

Variation in a simple trait of mangrove roots governs predator access to, and assemblage composition of, epibiotic sponges

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ABSTRACT: Many species create biogenic habitat that may vary in quality depending on its attributes. This variation may in turn affect species interactions among members of the attendant community. We describe a habitat-provisioning species that, with variation in a simple trait, produces dichotomous classes of habitat: one that serves as a predation refuge and the other that does not. Subtidal roots of the Caribbean red mangrove *Rhizophora mangle* are colonized by a diverse epibiont assemblage that includes many species of sponge. We experimentally demonstrated that roots touching the seafloor give benthic sea star predators access to their sponge prey living on the roots. After 6 wk, half of sponges on grounded roots were eaten, whereas sponges on suspended roots were uneaten. Correspondingly, in concomitant field surveys of mangrove root epibiont assemblages, we found very different sponge ensembles on the 2 root types. Even after standardizing for root area, suspended roots harbored 7 sponge species that covered an average of 91.3% of subtidal root length, while grounded roots, where sponges were exposed to sea star predation, had only 4 sponge species that covered 63.2% of root length. There was little overlap in species composition and a single sponge species *Chondrilla caribensis*, that was never eaten in our experiment, dominated grounded roots. This study suggests that a simple, dynamic trait of mangrove roots—groundedness—controls predator access, with consequences for assemblage composition.

KEY WORDS: Foundation species · Habitat-forming species · Biodiversity · Florida Keys · Everglades

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INTRODUCTION

Habitat-creating organisms alter the abiotic environment, ultimately controlling resources for other species (Jones et al. 1994, 1997, Byers et al. 2006). Although all species exhibit trait variability, trait variation among and within individuals that create habitat may be particularly influential, given their foundational role within an ecosystem. Specifically, trait-based influences of biogenic habitat can affect multiple species simultaneously, helping to shape entire communities (e.g. Miyashita & Takada 2007, Bishop et al. 2012, Bishop et al. 2013). For example, higher

grass stem densities reduce predation success by marsh killifish, which ultimately determines prey abundance and size distributions (Vince et al. 1976). As predation plays a strong role in shaping many marine communities (e.g. Connell 1961, Menge 1976, Underwood & Jernakoff 1981), living habitat that modifies predation may have a concomitantly influential effect.

The red mangrove *Rhizophora mangle* has aerial roots that originate from its branches and trunk and grow toward the sediment. *R. mangle* grows on Caribbean shorelines and island fringes, where portions of these aerial roots are often permanently sub-

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merged (Fig. 1). Submerged mangrove roots form the foundation of unique and diverse pelagic, benthic, and epibiotic communities (e.g. MacDonald et al. 2008, Nagelkerken et al. 2008, MacDonald & Weis 2013). These roots provide habitat in a soft-sediment environment largely devoid of other suitable hard substrate. Thus, where abiotic conditions are suitable, the intertidal and subtidal portions of mangrove roots are often heavily or completely colonized by sessile organisms such as algae, tunicates, bivalves, and sponges (e.g. Ellison & Farnsworth 1992, Rützler et al. 2000, Nagelkerken et al. 2008, Guerra-Castro et al. 2011, 2016).

Epibiont assemblage composition and diversity are determined by a variety of factors. Larval recruitment and abiotic factors differentiate assemblages on windward and leeward island sides and, on a larger scale, across different sites and regions of the Caribbean (e.g. Bingham 1992, Farnsworth & Ellison 1996, Wulff 2004). On a local scale, biotic interactions such as predation and competition (e.g. Wulff 2000, 2005, Engel & Pawlik 2005) may be more important for shaping individual root epibiont assemblages post-recruitment (e.g. Wulff 2000, 2005, Engel & Pawlik 2005; although Sutherland 1980, Farnsworth & Ellison 1996 both discuss small-scale impacts of larval dispersal and supply). Sponges are among the most abundant subtidal, root-dwelling epibiotic organisms (e.g. Rützler et al. 2000, Engel & Pawlik 2005, Hunt-

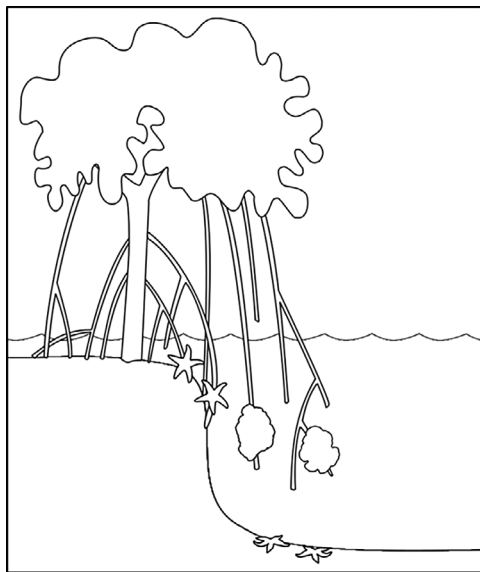


Fig. 1. Fringing red mangrove tree and typical marine mangrove habitat. For simplicity, we have depicted only the focal subtidal organisms of interest to this study. Diagram made with symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/)

ing et al. 2008, Nagelkerken et al. 2008, Guerra-Castro et al. 2011, 2016). Benthic sea stars, a dominant mangrove sponge predator (Wulff 2006a), may be limited to consuming sponges on roots grounded in the sediment, as Taylor et al. (1986) illustrated for algae species and their benthic predators in marine mangrove habitat. Furthermore, not all sponge species are equally palatable (e.g. Waddell & Pawlik 2000), and thus patterns may emerge due to differential consumption. Therefore, although the pool of subtidal epibiotic species living on roots at a particular site may be determined by a combination of larger-scale factors, at the site level, trait-dependent predatory access may act to differentially structure the sponge ensemble on grounded versus immediately adjacent suspended roots.

Thus, we seek to understand how variation in the trait of a habitat creator (1) affects the ability of that biogenic habitat to mediate predation and (2) influences the attendant assemblage structure. In this system, the habitat-creating mangrove seemingly produces habitat of dichotomous quality, which either serves as a predation refuge or exposes assemblage members to substantially higher predation rates. Specifically, once a mangrove root grows into the seafloor, benthic predators could possibly climb the roots and consume their epibiotic prey. Through an experiment and assemblage surveys, we compared the vulnerability to sea star predation of sponges living on suspended mangrove roots with that of those living on roots that have grown into the seafloor. Although qualitatively one might expect higher vulnerability on grounded roots, and such vulnerability is mentioned anecdotally in Nagelkerken et al. (2008), this issue has not, to our knowledge, been experimentally addressed. We hypothesized that sponges living on roots grounded into the sediment would experience more predation by sea stars than sponges living on roots suspended in the water column. We also predicted that the sponge ensemble on natural grounded roots would differ from the sponge ensemble on adjacent suspended mangrove roots, at least in part as a result of differential sea star access to these 2 root types.

MATERIALS AND METHODS

Predation susceptibility experiment

In summer 2009, we worked beneath the canopy of *Rhizophora mangle* trees at the edge of a mangrove island north of Key Largo, just inside the southern

border of the Everglades National Park (25.12876° N, 80.443811° W). Maximum tidal variation at this location is slightly less than 0.4 m and the mangrove island steeply slopes down (Fig. 1) to a mean water depth of approximately 1.4 m beneath the mangrove canopy where we worked. To evaluate the effects of root position and thus sea star *Echinaster sentus* predator access on sponge fate, we experimentally manipulated root position by controlling whether a root was grounded in the sediment or suspended in the water column (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m573p015_supp.pdf). Each treatment was represented twice in each of 10 blocks. Blocks were made using 2 rebar stakes to anchor either end of a clothesline (nylon string), with 4 root segments (all at least 0.5 m long) strung on the line hanging down vertically between the stakes. We spaced 2 suspended and 2 grounded roots at least 30 cm apart and alternated them to increase apparatus stability. The first root type on each block was randomly selected. The minimum distance between suspended root tips and the sediment was 30 cm. Sea stars on our experimental apparatus were unable to move between roots either on the clothes line or by reaching across neighboring roots, and so only had access to experimental sponges by climbing up roots from the seafloor. In 2 instances benthic debris acted as a ladder, allowing sea stars to gain access to suspended roots (see 'Discussion'), thus the 2 affected sponge replicates were excluded from analyses. Blocks were set up parallel to the edge of the island along a 14 m stretch underneath the mangrove canopy and amongst natural, suspended mangrove roots. No natural mangrove roots were removed to make space for this experiment. Instead, blocks were spaced strategically to separate them from natural roots by ≥ 30 cm.

For our experimental root segments, we used dead root segments of *R. mangle* found above the high tide line, none of which had epibionts. Guerra-Castro & Cruz-Motta (2014) demonstrated the efficacy of using inert, wooden substrates as artificial habitat for sponges in this system. We transferred 3 sponge pieces to each root; 1 individual of each of the 3 most abundant sponges (*Tedania ignis*, *Lissodendoryx isodictyalis*, and *Chondrilla caribensis*) around Key Largo (Engel & Pawlik 2005). *T. ignis* is one of the most abundant mangrove sponges in the Caribbean (Diaz & Rützler 2009, Wulff 2009 and references therein, Guerra-Castro et al. 2011, Diaz 2012). Each of the 3 sponge individuals was randomly assigned an attachment location (upper, middle, or lower) on each root because the lower (i.e. deepest) sponges

will necessarily be encountered first by climbing predators. From a source stock of sponges collected from roots outside the study area, sponge pieces were cut to a volume of approximately 50 ml each (measured by water displacement) and attached to experimental roots using zip ties. Asexual reproduction through fragmentation is a common reproductive method for sponges (Wulff 1991) and the sponge pieces reattached to the experimental roots within 48 h of transplantation.

To identify the agents of sponge damage and quantify consumption in our experiment, we photographed sponges approximately every 3 d for 6 wk (16 observations in total). Frequent photographic sampling ensured that all sponge tissue damage could be matched with its cause before that damage signature was lost. Loss of sponge tissue could readily be attributed to a specific agent based on unique signatures left in sponge tissue (see Wulff 2006a). Diseases or unsuitable environmental conditions cause sponges to turn pale, then disintegrate. Fish leave crater-like bite marks in the surface of sponges. Limpets do not eat sponges, but 'bulldoze' through them as they move along the root surface, leaving behind a groove in sponge tissue near the mangrove root. Sea stars eat sponges by digesting sponge tissue externally, then ingesting that broken-down tissue. Portions of sponges consumed this way are translucent in contrast to the usual orange, blue, or gray coloration of *T. ignis*, *L. isodictyalis*, and *C. caribensis*, respectively. Of all experimental sponge pieces, 20% were superficially damaged by fish (family Lutjanidae) and limpets *Diodora cayenensis* in isolated incidents (neither fish nor limpets persisted in damaging a sponge beyond taking a single bite or creating a single groove), and this damage quickly healed (see Bingham & Young 1995, Wulff 2012). Aside from these limited instances, observations during our experiment confirm that sponge condition was affected only by sea star predators and not by non-trophic factors.

Once a sponge lost more than 50% of its tissue volume to sea star predation, determined by estimating volume according to geometric approximation (sensu Wulff 2001), that sponge was removed from the experiment without replacement. Any sea stars eating that sponge at the time of removal were dropped to the seafloor beneath the root. These majority-eaten sponges were removed from the experiment, because once sea stars began eating a sponge, they did not leave that sponge under their own power until it was consumed. This removal practice focused the experiment on sea star predation choice rather than consumption volume. We recorded the sponge

pieces that had experienced any sea star predation by the end of this experiment. We compared sponge predation as a function of all 3 sources of variation examined (sponge species, treatment [grounded or suspended], and block) using a 3-way chi-squared contingency test.

To further elucidate the agent of damage to sponges, we enumerated sea star distributions on experimental sponge pieces and in the environment surrounding our experimental array. During our bi-weekly experimental observations, we quantified sea stars on our experimental sponges using the photographs of each sponge piece. Also, midway through the experiment, we quantified sea star abundances on the seafloor beneath our experiment using 15 haphazardly thrown 0.25×0.25 m quadrats systematically spaced around experimental root segments. All sea star counts were performed diurnally. As experimental blocks were placed amid naturally occurring mangrove roots, systematically spacing the quadrats around our experiment ensured that we captured sea star abundances beneath naturally occurring suspended mangrove roots.

Natural epibiont assemblage surveys

To investigate how sponge ensemble structure varies according to the groundedness trait of mangrove roots, we documented natural sponge distributions at our site as a function of root position. These surveys also explored how the mechanisms uncovered by the predation experiment may influence natural root assemblages. We surveyed natural epibiont assemblages on the subtidal portion of 10 haphazardly selected grounded roots and 10 haphazardly selected suspended roots along the 14 m of island edge where our experiment was conducted. We photographed the root surface facing away from the bank of the mangrove island (as this was the only part of the grounded roots feasible to survey accurately). Photographs were taken down the length of each root and then stitched together in Adobe Photoshop (CS6). The percent coverages of all epibionts (sponge and non-sponge species, including hydroids, anemones, and algae) were quantified in the photos using the analytical software package ImageJ (Schneider et al. 2012). Root contours were traced from the mean tide line to the tip of the root. The length of root covered by sponges and other epibionts was quantified (bare space was negligible). Only primary space-occupying species were counted. For example, anemones that colonized a

sponge were not counted for our analyses because the sponge was the primary space occupant, i.e. contacting the root. Sponges were preliminarily identified to species level using photographic identification aides (Smithsonian Tropical Research Institute 2006, Zea et al. 2009). Species identities were confirmed using spicule plates except for *Halichondria* cf. *magniconulosa*, which was only identified using photographic sponge guides.

We used a *t*-test to compare the percent coverage of all sponge species combined on subtidal root lengths between the 2 root types. We also calculated several standard biodiversity statistics (discussed below). For these, we used only the percent cover of sponges and did not include non-sponge species in our analyses, because sponges were the predominant root-colonizing taxa in our study area. Thus, the focus of this study was to describe sponge ensembles specifically. The average subtidal portion of grounded roots was 0.60 ± 0.1 m long (mean \pm SD) and the average subtidal portion of suspended roots was 0.92 ± 0.2 m long (from the water's surface to root tip; Fig. 1). As species richness generally scales with area, we equalized the areas being compared between the 2 root types by analyzing the full subtidal length of all grounded roots and only the upper subtidal portion of suspended roots, from the mean tide level to the average water depth attained by grounded roots (0.6 m). This allowed us to standardize for the influence of water depth in addition to area. As a supplementary analysis—although not an equal comparison—to see if the longer suspended roots harbored overall more diversity compared to grounded roots, we repeated our statistical calculations using the sponge ensemble on the entire subtidal length of suspended roots.

We calculated standard diversity metrics both for suspended and grounded roots, including species richness, evenness, and the Shannon diversity index. For the latter, we compared the index values between the 2 root types using a *t*-test. We evaluated the assumptions of the *t*-test as they applied to our data and, while variances were homogeneous, residuals were only near-normally distributed. However, this is possibly to be expected given our relatively low sample size ($n = 10$ roots of each type). We considered the *t*-test robust enough to use in this case. We also compared assemblages on the 2 root types using ANOSIM calculated with the Bray-Curtis dissimilarity index using the vegan package (Oksanen et al. 2017) in the statistical program R (R Core Team 2016). Percent cover data (already treated by relativizing) were used to complete this analysis. Data

were further subjected to square root transformation and Wisconsin double standardization before plotting using a permutational transformation function.

Finally, to compare cumulative epibiont assemblages between the 2 root types, we used percent similarity, which we calculated using Renkonen's (1938) formula (the proportional index of community similarity).

RESULTS

Predation susceptibility experiment

The 3-way contingency test revealed that only sponges on grounded roots were eaten by *Echinaster sentus* sea stars, with a total of 34% of all grounded sponge pieces preyed upon and 0% of suspended sponges ($\chi^2_{1,118} = 37.5$, $p < 0.0001$; Fig. 2). These rates are highly species-specific as *Chondrilla caribensis* was never eaten by sea stars, and *Tedania ignis* and *Lissodendoryx isodictyalis* were eaten frequently by sea stars ($\chi^2_{1,118} = 26.0$, $p < 0.0001$; Fig. 2). Nearly half (51%) of individuals of *T. ignis* and *L. isodictyalis* in the grounded treatment experienced predation. *T. ignis* and *L. isodictyalis* were preyed upon almost equally (58 and 45% of individuals on grounded roots, respectively). Block did not have a significant effect on sponge predation ($\chi^2_{1,118} = 15.4$, $p = 0.08$).

Sea star distributions aligned with the documented predation patterns. We saw an average of 2.2 and 1.5 ind. d⁻¹ on each individual of *T. ignis* and *L. isodictyalis*, respectively, versus just 0.1 ind. d⁻¹ on each individual of *C. caribensis*. There were 86 ± 85 ind. m⁻² on the seafloor beneath our experiment.

Natural epibiont assemblage surveys

Collectively, we found a total of 9 sponge species on surveyed mangrove roots, but suspended roots

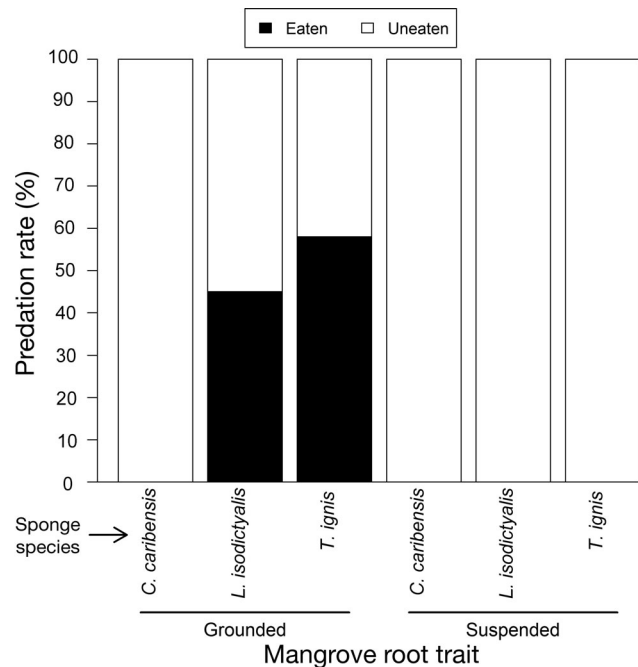


Fig. 2. Sea star predation rates (the percentage of individual sponge pieces exhibiting any sign of sea star predation) for the 3 sponge species (*Chondrilla caribensis*, *Lissodendoryx isodictyalis*, and *Tedania ignis*) on experimentally grounded and suspended mangrove root segments in our 6 wk experiment

had almost twice the species richness and much higher sponge coverage. In our equalized length comparison of roots (Fig. 3, Table S1 in the Supplement at www.int-res.com/articles/suppl/m573p015_supp.pdf), 7 sponge species covered 91.3% of subtidal suspended root length and 4 sponge species covered 63.2% of the subtidal grounded root length, a significant difference ($t = 2.89$, $df = 18$, $p < 0.01$). Root length not occupied by sponges was primarily covered by turf algae on both types of root. Suspended roots were dominated by massive, fleshy sponges, while grounded roots were occupied by more encrusting sponge species (Fig. 4). Of the 3

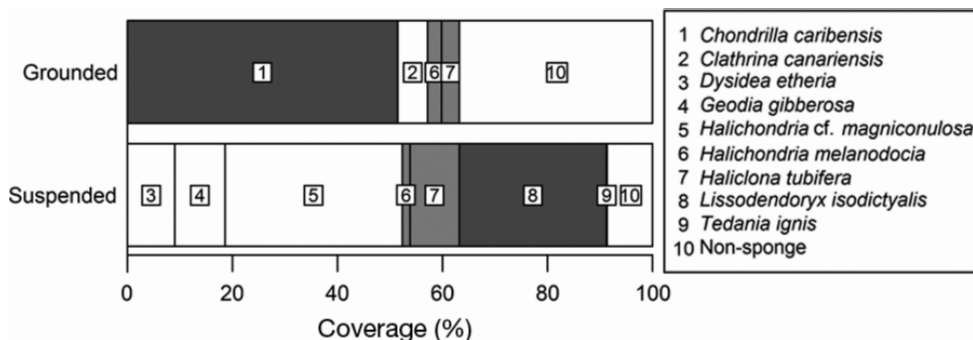


Fig. 3. Sponge ensembles constructed from cumulative percent coverage on surveyed natural roots at the study site. We compared segments of equal length (0.6 m) from grounded and suspended roots. Sponge species are listed in alphabetical order from 1 to 9. Dark gray shading highlights the species used in our experiment and light gray shading highlights the sponge species seen on both suspended and grounded roots. The 'non-sponge' category includes hydroids, anemones, and algae

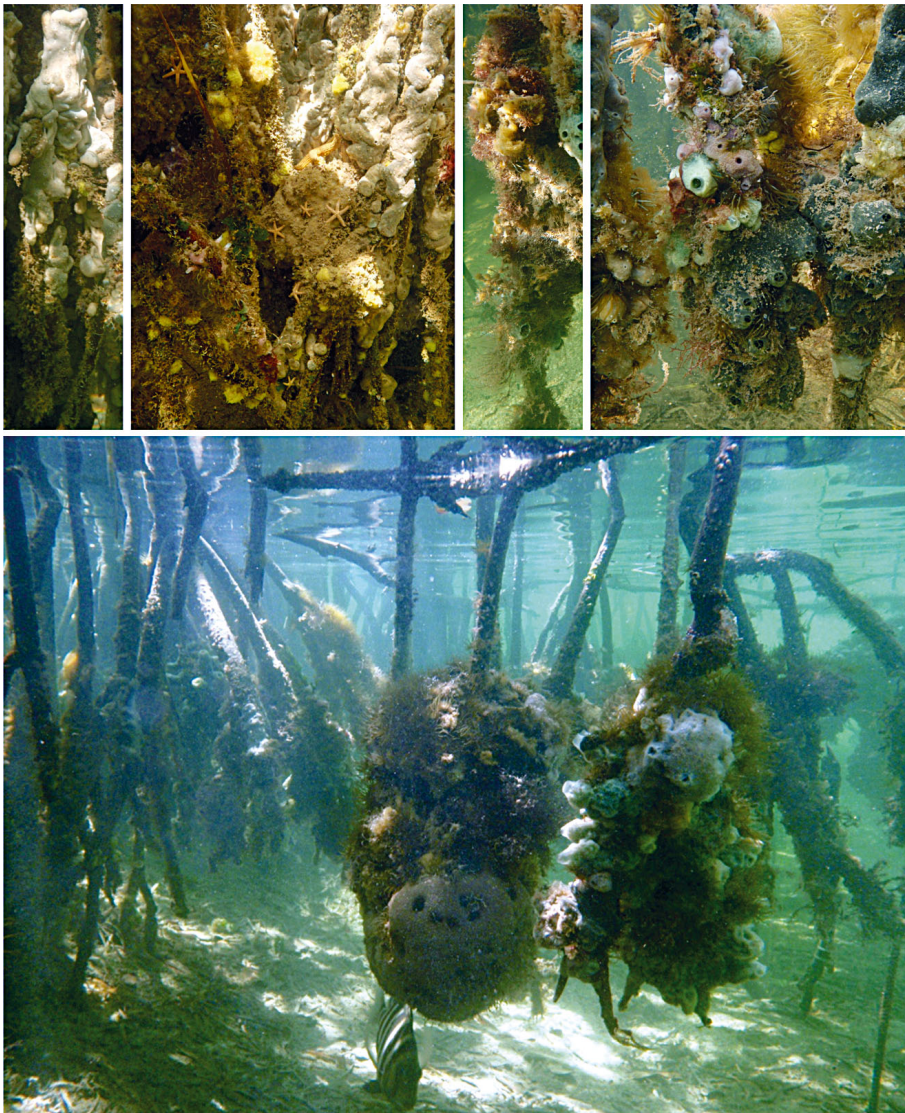


Fig. 4. Sponge epibiont assemblages at our site in the Florida Keys. From left to right, the top row shows one grounded root with a typical less-diverse sponge community (note the area covered by the beige, globular sponge *Chondrilla caribensis*), multiple grounded roots with an abundance of sea stars, one suspended root with a typical heterogeneous sponge community, and multiple suspended roots that depict the increased sponge coverage on suspended roots in general. The bottom photo was taken at high tide and shows grounded roots on the left and suspended roots on the right. At this site, as in most subtidal red mangrove ecosystems in the Caribbean, roots of *Rhizophora mangle* are virtually the only hard substrate available

sponge species used in our experiment, 2 (*T. ignis* and *L. isodictyalis*) were found only on suspended roots and the third species (*C. caribensis*) was found only on grounded roots.

Suspended and grounded roots of *Rhizophora mangle* supported different sponge species ensembles (Table 1). Of the 9 species seen overall, 5 were found only on suspended roots, 2 were seen only on grounded roots, and 2 species were found on both types of root (Fig. 3). Species evenness was lower on grounded roots (mean \pm SD: 0.64 ± 0.26) than on suspended roots (0.77 ± 0.25) (Table 1). The Shannon diversity index was (mean \pm SD) 0.37 ± 0.35 for sponge ensembles on grounded roots and 0.72 ± 0.41 for ensembles on suspended roots, a significant difference ($t = 2.45$, $df = 18$, $p < 0.05$). A Bray-Curtis

Table 1. Biodiversity indices for sponge epibiont communities on grounded and suspended mangrove roots of equalized length (entire lengths of grounded roots and only 0.6 m of suspended roots as measured from the water line at mean tide level down the root). Statistics in this equalized length analysis were calculated using only the portion of suspended roots equal to the length of the average grounded root. Whole-assemblage indices are based on percent cover as a proportion of cumulative subtidal root length covered by sponges on all 10 roots of each type, while per-root values represent the means and standard deviations of indices calculated using the percent coverage of sponges at the level of individual roots

Index	Total species richness	Evenness	Shannon diversity index	Bray-Curtis analysis of similarity	Similarity (%)
Whole assemblage					
Grounded	4	0.49	0.67		6.97
Suspended	7	0.77	1.5		
Per root					
Grounded	1.9 ± 0.74	0.64 ± 0.26	0.37 ± 0.35	$R = 0.87$, $p < 0.001$	
Suspended	2.8 ± 1.03	0.77 ± 0.25	0.72 ± 0.41		

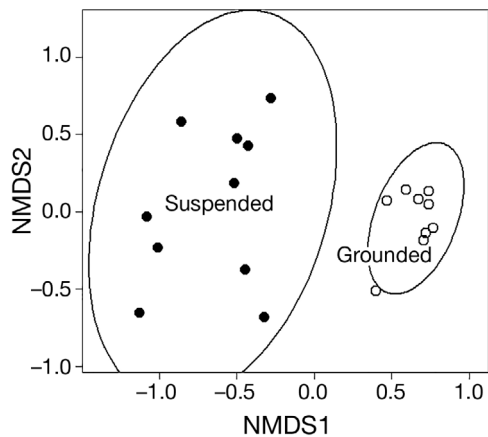


Fig. 5. Bray-Curtis analysis of similarity (performed on equalized root lengths) indicated that root position significantly affected root ensemble composition ($R = 0.87$, $p < 0.001$). Root position designations are plotted at the centroid of scores for each root type and circles show the 95% confidence intervals for the standard error around these centroids. The larger circle around the points representing suspended roots indicates higher variance in sponge ensembles between roots (compared to ensembles on grounded roots)

analysis of similarity indicated that the ensembles on the 2 root types were significantly different ($R = 0.87$, $p < 0.001$; Fig. 5). Percent similarity (comparing cumulative percent coverages of species over all 10 roots rather than at the level of individual roots) between sponge ensembles on suspended and grounded roots was only 6.97%. Diversity statistics were virtually unchanged for our less conservative comparison between grounded roots and the (longer) whole length of suspended roots (Table S2, Figs. S2 & S3).

DISCUSSION

Mangrove root position relative to the seafloor significantly affected sea star predation on epibiotic sponges and assemblage composition. The diversity and evenness of sponge epibionts on natural, suspended mangrove roots was high. In contrast, grounded roots had sharply reduced sponge diversity and were dominated by one unpalatable sponge, *Chondrilla caribensis* (see Waddell & Pawlik 2000 for more details on sponge palatability). The sponge species assemblages on the 2 types of root were distinct from one another. Our experiment suggested that differential predation by sea stars on their highly favored prey species may help to drive differences in assemblage structure among grounded and suspended roots. Specifically, *Lissodendoryx isodictyalis*

and *Tedania ignis* were exclusively preyed upon in our experiment and were completely absent in surveys of natural grounded roots.

Epibiotic sponges that live in marine mangrove environments heavily colonize mangrove roots because subtidal mangrove ecosystems are typically devoid of alternative, predator-free settling surfaces. Highly palatable sponges on aerial roots are protected from benthic sea star predators, but the closer a root is to the sediment, the more likely it is that benthic sea star predators will gain access to these sponges. Roots need not anchor into the sediment to lose their status as refugia, as debris on the seafloor will form a bridge between the benthos and roots. This happened twice to experimental roots during this study and each time, sea stars quickly used the bridge to gain access to and consume palatable sponges on suspended roots.

Palatable sponges are not excluded altogether from the system by predation, however, because of inconsistent root accessibility and variable sea star abundances. Mangrove roots commonly terminate growth above a critical height off the seafloor and may never grow close enough to the sediment that sea star predators can access palatable sponges. This is more common in deeper water, where the distance to the seafloor is greater. Even in shallower water, owing to the constant production of new aerial roots, the suspension of aerial roots is a dynamic trait that varies with the age and ontogeny of the mangrove tree. The uneven age structure of roots and trees in a typical mangrove forest helps to produce a mosaic of grounded and suspended roots, each with its own distinct assemblage, leading to a diverse community. Furthermore, *Echinaster sentus* and other sponge-eating sea stars (Wulff 2000, 2006a,b) are found throughout the Caribbean, but their spatial and seasonal abundance can vary greatly. Underneath just the 14 m stretch of mangrove canopy used for this experiment, sea star abundances varied from 288 to 0 ind. m^{-2} . Also, temporal variation, for example due to recruitment events, could influence seasonal predation pressure of sea stars on sponge epibionts.

Our experimental and survey results suggest that at our study site, sea star predation contributes to sponge community differences between suspended and anchored roots. Certainly on larger spatial scales, abiotic variables such as hydrology, oxygen, temperature, and salinity affect sponge recruitment and distributions (e.g. Wulff 2004, Diaz & Rützler 2009, Guerra-Castro et al. 2011, 2016), and determine the pool of species living at a site like our

study location. Even highly localized factors such as chemical signatures, light exposure, sponge larval settlement preferences, or root assemblage successional stage, among others, may contribute to the composition and abundance of sponge species living on a particular type of root (Hunting et al. 2010, Guerra-Castro et al. 2016). However, such localized factors would have to vary systematically within roots of each type for them to help explain the strong differences between root types that we found in our study over a small spatial scale.

Ours is not the first evidence that sponge communities in particular (Wulff 2000, 2004, 2005, 2009), and root epibiont ensembles more generally (Taylor et al. 1986, Perry 1988), on the scale of meters, may be influenced more by localized post-settlement processes (such as predation and competition) than recruitment. The horizontal distance in our study between surveyed grounded and suspended roots was not more than 1.5 m, and depth was kept constant. In addition to our experimental evidence for predation, competition also seemed to influence the root assemblages in our study. Namely, faster-growing, palatable, massive sponges such as *Haliclondria* cf. *magniconulosa* and *L. isodictyalis* presumably pre-empted space from the unpalatable sponge *C. caribensis* and likely explain the absence of this species on suspended roots (see Wulff 2005).

The subtidal roots of *Rhizophora mangle* provide the only consistent source of hard substrate for sponge settlement in soft-sediment Caribbean mangrove ecosystems (Wulff 2012 and references therein). The suitability of mangrove roots as habitat for many sponges is dynamic, dichotomous, and dictated by a subtle but simple trait. Root habitat may terminate above the seafloor and serve as a predation refuge, or it may anchor into the sea floor, giving sea star predators access to sponges. Our study suggests that where sea stars are abundant and water depth is shallow, root position relative to the seafloor dictates dramatic differences in epibiotic sponge ensembles. More broadly, the specific characteristics of structure produced by a habitat-provisioning species can influence the interactions of attendant species, ultimately affecting community composition.

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