exhibited higher rates of isopod colonization in cages than Belize and Panama, even though the cages were mostly intact (Appendix S2: Fig. S1). Root growth varied strongly between sites ($P < 0.001$, $F_{1,7} = 194.25$, Fig. 3) and was considerably higher in Panama and Belize than Florida sites. The proportional difference in growth between caged and uncaged roots was relatively similar across sites, except one Florida site (Brad) that experienced very low levels of growth in isopod-bored roots (Appendix S2: Fig. S2). Overall, 15% of the caged roots among sites became anchored in the mud seafloor off from the peat bank (10/66 caged roots) by the end of the experiment, whereas no uncaged isopod-bored roots became anchored (0/76 uncaged roots), representing a significant difference ($P < 0.001$). Most roots anchored in the Maya site (7 roots, mean site depth: 188 cm), but roots also anchored in Alcove (1, depth: > 250 cm), BDD (1, depth: 179 cm), and Brad sites (1, depth: 106 cm).

We detected longer mean root tip lengths and longer maximum depths of roots in caged treatments than control roots (Fig. 4, Table 1; Appendix S2: Fig. S3). The magnitude of these differences was lower in Florida than Belize and Panama sites (Fig. 4). While the numbers of new root tips were significantly different between locations (Table 1), the differences were not consistent among the sites and not significantly different after FDR correction (Fig. 4). The number of damage nodes did not differ consistently between treatments, although there was a difference between sites.

Discussion

The boring isopod *S. terebrans* has widespread non-consumptive effects on red mangrove habitats across the Caribbean and Florida. When isopods were excluded, mangrove roots grew 2.5–19 times longer than control roots and these results were consistent across tropical and subtropical mangrove populations with different overall root growth rates (Hypothesis 1). Our data also partially support Hypothesis 2: The isopods altered root morphology, by reducing the length and depth of the roots in the water and mean root tip length, but not the numbers of root tips or damage nodes. The lack of differences in the numbers of root tips created and damage nodes between treatments indicates these responses to damage were highly variable (even in unclipped roots, Appendix S3). Furthermore, in support of Hypothesis 3, 15% of the isopod-excluded roots grew enough during our experiment to anchor in the sediment, while no control roots and no other adjacent (isopod-inhabited) roots became anchored during the study period. As the nature of the system limited us from using a proper cage control, we cannot fully discount the alternative hypothesis that cages may have somehow promoted growth independently while also excluding isopods. However, this appears extremely unlikely because (1) similar previous studies, including our own, did not find evidence of a cage effect (Perry 1988; T. M. Davidson, unpublished manuscript), (2) fouling organisms known to promote mangrove growth (e.g., sponges found on mangroves in euryhaline waters Ellison et al. 1996) were not present on the cages or roots at our brackish water sites, and (3) fouling on the cages could, if present, reduce root growth (as with barnacles on roots, Perry 1988) and our
ability to detect a treatment effect, but this runs counter to the pattern observed.

While other studies suggest isopod boring affects the mangrove edge (Rehm and Humm 1973, Svavarsson et al. 2002), we provide quantitative experimental evidence that the non-consumptive effects of introduced isopods inhibit root anchorage and mangrove encroachment into tidal creeks across Caribbean and Florida mangroves. Furthermore, our study is consistent with a wide body of literature documenting how consumers delineate the extent and structure of habitats and ecotones (Silliman et al. 2013), including intertidal zonation (Paine 1966, He et al. 2015). However, our results are distinct in that they highlight the role of non-consumptive interactions by a widespread introduced species.

Fig. 4. Morphological differences in aerial roots (A) excluded from boring isopod attack (black) and exposed to isopod colonization (red). An asterisk represents evidence of a difference between treatments \((P < 0.05)\), while a period represents weak evidence \((0.05 < P < 0.10)\) (see Appendix S2: Table S1 for exact \(P\) values). The bars represent means, and error bars represent SE. Depiction of root morphology (B) approximating the observed differences between treatments based on the data in 3A. Mean numbers of root tips and damage nodes were rounded to the nearest whole number.
Seaward extent

Our results suggest that by reducing growth and preventing anchorage of mangrove roots into the sediment, *S. terebrans* could limit the seaward encroachment of mangroves in shallow estuaries and may even help maintain tidal creeks. Because new mangrove roots grow adventitiously from anchored ground roots, the anchorage of a single root can propagate many additional ground roots. Successive iterations of roots growing outward increase habitat complexity and cause abiotic changes associated with increasing root structure (e.g., hydrodynamics, sedimentation, light changes). Interestingly, in contrast to our experiments, observational studies by Brooks and Bell (2002) found 23% of isopod-colonized roots became anchored in only 14 weeks in Tampa, Florida. Such differences may be due to site (e.g., depth, nutrient levels/mangrove growth) or methodological differences (e.g., monitoring roots hanging above the peat bank vs. hanging above open water). The rate of encroachment should depend on water depth and is likely limited in deeper areas in the middle of a creek that experience significant tidal movement and scouring during ebbing tides (Wolanski et al. 1980). However, in our experiment, uncaged roots failed to anchor across all sites including relatively shallow Florida sites. Thus, while local hydrodynamics and bathymetry can affect root anchorage, these effects can be offset if the impacts of boring isopods are strong, as evidenced by consistent effects across all of our experimental sites from Panama to Florida.

Implications of habitat alteration

As the complex root systems of red mangroves provide critical habitat (structure, refuges, nurseries, etc.) for marine species (Odum and Heald 1972, Ellison and Farnsworth 1992, Nagelkerken et al. 2008), the non-consumptive root alterations by these isopods may have indirect consequences on the surrounding community. For example, the species composition, abundance, and diversity of fish and crustaceans using root habitats vary in response to different root morphologies (Rönnbäck et al. 1999, Nagelkerken et al. 2010). Nagelkerken et al. (2010) used PVC pipes as root-mimics to infer how root spacing, orientation, and length may affect root use by fish. Interestingly, short, vertically hanging pipes (structurally similar to our...
unanchored isopod-bored aerial roots) hosted fewer species and a lower abundance of fish than full-length (80 cm) pipes that mimic anchored roots (Nagelkerken et al. 2010). In addition, by preventing roots from anchoring in the sediment, isopods should reduce access to the root by benthic predators that prey on root-epibiont communities (Taylor et al. 1986, Perry 1988, Schutte 2014). Thus, non-consumptive effects by isopods may also influence connectivity and trophic interactions between mangrove root and benthic communities. Furthermore, alterations in root morphology and density caused by isopods may elicit abiotic changes such as sedimentation and erosion (Kathiresan 2003, Krauss et al. 2003), changes in hydrodynamics (Wolanski et al. 1980), and light levels (Farnsworth and Ellison 1996, Granek and Ruttenberg 2008). Such abiotic factors, in turn, can influence the composition of mangrove root communities (Bingham and Young 1995, Farnsworth and Ellison 1996).

The effects of isopod root damage are likely greatest in sites where isopod prevalence and density are high and roots are a limiting resource for other species. Isopods are widespread and common; we found them in >90% of the roots in nearly every brackish creek examined (T. M. Davidson, unpublished manuscript). However, the amount of root substrata available and the coverage of epibionts (which presumably affect isopod colonization through space competition) can vary widely in mangroves (Farnsworth and Ellison 1996; T. M. Davidson, unpublished manuscript), suggesting that the community effects of isopod alterations may vary across sites.

Conclusions

The effects of consumers on controlling the extent and structure of habitat-forming species and ecotones are well documented (Silliman et al. 2013). However, we demonstrate that non-consumptive effects of boring isopods can have similar outcomes across a broad geographic range. While our experiments focused on local-scale (root-level) effects, albeit across a large geographic range, it is possible that these cumulative root-level effects may scale up to cause larger landscape and community level changes in brackish mangroves. However, larger-scale and multiyear studies are needed to further evaluate the processes that affect mangrove roots on the landscape scale and determine the extent to which isopods limit mangrove encroachment into estuarine waters.

Acknowledgments

We are grateful for the field, laboratory, and logistical support provided by Andrew Sellers, Carmen Schloeder, and Amanda Fenner. We thank Adrian Vernon, Juhyung Lee, Christian Harris, Brittney Kosar, Allyson Tombesi, Samantha Flounders, Taylor Jackson, and Nicole Yamase for their help in the field and Donna and Roger Davidson for helping to sew dozens of cages. Jill Schmid, Victoria Vazquez, and Kevin Cunniff, at the Rookery Bay National Estuarine Research Reserve, provided key logistical support and expert local knowledge. We thank Ernie Estevez for the many insightful discussions on isopod–mangrove interactions and for the use of his boat and site access. Critical comments by two anonymous reviewers and Brian Turner improved an earlier draft of this manuscript. The primary funding for this research was provided by the Smithsonian Institution Marine Science Network Postdoctoral Fellowship. Additional support was provided by the National Science Foundation Ocean Sciences Postdoctoral Fellowship (OCE-PRF 1323429). This article is devoted to the memory of Adrian Vernon, a skilled naturalist and strong ally of mangrove conservation in Belize. We declare no conflicts of interest.

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**Supporting Information**

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecos.1430/supinfo