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Epibiont community composition of red mangroves *Rhizophora mangle* are contingent on root characteristics

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ABSTRACT: Foundation species traits that structure communities are rarely experimentally examined; thus, a predictive understanding of their functions lags behind patterns of observed species associations. Red mangrove *Rhizophora mangle* roots form complex living habitats that support diverse epibiont communities, making them a model system for testing links between variation in foundation species traits and associated biodiversity. Here, we compared epibiont community composition between living and non-living mangrove roots, as well as root mimics, to test how foundation species traits affect community structure. We also quantified the community structure of associated mobile invertebrates to examine their relationship with secondary foundation species (e.g. sponges, bivalves) that grow on the roots. After 14 mo of colonization and succession, substrate composition (i.e. mangrove, wood, PVC) had significant effects on community composition, richness, and abundance of sessile epibionts and mobile invertebrates. Non-living mangrove roots were 5 times more likely to deteriorate, and consequently had the lowest epibiont richness and abundance. We found strong positive relationships between mobile invertebrate richness and the abundance, measured as biomass, and richness of sponges and bivalves, suggesting that variation among roots in secondary foundation species play an important role in mediating mobile invertebrate community composition. This study highlights the functional role of habitat structure and how rapidly that function can be lost without biogenic maintenance. Our results indicate the importance of facilitation cascades in fostering diverse mobile invertebrate communities and highlight both advantages and limitations in using artificial structures in restoration programs.

KEY WORDS: Facilitation cascades · Foundation species · Mangrove · Fouling community · Epifauna · Artificial structure · Bocas del Toro

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1. INTRODUCTION

Foundation species (sensu Dayton 1972) play a disproportionately important role in structuring communities by creating biogenic habitat, modifying environmental conditions, and altering resource availability and species interactions (Dayton 1972, Ellison et al. 2005, Angelini et al. 2011, Altieri & Van De Koppel 2013). Variation in foundation species traits such as structural complexity, age, and patch size can determine the strength of facilitation, defined here as the degree to which environmental conditions are modified or stress is ameliorated, and the subsequent effects on associated species composition and interactions (Irving & Bertness 2009, Bishop et al. 2013, Schutte & Byers 2017). For example, variability in the density and structural complexity of foundation species (e.g. seagrass, marsh grass, macroalgae, coral) can modify water flow velocity, turbulence, and sediment characteristics, as well as reduce predation intensity, which can affect growth rates, survivorship, body size, and population density of associated species (Bruno & Bertness 2001, Bruno et al. 2003).

In a facilitation cascade (sensu Altieri et al. 2007), the primary foundation species enables the colonization of a secondary foundation species, thereby providing complementary facilitative functions to support diverse species assemblages. These types of assemblages can exist in both terrestrial and marine ecosystems, and function through a suite of positive interactions such as reducing predation pressure by increasing habitat complexity, altering the physical environment to provide protection from abiotic stress (e.g. canopy shading), and modifying nutrient availability (Angelini et al. 2011, Hughes et al. 2014, Thomsen et al. 2018). One way to study the relationship between primary and secondary foundation species and their associated organisms is by isolating primary foundation species traits with the use of mimics to experimentally identify which traits impact community composition of associated organisms (Angelini et al. 2011). Understanding links between foundation species traits and their associated assemblages is also important in the context of recovery and restoration efforts that involve artificial substrates that mimic foundation species.

In coastal systems, hard infrastructure such as artificial reefs, seawalls, and breakwaters are increasingly used for coastal protection and to mitigate other repercussions of lost foundation species (Gittman et al. 2015). A mechanistic understanding of the effectiveness of such hard infrastructure, including their cascading effects on the ecosystem, is needed for effective design and planning of coastal resource management (Dafforn et al. 2012, 2015, Morris et al. 2018, Vozzo et al. 2021). Experimental studies examining foundation species mimics as hard infrastructure can inform habitat restoration and enhancement efforts, because they allow for traits of foundation species to be isolated to assess their impact on associated biodiversity. For example, the physical structure of a mimic may be more durable under stressful conditions (e.g. high wave energy) that would deteriorate or erode a foundation species (e.g. break mangrove roots or topple coral colonies), allowing habitat structure to persist in the system. In contrast, artificial infrastructure may lack important characteristics, such as chemical cues that are important for inducing recruitment of the desired species assemblage, or contain additives that inhibit settlement (Dennis et al. 2018). Consequently, differences in communities have also been observed between foundation species and hard infrastructure, including a greater presence of non-indigenous species on hard infrastructure than on foundation species (Ellison et al. 1996, Chapman 2003, Bulleri & Airoldi 2005, Glasby et al. 2007, Tyrrell & Byers 2007, Mineur et al. 2012, Airoldi et al. 2015). In this study, we examined how those differences can arise from variation in traits of foundation species and associated facilitation cascades.

We used red mangroves *Rhizophora mangle* as a model system for testing links between foundation species traits and associated biodiversity. Mangrove aerial roots form living subtidal habitats recognized for their diverse fish and epibiont communities, with the aerial roots providing a complex habitat and hard, stable settlement surface in an otherwise simple and unstable sedimentary environment (Farnsworth & Ellison 1996, MacDonald & Weis 2013). A number of studies on mangroves and their associated biodiversity have focused on associations between mangrove root traits and fish communities (Nagelkerken et al. 2010) or relationships between epibionts and fishes (MacDonald et al. 2008, MacDonald & Weis 2013). Other studies have examined the relationships between epibionts and mangroves (Pawlik et al. 2007, Guerra-Castro et al. 2011, 2021, Guerra-Castro & Cruz-Motta 2018, Hunting et al. 2013a, 2013b) or epibionts and environmental factors (Castellanos-Pérez et al. 2020) to better understand what factors account for the diversity in epibiont communities. For example, some studies have tested the importance of substrate by comparing epibiont communities between natural mangrove roots and either mangrove root mimics (e.g. PVC, wooden

stakes) or hard infrastructure (e.g. concrete dock pilings, seawalls) (Hunting et al. 2013a, Guerra-Castro & Cruz-Motta 2014, Janiak et al. 2018). These previous studies using root mimics or hard infrastructure have demonstrated that they have communities distinct from natural mangrove roots, at local and regional scales (Guerra-Castro & Cruz-Motta 2014, 2018). However, there remains a lack of experimental tests addressing how root traits predict their function in shaping the composition of associated organisms. Sponges and bivalves are dominant groups found on subtidal mangrove roots within the Caribbean (Guerra-Castro et al. 2016) and are often assumed to be secondary foundation species (Altieri & Van De Koppel 2013, Aquino-Thomas & Proffitt 2014) because of the structural complexity they add to the mangrove system, which can provide refuge to a speciose invertebrate community (Henkel & Pawlik 2011, Rebolledo et al. 2014). Additionally, specific sponge species may serve as biological indicators of mangrove epibenthic community health (e.g. presence of pollution) (Diaz et al. 2004). However, few studies have quantified the importance of these secondary foundation species on associated mobile community structure within mangrove roots.

The objective of this study was to test for links between foundation species traits and the biodiversity of associated epibionts to better understand the mechanisms that determine community assemblage in this speciose and functionally diverse system. We were interested in chemical, physical, and biological traits, so we used a variety of treatments. Living versus non-living mangrove roots were used to study the chemical cues of the mangrove itself, independent of structure, and their role in mediating settlement and growth. Non-living root mimics of a foreign wood were used to compare biological traits (e.g. porous material), while PVC was used as a physical comparison to assess the importance of structure (i.e. erosion control) relative to the scraped mangrove treatment. Our study expands the growing literature examining the influence of mangrove root traits and mechanisms in supporting community biodiversity by focusing on substrate composition and whether roots are alive or dead. Previous works have focused on leaching of organic matter (Hunting et al. 2010, 2013b), root complexity (Nagelkerken et al. 2010, Vorsatz et al. 2021), root contact with the ground (Schutte & Byers 2017), and root density (Nanjo et al. 2014). By tracking community development of these treatments until one of them lost 50% of replicates to complete decay, we were able to examine the importance of other factors that came to vary among root treatments, including root length and the presence of secondary foundation species (e.g. sponges, bivalves), in determining community structure. To address our objective, we examined the following questions: (1) are epibionts more likely to grow on living than on non-living mangrove roots; (2) can root mimics offer suitable habitat for commonly found taxa, and does mimic type matter (e.g. wood, PVC); (3) are ecologically and conservation relevant time scales, determined by the decay time of one or more treatments, sufficient for the development of the epibiont community to approach its original state; and (4) are there links between secondary foundation species (bivalves and sponges) and the mobile invertebrate community? Through these comparisons, we can isolate complex foundation species traits to understand the characteristics that influence community composition and what this means for conservation and management of these dynamic environments.

2. MATERIALS AND METHODS

2.1. Study sites

We conducted our field experiment in the fringe red mangrove *Rhizophora mangle* forest on Solarte Island in the Bocas del Toro Archipelago on the Caribbean coast of Panamá from April 2017 to May 2018 (Fig. 1a). We haphazardly selected 2 representative mangrove coves (Coco and Corales), both with similar average depth of 1.2 m and where aerial roots hanging from the branches were permanently inundated and encrusted with rich epibiont communities (Fig. 1b,c). Each site was in a cove facing Almirante Bay and was protected from wave exposure by islets and reef.

2.2. Experimental design and mangrove root treatments

At each site, 5 root treatments, with 10 replicates each, were assigned in a random order >2 m apart. Treatments consisted of: (1) 'natural', an unmanipulated mangrove root control; (2) 'scraped', a mangrove root cleared of epibionts at the beginning of the experiment; (3) 'cut', a cleared mangrove root that was cut from the tree, dried for 3 wk, and reattached to a mangrove branch; (4) 'wood', an untreated wooden dowel (poplar); and (5) 'PVC', pipe made of polyvinyl chloride (Fig. 1d). The 2 root mimic treatments consisting of wood (Eston et al. 1992,

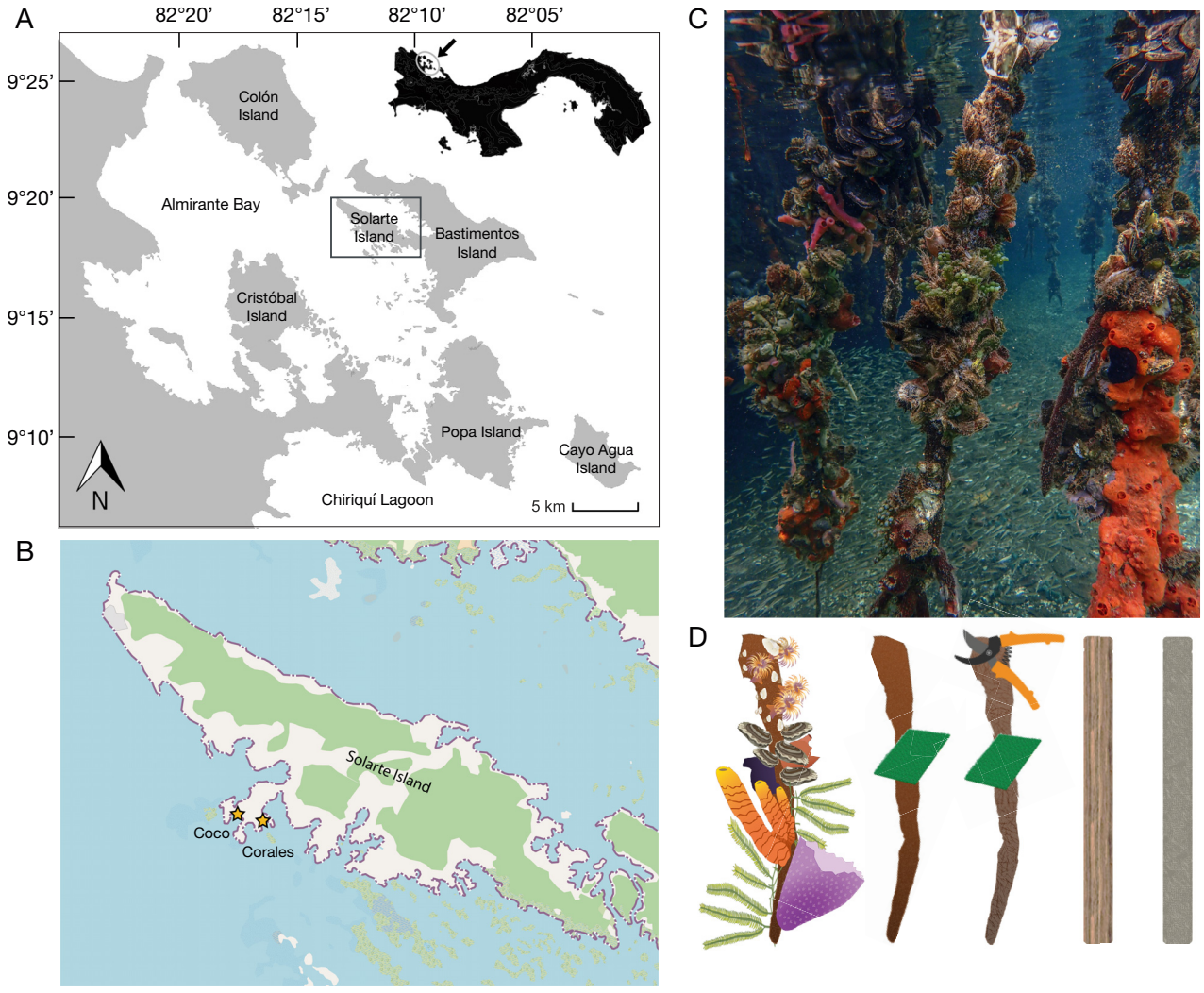

Fig. 1. Experimental study sites. This research was conducted on (A) Solarte Island of the Bocas del Toro Archipelago on the Caribbean coast of Panama. (B) The 2 mangrove sites (Coco and Corales, marked with yellow stars) were selected because of their similar, rich epibiont communities (C) to test for links between traits of foundation species and associated epibiont biodiversity. (D) Root treatments consisted of natural mangrove root control, scraped living mangrove root, cut and scraped non-living mangrove root, and 2 root mimics of wooden rod and PVC pipe (left to right)

MacDonald et al. 2008, Guerra-Castro & Cruz-Motta 2014, 2018) and PVC (Eston et al. 1992, Verweij et al. 2006, Nagelkerken et al. 2010) have been used in previous mangrove studies and allow for a direct comparison of common materials assumed to be surrogates for natural mangrove roots. Pairwise comparisons between subsets of treatments allowed us to test our specific research questions for a variety of response variables (see Table 1). Natural roots were controls used as a reference of the natural community and allow comparisons to scraped roots to document succession. Cut treatments were used to compare with scraped treatments to test whether living or dead roots affected community development over time. Wood and PVC treatments were used to compare whether artificial wood type (wood treatment) or commercially available products mimic community development and composition over the experimental period. The study lasted 14 mo, at which point we terminated the experiment because one of the treatments (cut mangrove root) lost more than 50% of replicates to complete decay. Termination of the experiment at this point allowed for inclusion of the cut mangrove treatment in all forms of sampling and analysis.

We standardized root diameter at the beginning of the experiment, since root diameter can be an important factor in determining available substrate for epibionts. To minimize potential differences caused by root complexity, we only selected non-bifurcated

mangrove roots for the natural, scraped, and cut treatments. The wooden rods had a weight added to their tip as ballast to maintain a vertical orientation. PVC pipes were lightly sanded to roughen their surface and partially closed at the ends to prevent predators (e.g. crabs) from residing inside while allowing water to enter to mitigate effects of buoyancy on root orientation. To control for potential variation in access by walk-on predators from below (Guerra-Castro & Cruz-Motta 2018), none of the roots were in contact with the sediment or other roots. We were able to control the length of the cut and mimic root treatments, but not the length of the scraped or natural mangrove roots without damaging the root itself. Therefore, we selected roots of a similar length to other treatments and then recorded initial root length to use as a covariate in analyses to account for any effect this may have had on initial settlement. We labeled each root with a numbered tag and marked the mean higher high water (MHHW) level with a horizontal colored nylon cable tie to denote the top of the sampled portion of each root. We attached roots to branches using cable ties so that the root tip was 60 cm below MHHW, which was the average submerged length of non-bifurcated mangrove roots in the area. Roots were monitored monthly to re-secure cable ties and to record any roots that rotted away above the MHHW. In both *in situ* and laboratory sampling, only the area below the MHHW was sampled.

2.3. Root growth and deterioration

To account for growth and deterioration of the roots over the course of the experiment, we measured the final root length *in situ*, which by necessity included the epibiont community growing on the roots (because overgrowth made it impossible to locate the end of the root without disturbing the epibionts). The initial length was subtracted from the final length to calculate the change in root length. This is important in quantifying available substrate for epibionts to colonize and measuring how the roots were affected by degradation due to boring invertebrates such as the isopod *Spaeroma terebrans* or shipworms (marine bivalves in the family Teredinidae). We recorded signs of boring (e.g. openings from *S. terebrans* or calcareous burrows of shipworms) as present or absent when roots were sampled in the laboratory. Because of the loss of some roots to deterioration, only 73 of the original 100 roots could be sampled at the conclusion of the experiment. Since community composition can be linked to available area (i.e. root length), and root treatments may have differed in final length, we examined how change in root length and survival of roots differed among treatments and the relationship between final root length and community composition.

2.4. *In situ* percent cover, community composition, and richness

Prior to collection of roots at the end of the 14 mo experiment, we conducted *in situ* surveys of sessile epibiont percent cover to compare treatments. *In situ* surveys are commonly used in the mangrove habitat to study epibiont communities (Ellison & Farnsworth 1990, MacDonald et al. 2008, Guerra-Castro & Cruz-Motta 2018, Janiak et al. 2018) and allow for evaluation of encrusting species, which may be difficult to accurately quantify through destructive sampling. We collected *in situ* data to account for these encrusting taxa and to capture any epibiota that may have been damaged during sampling. Further, by collecting both *in situ* and laboratory data, we could test whether differences in root treatments could be detected with both methods. We first recorded the total length of each root to account for growth or deterioration of non-PVC root treatments. We then used a ruler to measure the linear proportion of space on the root dominated by each of the following 13 categories: empty space, barnacle, bivalve, green algae, red algae, crustose coralline algae, cyanobacteria, sponge, tunicate, tube worm, hydroid, anemone, and bryozoan. Where there were overlapping epibionts, the outermost layer of epibionts was used for the percent cover score. The percent cover of both sides of the roots (i.e. facing ocean, facing island) was measured, but no significant difference was found; therefore, the side facing the ocean was used in all subsequent analyses.

2.5. Sessile community composition and richness

At the end of the experiment, the roots and mimics were collected (at a rate of ~4 randomly selected roots/sampling day). For collection, we enclosed each root in a large fabric bag with zip ties to retain all epibionts. Roots were transported to the laboratory in a cooler filled with aerated seawater. Once in the laboratory, root epibionts were removed and identified to the lowest possible taxonomic level, henceforth referred to as morphospecies. We recorded individual and total wet mass for each morphospecies and ob-

tained total biomass of all epibionts per replicate. However, it should be noted that the masses of encrusting taxa (e.g. encrusting bryozoans, crustose coralline algae, hydroids) may underrepresent their abundance due to their lack of structural integrity. Biomass analyses were thus done both with and without these groups included, and results were similar. The following metrics were quantified for the epibiota of each root: species richness, community composition, and biomass. Species richness, quantified as the number of morphospecies per root treatment, served as a metric for α-diversity. Variation in community composition served as a metric for β-diversity. We recorded biomass of each replicate to compare how treatments varied in their functioning as habitat. We employed destructive sampling in addition to the *in situ* percent cover to provide a more in-depth understanding of community assemblage as it accounts for the complex multi-layered epibiont community and allows for mobile invertebrate species to be quantified.

2.6. Mobile community composition, richness, and abundance

To explore the effects of primary (mangrove root treatment) and secondary foundation species (epifaunal sponges and bivalves) on the associated mobile fauna on roots, mobile invertebrates were collected and identified to the lowest possible taxonomic level. During destructive root sampling, secondary foundation species (e.g. bivalves, sponges, and tunicates) were dissected to separate their associated endobionts from non-associated organisms. Visible mobile invertebrates were collected from the sessile epibionts and kept in separate aerated tanks to prevent predation. After all sessile epibionts were removed from the root, the epibionts and root were rinsed, and the water was sieved to collect mobile invertebrates that may have been missed previously. We quantified richness of the mobile community as the number of morphospecies per treatment and site. We calculated abundance of mobile fauna as count data.

2.7. Secondary foundation species

Based on our visual estimates of percent cover, sponges and bivalves were dominant, and we tested whether root treatment or site affected their biomass and richness. Since the existing literature suggests sponges and bivalves are secondary foundation species (Altieri & Van De Koppel 2013, Aquino-Thomas & Proffitt 2014), we conducted isolated analyses to test whether they appear to have similar function when the substrate they are growing on is altered.

2.8. Analyses

To address our questions, we used permutational multivariate analyses of variance (PERMANOVA) (Anderson 2017) with *in situ* percent cover and biomass of sessile epibionts and count data of mobile invertebrates to compare community composition across treatments. Then we used generalized linear models (GLMs) with response variables of sessile richness and biomass as well as mobile richness and numerical abundance. Root treatment and site were fixed factors in all analyses. While ideally site would be treated as a random effect, to establish the generality of our results, it is recognized that random-effect models are not suitable below a certain number of levels within the random variable, often given as 10–15 (Luke 2017). Thus, we analyzed site as a fixed factor, and acknowledge that this is a caveat on the generalization of our results. Results, as they apply to our specific questions, are summarized in Table 1. To address the questions of whether epibionts are more likely to grow on living or non-living mangrove roots, we compared scraped mangrove roots to cut mangrove roots. Comparisons of scraped mangrove root to wood and then to PVC addressed the question of whether root mimics offer suitable habitat for commonly found taxa and whether mimic type matters. Finally, scraped mangrove roots were compared to natural mangrove control roots to test whether the decay time of one or more treatments was sufficient for the epibiont community of mangrove roots to return to its approximate original state. All data were analyzed with R version 4.1.1 (R Core Team 2021). The following sections provide details of each statistical procedure for each component of the study.

2.8.1. Root growth and deterioration

To examine how treatment affected change in root length (difference between initial and final root length), we fit GLMs using the glm function with the main effects of root treatment and site and the response variable of change in root length. Roots that completely deteriorated were included as a final root length value of zero, for a change in root length of −100%. A subsequent binominal GLM on all treatments excluding PVC was used to examine the main

Table 1. Results of multiple community analyses to address 3 of the 4 research questions regarding the role of foundation species traits in shaping community assemblage. All response variables in this table were significantly affected by root treatment. How results from pairwise comparisons in post hoc analyses address the question (no versus yes) is indicated after each question. Sessile community composition was quantified as both percent cover and biomass, differences in the response with those metrics are separated with a "/". Similarly for bivalve biomass and richness. Species richness is quantified as the average number of morphospecies per root treatment

Root A	Root B	Question	Sessile community composition (% cover/biomass)	Mobile richness	Sponge richness	Bivalve biomass/ richness
Scraped	Cut	Are epibionts more likely to grow on living than on or non-living mangrove roots? ($p < 0.05$ = Yes)	No/Yes	No	No	No/No
Scraped	PVC	Can root mimics offer suitable habitat for commonly found taxa, and does mimic type matter? ($p < 0.05$ = No)	Yes/No	Yes	Yes	Yes/Yes
Scraped	Wood		Yes/Yes	Yes	Yes	Yes/Yes
Natural	Scraped	Is the decay time of one or more treatments sufficient for the epibiont community of mangrove roots to return to approximately its original state? ($p < 0.05$ = No)	Yes/No	No	No	No/Yes

effects of root treatment and site on presence of boring invertebrates. Overall significance of each factor in the model was assessed by a Wald test with a chi-square error distribution using the Anova function from the package car (Fox & Weisberg 2019) with a Type III sum of squares. If differences were detected, we utilized the glht function of the multcomp package (Hothorn et al. 2008) to provide Tukey post hoc multiple comparisons of means with adjusted p-values. To examine the effect of final root length (as a proxy for available area on root) on sessile and mobile community composition (e.g. richness and biomass) within each treatment, we used the ggscatter function within the ggpubr package (Kassambara 2020) to plot linear regressions with 95% confidence intervals and to calculate a Pearson's r correlation coefficient within each treatment.

2.8.2. *In situ* percent cover community composition and richness

To examine treatment differences in the community composition data based on *in situ* sampling of roots, we created a Bray-Curtis dissimilarity matrix using root treatment and site as main effects. A square-root transformation was used to reduce distributional asymmetry before subjecting it to further analysis as per Legendre & Borcard (2018). To test for an overall estimate of similarity between the 2 Bray-Curtis matrices, we used Spearman rank correlations with the function cor.test. The functions permutest and betadisper were used to analyze the multivariate homogeneity of group dispersion as a multivariate analogue of Levene's test for homogeneity of variances. We conducted a PERMANOVA using the adonis2 function from the vegan package (Oksanen et al. 2020) to test for differences in community composition with the main effects of root treatment, site, the interaction of treatment and site, and a covariate of initial root length, to account for variation within natural (mean ± SE root length = 73.2 ± 2.4 cm) and scraped roots (74.8 ± 2.6 cm). Other parameters were left as default, including number of permutations at 999. For *in situ* surveys, the abundance of taxa was estimated as percent cover of major taxonomic groups. Post hoc pairwise comparisons were made using the pairwise.adonis function of the pairwiseAdonis package (Martinez Arbizu 2017), which returns adjusted p-values. To test for the main effects of root treatment, site, the interaction of treatment and site, and a covariate of initial root length on species richness, we used a GLM with Poisson distribution.

2.8.3. Sessile community composition and richness

We used the same data pretreatments and identical methodology as for the *in situ* data to conduct a second PERMANOVA from the destructive sampling, using biomass of each of the 86 sessile epibiont morphospecies identified as a representation of their abundance. For the same sessile community data, similarity percentage analyses (SIMPER) (Clarke 1993) were used to determine which taxonomic groups and species had the greatest contribution to dissimilarity

in the community composition. The first SIMPER compared 10 major taxonomic groups (i.e. bivalve, sponge, tunicate, barnacle, red algae, green algae, cyanobacteria, hydroid, tubeworm, and sea anemone), whereas the second SIMPER compared all 86 morphospecies.

For sessile community data from collected roots, we used a GLM with main effects of root treatment, site, the interaction of treatment and site, and a covariate of initial root length to detect effects on species richness with Poisson distribution. We then used the Anova function from the car package with a Type III sum of squares to run a Wald test with a chi-square error distribution to test for significance of the main effects and their interaction on richness, and to compare coefficients.

2.8.4. Mobile community composition, richness, and abundance

For the mobile community, we conducted a third PERMANOVA using count data of invertebrate morphospecies with main effects of root treatment, site, the interaction of treatment and site, and a covariate of initial root length. The same methodology was utilized for all PERMANOVAs. Additionally, 2 response variables (morphospecies richness and abundance) were assessed using GLMs with main effects of root treatment, site, the interaction of treatment and site, and a covariate of initial root length. We then tested how root treatment indirectly affected the mobile community through secondary foundation species interactions. We used GLMs with main effects of sponge and bivalve richness and biomass to assess the response variable of mobile invertebrate richness.

2.8.5. Secondary foundation species

Variation in secondary foundation species (i.e. sponges and bivalves) richness and biomass among root treatments was assessed using GLMs, with main effects of root treatment, site, the interaction of treatment and site, and a covariate of initial root length.

3. RESULTS

3.1. Root growth and deterioration

We found an effect of root treatment ($p < 0.001$, chi-square test) but not site ($p = 0.748$) on change in root length (e.g. growth or deterioration). Cut roots were the shortest of all treatments by the end of the experiment, and post hoc pairwise comparisons of root treatments indicated that cut roots had a significantly greater decrease in root length compared to other treatments. Scraped and wood treatments had similar decreases in root length to each other and were significantly shorter than PVC (Fig. 2). During the experiment, there were noticeable signs of deterioration (e.g. rotting and/or boring by invertebrates) starting in month 8. By the end of the experiment, 70% of the cut mangrove roots had completely deteriorated, which was nearly 5 times more than the living mangrove treatments, while only one wood treatment completely deteriorated (Fig. 2). Since we monitored the roots over time, we observed that roots were lost from progressive deterioration rather than other factors such as sudden dislodgment in storms. We found a significant effect of root treatment ($p < 0.001$) on the presence of boring, but no effect of site ($p = 0.570$), with greater frequency of boring observed in wood compared to the cut, scraped, and natural mangrove root treatments. Initial root length was used as a covariate in all analyses, but never had a significant effect.

3.2. *In situ* percent cover community composition and richness

The PERMANOVA based on percent cover of encrusting epibionts revealed that root treatment ($p = 0.001$) and site ($p = 0.001$) had significant effects on community composition (Table 2A, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m686p015_supp.pdf), with natural mangrove roots having the highest percent cover. There was no effect of the interaction of treatment and site ($p = 0.177$), nor initial root length ($p = 0.202$). The permutation test for homogeneity of multivariate dispersions found no difference in dispersion between groups ($F = 0.605$). The dominant sessile epibiont group, with the highest percent cover across all treatments, was sponges, followed by red algae, which, together with empty space, contributed to the most dissimilarity between root treatments. The post hoc analysis revealed that epibiont composition of natural mangrove roots differed from that of cut mangrove roots and root mimic treatments ($p = 0.036$; Table 2B), but not scraped mangrove roots ($p = 0.216$; Table 2B, Fig. 3A). No differences in the epibiont composition were detected between scraped and cut mangrove roots ($p = 0.556$), PVC ($p = 0.065$), nor wood ($p = 0.556$). Additionally,

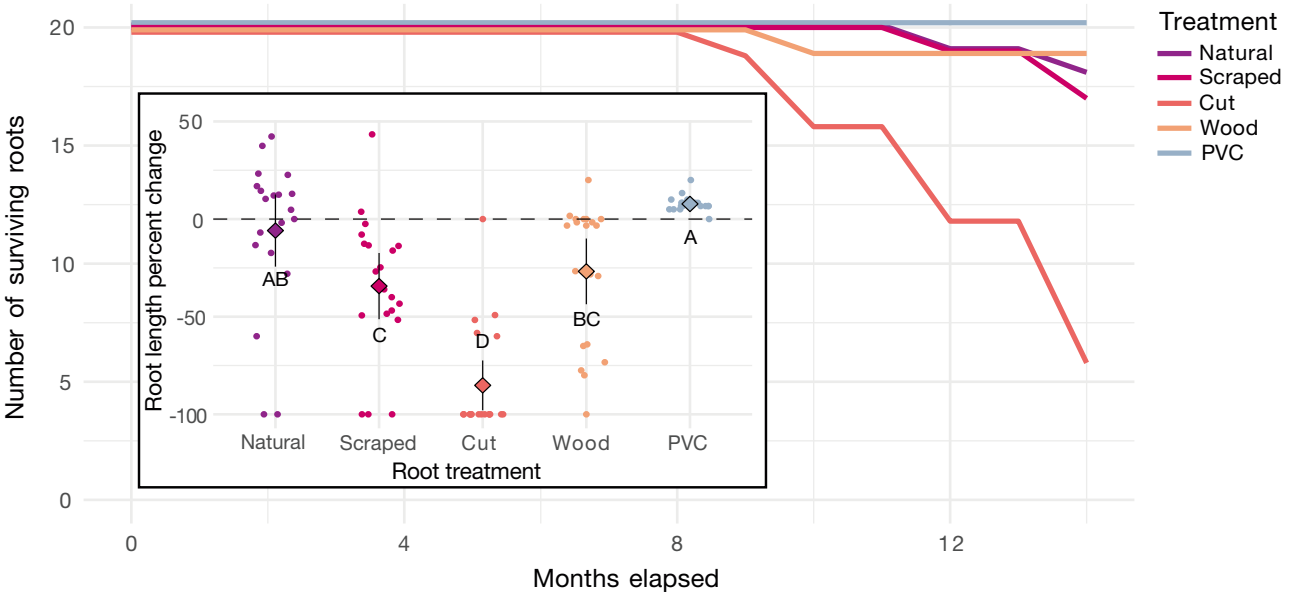

Fig. 2. Root treatment survival and percent change in root length. Survival curve of total roots for both sites combined over the experiment duration based on complete loss of roots, with inset of root length percent change. Lost roots are those that deteriorated away completely or to the mean higher high-water level, such that they could not be sampled. Lost roots were included in the root length change calculations as 100 % reduction in length. Change in root length includes added length of epibionts at the tip, which explains why there was an apparent increase in length for the PVC and some wood replicates. Treatments within each plot with different letters were found to differ in the post hoc analyses ($p < 0.05$)

no difference in epibiont composition was found between cut mangrove roots and the wood treatment. Overall mean (±SE) sessile species richness across all root treatments was 4.568 ± 2.923. Sessile richness of *in situ* data (i.e. 12 major taxonomic groups) revealed no significant effects of root treatment ($p = 0.272$), site ($p = 0.814$), interaction of treatment and site ($p = 0.904$), or initial root length ($p = 0.629$).

3.3. Sessile community composition and richness

The Bray-Curtis distance matrix based on *in situ* percent cover and biomass had an overall moderate positive correlation with rho = 0.415, $p < 0.001$. Mean (±SE) biomass (i.e. wet mass) for the root treatments were: 763.546 ± 180.715, 292.623 ± 37.797, 173.709 ± 73.375, 163.090 ± 35.091, and 22.616 ± 10.934 g for natural mangrove roots, PVC, scraped mangrove roots, wood, and cut mangrove roots, respectively.

Table 2. PERMANOVA analyses based on *in situ* percent cover data collected in the field. (A) Results found differences in mangrove epibiont communities among root treatments and sites. (B) Pairwise comparisons of root treatments from PERMANOVA using a Bray-Curtis dissimilarity matrix on square-root transformed data used to test for differences in mangrove root communities. Significant p-values ($p < 0.05$) are in **bold**. Adjusted p-value: Holm-Bonferroni correction

(A)	df	SS	pseudo-*F*	R^2	Pr(>*F*)
Treatment	4	1.216	3.263	0.132	**0.001**
Site	1	0.860	9.230	0.093	**0.001**
Initial root length	1	0.136	1.459	0.015	0.196
Treatment:Site	4	0.489	1.311	0.053	0.170
Residual	70	6.522		0.707	
Total	80	9.223		1.000	

(B) Pairs	df	SS	pseudo-*F*	R^2	p	Adj. p
Natural vs. Scraped	1	0.267	2.198	0.062	0.054	0.216
Natural vs. Cut	1	0.291	2.879	0.111	**0.004**	**0.036**
Natural vs. PVC	1	0.351	3.808	0.096	**0.004**	**0.036**
Natural vs. Wood	1	0.480	4.144	0.106	**0.005**	**0.036**
Scraped vs. Cut	1	0.098	0.872	0.038	0.528	0.556
Scraped vs. PVC	1	0.323	3.251	0.089	**0.013**	0.065
Scraped vs. Wood	1	0.156	1.261	0.036	0.278	0.556
Cut vs. PVC	1	0.384	4.936	0.165	**0.002**	**0.020**
Cut vs. Wood	1	0.223	1.995	0.077	0.103	0.309
PVC vs. Wood	1	0.386	3.883	0.095	**0.005**	**0.036**

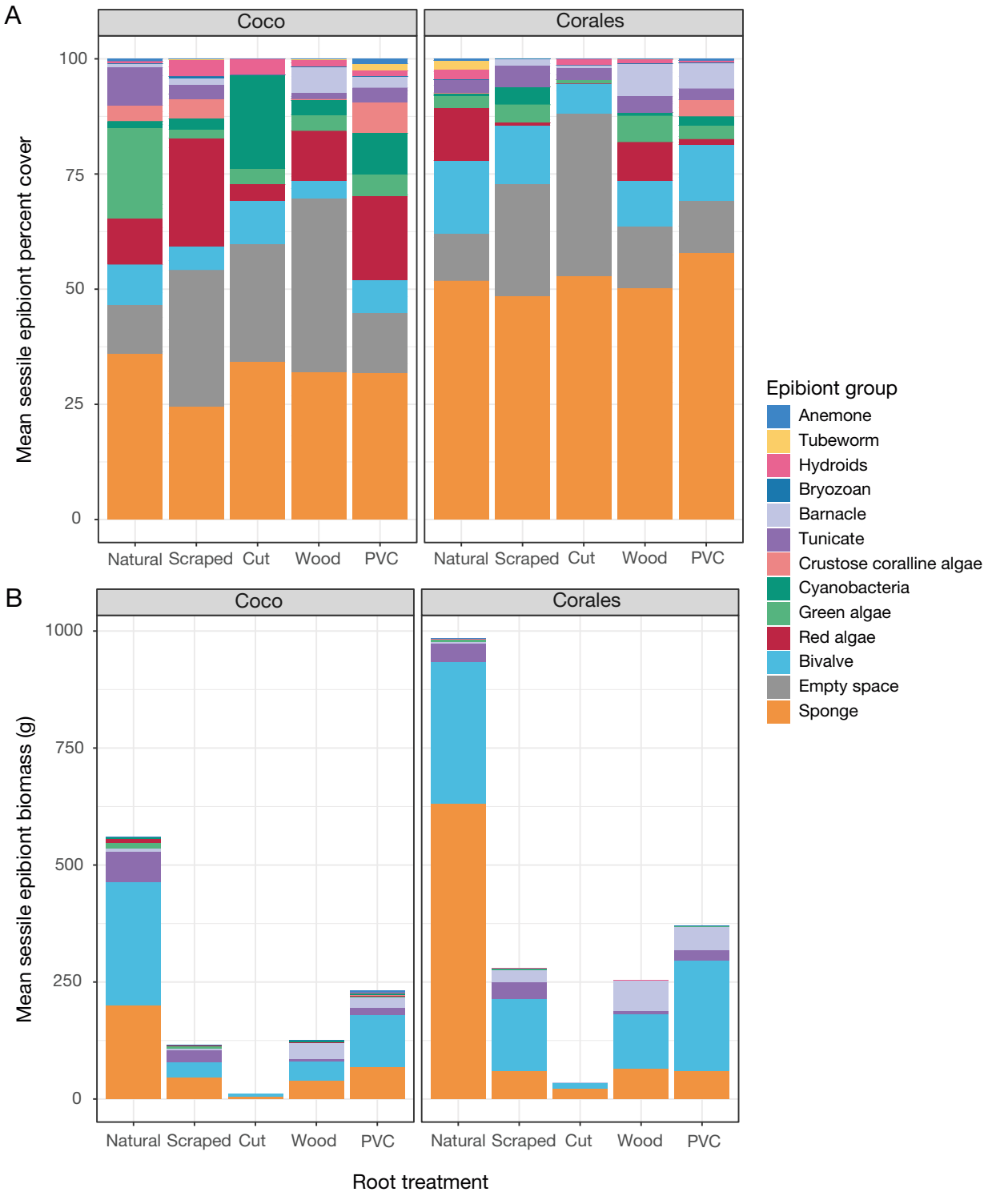

Fig. 3. Community composition comparisons of mean (A) percent cover of sessile epibionts and empty space and (B) sessile epibiont biomass of 5 root treatments across 2 sites (Coco and Corales). Root treatment consisted of natural mangrove root control, scraped living mangrove root, cut and scraped non-living mangrove root, and 2 root mimics of wooden rod and PVC pipe Percent cover differed among treatments and sites, with pairwise comparisons revealing significant differences between PVC and natural and PVC and cut mangrove roots. Composition of sessile epibiont biomass differed among treatments and sites, with pairwise comparisons revealing differences between natural mangrove roots and PVC from all other treatments as well as each other

Table 3. PERMANOVA analyses based on sessile species biomass data collected from the laboratory. (A) Results found differences in mangrove epibiont communities among root treatments and sites. (B) Pairwise comparisons of root treatments from PERMANOVA using a Bray-Curtis dissimilarity matrix on square-root transformed data used to test for differences in mangrove root communities. Significant p-values ($p < 0.05$) are in **bold**. Adjusted p-value: Holm-Bonferroni correction

(A)	df	SS	pseudo-*F*	R^2	Pr(>*F*)	
Treatment	4	2.846	4.579	0.206	**0.001**	
Site	1	0.602	3.874	0.044	**0.001**	
Initial root length	1	0.154	0.992	0.011	0.382	
Treatment:Site	4	0.586	0.943	0.042	0.521	
Residual	62	9.635		0.697		
Total	72	13.823		1.000		
(B) Pairs	df	SS	pseudo-*F*	R^2	p	Adj. p
Natural vs. Scraped	1	0.740	4.023	0.130	**0.002**	**0.010**
Natural vs. Cut	1	1.240	7.009	0.260	**0.001**	**0.010**
Natural vs. PVC	1	0.580	4.006	0.108	**0.001**	**0.010**
Natural vs. Wood	1	0.974	5.158	0.135	**0.001**	**0.010**
Scraped vs. Cut	1	0.420	2.538	0.130	**0.016**	**0.048**
Scraped vs. PVC	1	0.632	4.680	0.135	**0.001**	**0.010**
Scraped vs. Wood	1	0.227	1.239	0.040	0.235	0.235
Cut vs. PVC	1	1.288	11.282	0.329	**0.001**	**0.010**
Cut vs. Wood	1	0.469	2.646	0.103	0.037	0.074
PVC vs. Wood	1	0.663	4.492	0.111	**0.003**	**0.012**

The PERMANOVA based on epibiont biomass revealed that community composition differed by root treatment ($p = 0.001$) and site ($p = 0.001$; Table 3A, Fig. 3, Fig. S2 in the Supplement), but there was no significant effect of root length ($p = 0.382$) or the interaction of treatment and site ($p = 0.521$). Scraped mangrove roots differed in community composition from natural mangrove roots ($p = 0.010$), PVC ($p = 0.010$), and cut mangrove roots ($p = 0.048$), but not wood ($p = 0.235$; Table 3B). No difference in community composition was detected between cut mangrove roots and wood treatments ($p = 0.074$; Table 3B). The permutation test for homogeneity of multivariate dispersions found differences in dispersion among groups ($F = 0.017$). PVC and cut treatments had lower dispersions than other treatments. The first SIMPER analysis on the same broad taxonomic epibiont categories used in the *in situ* surveys, excluding empty space, revealed that bivalves and sponges had the greatest contribution to the dissimilarity of community composition across all pairwise comparisons of treatments, making up 71–85% of the cumulative contribution (Table 4). Bivalves accounted for 44–59% of the dissimilarity, and sponges accounted for 19–34%, followed by tunicates (3–11%) and barnacles (1–19%). Barnacles had a greater contribution to community composition in root mimic treatments than mangrove roots, living or non-living. In comparison, tunicates had a greater contribution to community composition in living mangrove roots than other treatments. Of the 2 sites, bivalves, barnacles, and sponges had a greater contribution to community composition in Corales than in Coco.

Using a second SIMPER analysis on morphospecies, we found that 17 of the 86 taxa accounted for the largest dissimilarities among treatments in sessile epibiont communities (Table 4). Of these 17 taxa, there were 5 bivalves — *Ostrea stentina*, *Pinctada imbricata*, *Crassostrea rhizophorae*, *Dendostrea frons*, and *Isognomon alatus* — all of which were also among the most commonly found species, detected on >50% of roots (Table S1). Eight sponges were among the taxa with the largest percent contribution to dissimilarity, of which 2 were common species, *Tedania ignis* and *Mycale microsigmatosa*. Barnacles, 2 species of tunicates (*Phallusia nigra* and *Herdmania pallida*), and the green algae *Caulerpa verticillata* were also among the taxa with the largest percent contribution to dissimilarity.

A total of 86 sessile morphospecies were observed on the roots, representing the classes Demospongiae (sponge), Ascidiacea (tunicate), Bivalvia (bivalve), Polychaeta (tubeworm), Cyanophyceae (cyanobacteria), Hexanauplia (barnacle), Hydrozoa (hydroid), and Anthozoa (sea anemone), and the phyla Chlorophyta (green algae), Rhodophyta (red algae), and Bryozoa (bryozoan). No taxa were present on all roots. The sessile morphospecies detected on >50% of all roots, henceforth referred to as 'common', were the barnacles *Amphibalanus* spp. and the oyster *O. stentina*, which were found on every PVC root, and the ascidian *Eudistoma olivaceum*, which was found on every natural and cut mangrove root (Table S1). The most common sponges included *T. ignis*, *Haliclona manglaris*, *M. microsigmatosa*, which were found in all root treatments, and *H. piscaderaensis*, which was in all treatments except cut mangrove root. Morphospecies with the greatest biomass across all treatments were *T. ignis* (maximum mass = 1926.544 g, mean ± SE mass = 124.855 ± 57.735 g), *T. klausi* (571.705, 85.199 ± 49.985 g), *Haplosclerida* spp. (399.882, 156.283 ± 67.706 g), *O. stentina* (335.573, 90.241 ± 11.784 g), *Pinctada imbricata* (266.130, 32.535 ± 6.710 g), and *Niphates erecta* (258.687, 59.512 ± 35.467 g).

Table 4. Percent contributions of most influential taxa to dissimilarity of community composition based on pairwise comparisons of root treatments. Results are from SIMPER run on biomass data from root collections. **Bold** indicates species found on >50% of the roots in multiple treatments. Bivalves and sponges formed the majority of community biomass regardless of treatment, making up 71–87%

Class	Taxa	Natural vs. Scraped	Natural vs. Cut	Natural vs. PVC	Natural vs. Wood	Scraped vs. Cut	Scraped vs. PVC	Scraped vs. Wood	Cut vs. PVC	Cut vs. Wood	PVC vs. Wood
Bivalvia (Bivalves)	All species	43.69	48.31	42.78	42.16	48.99	49.71	45.35	56.67	46.85	50.47
	Ostrea stentina	21.08	24.20	20.44	20.57	19.62	31.46	19.69	38.45	20.94	32.52
	Pinctada imbricata	7.21	6.09	5.96	6.46	8.30	8.29	9.87	6.85	6.82	8.02
	Crassostrea rhizophorae	4.85	6.37	3.10	5.34	10.36	3.77	8.34	3.50	13.11	3.87
	Dendostrea frons	4.73	4.26	4.41	4.12	9.79	5.71	7.25	5.01	2.78	5.40
	Isognomon alatus	2.43	2.33		2.38	2.58		2.26		2.77	
Demospongiae (Sponges)	All species	40.65	38.87	38.01	38.82	30.64	23.75	25.44	20.24	29.30	23.35
	Tedania ignis	17.13	18.31	18.07	18.63	10.18	4.55	9.21	5.73	15.75	7.41
	Tedania klausi	3.59	3.53	5.14	3.68		2.62		2.77		2.80
	Haliclona spp.	2.75				8.67	3.57	5.29			
	Haplosclerida			5.79	2.41		6.48		7.03	1.60	6.68
	Mycale microsigmatosa				2.53	5.23		5.43	2.27	4.81	3.62
	Halichondria magniconulosa	2.46	3.30							2.56	
	Haliclona implexiformis		2.43	2.13							
	Niphates erecta			2.17							
Cirripedia (Barnacles)	All species	2.01	0.98	7.79	8.11	3.78	13.44	16.50	13.74	19.27	16.46
	***Amphibalanus* spp.**			6.13	7.11	3.49	11.13	14.54	12.94	17.52	13.43
Ascidiacea (Tunicates)	All species	9.26	7.42	7.75	7.11	10.29	10.16	8.32	7.05	2.93	7.04
	Phallusia nigra						2.55		2.79		2.55
	Herdmania pallida					2.96		2.39			
Chlorophyta (Green alga)	All species	3.20	3.76	2.10	2.87	2.22	0.52	1.31	0.24	0.18	0.27
	Caulerpa verticillata	2.62	3.34								

Natural mangrove roots and PVC had greater richness than all other treatments, 70 and 69 total morphospecies, respectively, and did not differ from one another ($p = 0.777$, mean richness). Average species richness was greatest in natural mangrove roots (22.9 ± 2.1, mean ± SE) and PVC (21.5 ± 0.9). In comparison, wood (11.9 ± 1.6), scraped (13.5 ± 1.9), and cut mangrove roots (9.5 ± 0.7) had approximately half the average richness of natural mangrove roots. There was a significant interaction between root treatment and site ($p < 0.001$, chi-square test), as well as an effect of initial root length ($p = 0.032$) on sessile epibiont morphospecies richness. We found a significant positive correlation between sessile epibiont richness and final root length within scraped ($r = 0.738$, $n = 13$, $p = 0.004$) and wood ($r = 0.765$, $n = 19$, $p < 0.001$) treatments (Fig. S3).

Total sessile epibiont biomass (i.e. wet mass) differed among sites ($p = 0.026$), but not root treatments ($p = 0.057$). Neither the interaction of treatment and site ($p = 0.714$) nor initial root length ($p = 0.717$) showed significant effects. Corales had greater overall biomass than Coco, with generally more sponges and bivalves. Within scraped mangrove roots ($r = 0.628$, $p = 0.021$) and wood treatments ($r = 0.722$, $p < 0.001$), there were positive correlations between total sessile epibiont community biomass and final root length (Fig. S4).

3.4. Mobile community composition, richness, and abundance

The community composition of mobile invertebrates differed among root treatments ($p < 0.001$, PERMANOVA) and between sites ($p < 0.001$), but the interactions of treatment and site ($p = 0.101$) and root length ($p = 0.783$) were not significant (Table 5A). The mobile community composition differed between natural and cut mangrove roots ($p = 0.010$), between PVC treatments and wood ($p = 0.016$), and between PVC treatments and cut mangrove roots ($p = 0.010$). However, no differences were detected between the mobile community composition of scraped mangrove roots and the other root treatments (Table 5B). The richness of mobile inver-

Table 5. PERMANOVA analyses based on mobile species count data collected from destructive sampling of epibionts in the laboratory. (A) Results found differences in mangrove mobile communities among root treatments and sites. (B) Pairwise comparisons of root treatments from PERMANOVA using a Bray-Curtis dissimilarity matrix on square-root transformed data were used to test for differences in mangrove root communities. Significant p-values ($p < 0.05$) are in **bold**. Adjusted p-value: Holm-Bonferroni correction

(A)	df	SS	pseudo-*F*	R^2	Pr(>*F*)	
Treatment	4	2.022	2.551	0.125	**0.001**	
Site	1	0.845	4.264	0.052	**0.001**	
Initial root length	1	0.128	0.645	0.008	0.783	
Treatment:Site	4	1.036	1.307	0.064	0.101	
Residual	61	12.088		0.750		
Total	71	16.119		1.000		
(B) Pairs	df	SS	pseudo-*F*	R^2	p	Adj. p
Natural vs Scraped	1	0.452	2.261	0.077	**0.011**	0.066
Natural vs Cut	1	0.860	4.019	0.167	**0.001**	**0.010**
Natural vs PVC	1	0.237	1.673	0.048	0.069	0.276
Natural vs Wood	1	0.507	2.183	0.064	**0.023**	0.115
Scraped vs Cut	1	0.316	1.181	0.065	0.272	0.318
Scraped vs PVC	1	0.348	2.110	0.066	**0.008**	0.056
Scraped vs Wood	1	0.428	1.614	0.053	0.097	0.291
Cut vs PVC	1	0.933	5.601	0.196	**0.001**	**0.010**
Cut vs Wood	1	0.436	1.457	0.062	0.159	0.318
PVC vs Wood	1	0.643	3.226	0.084	**0.002**	**0.016**

tebrates differed among root treatments ($p < 0.001$, chi-square test) but not between sites ($p < 0.071$). The interactions of treatment and site ($p = 0.303$) and root length ($p = 0.897$) were not significant. Cut roots had the lowest mean richness. Within scraped mangrove root ($r = 0.633$, $p = 0.02$) and wood treatments ($r = 0.793$, $p < 0.01$), mobile richness was positively correlated with final root length (Fig. S3). Mobile community richness was also positively correlated with the biomass of bivalves ($p < 0.001$) and sponges ($p = 0.006$) (Fig. S5). The most frequently detected mobile invertebrates were the shrimp *Cuapetes americanus* (found on every natural mangrove root and over 85% of scraped mangrove and PVC treatments), polychaete worms of the family Nereididae (found on every PVC root and 94% of the natural roots), amphipods (found on every PVC and natural root), isopods from the genus *Paracerceis* (found on over 85% of

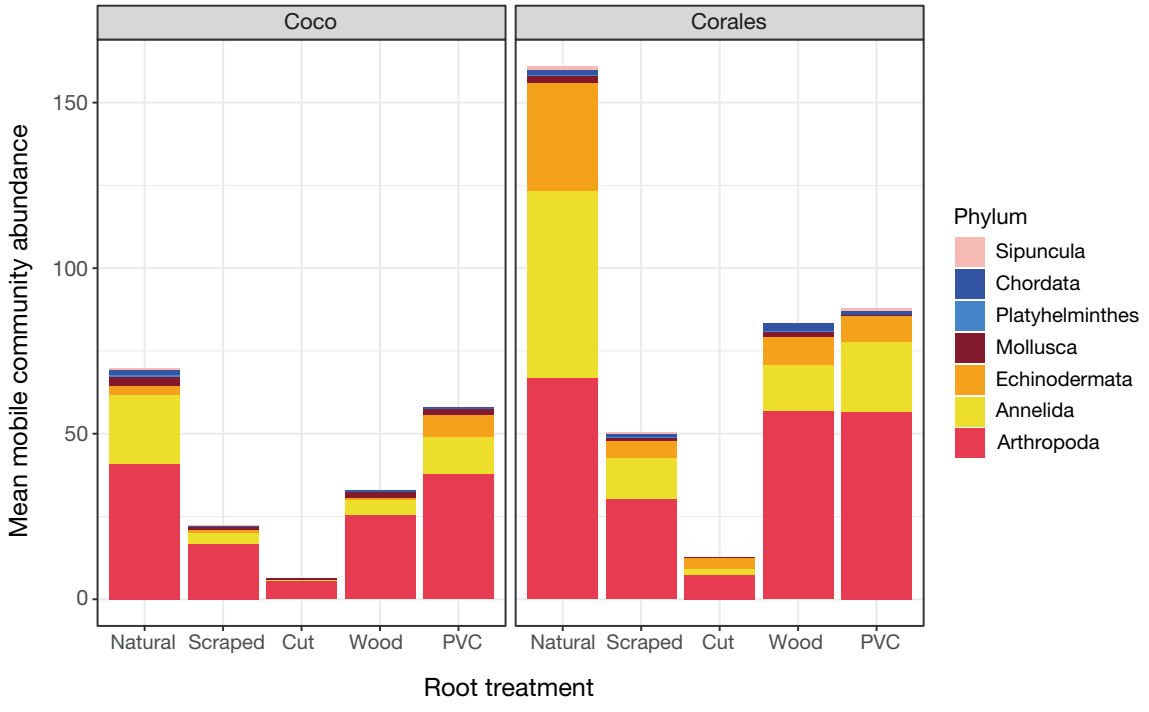

Fig. 4. Mean mobile community abundance by treatment, averaged across roots. Site ($p = 0.008$) had a significant effect on mean mobile community abundance, while richness of mobile invertebrates differed among root treatments ($p < 0.001$), but not between sites ($p < 0.071$)

natural, scraped and PVC roots), and the snapping shrimp *Synalpheus apioceros* (found on over 80% of natural mangrove roots; Table S2). Mean mobile community abundance differed between sites ($p = 0.008$), but not among root treatments ($p = 0.379$); and neither of the interactions of treatment and site

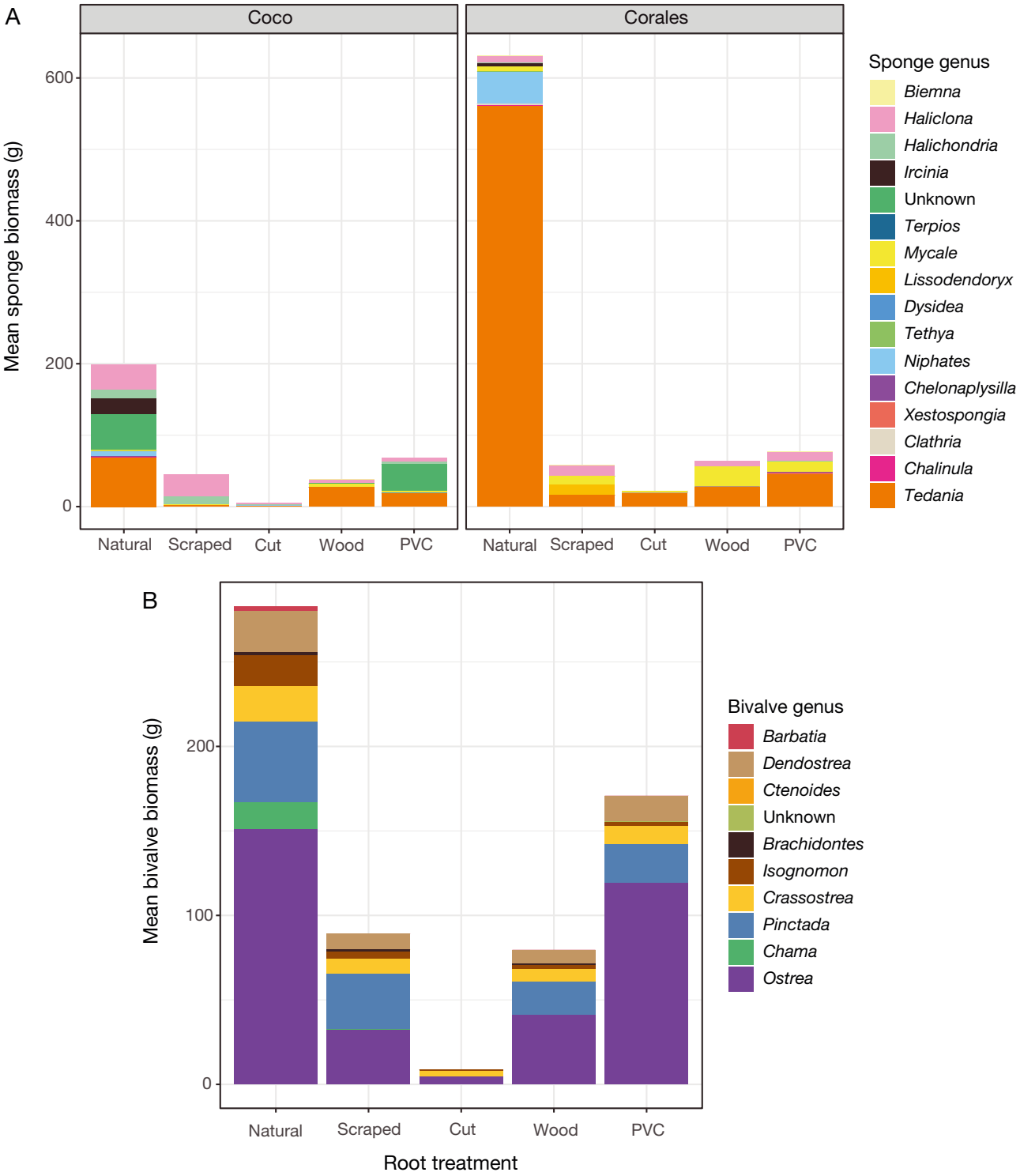

Fig. 5. Mean biomass of (A) sponge and (B) bivalve species by root treatment and site. Root treatment had significant effects on richness and bivalve richness and biomass. Site had a significant effect on sponge biomass, with Corales having greater biomass than Coco

($p = 0.577$) or root length ($p = 0.905$) were significant. Corales had a greater abundance of mobile fauna than Coco (Fig. 4).

3.5. Secondary foundation species

The SIMPER analysis indicated that bivalves and sponges had the greatest influence on sessile epibiont community structure, and therefore we explored how these taxa were affected by root treatments. There were significant effects of root treatment on sponge richness ($p = 0.003$), bivalve richness ($p = 0.027$), and bivalve biomass ($p = 0.004$). Only site influenced sponge biomass ($p = 0.002$), and the interaction of treatment and site had no effect on either of the secondary foundation taxa (Table S3, Fig. 5). The Corales site had greater sponge biomass than Coco. Scraped mangrove roots had lower sponge richness than natural roots ($p = 0.049$, *z*-test), and wood had lower sponge richness than natural roots ($p = 0.046$).

4. DISCUSSION

Foundation species play an essential role in ecosystems, but little is known regarding how their traits shape the associated community composition. Our treatments represented variation in both substrate composition and whether the foundation species was alive or dead, allowing us to answer a series of complementary questions about mangrove traits and community structure of epibionts (Table 1). We compared living mangrove roots (i.e. scraped treatments) to non-living mangrove roots (i.e. cut treatments) and root mimics (i.e. wood and PVC) and found some evidence for biotic controls (e.g. nutrient exchange) shaping the associated community, but only with destructive sampling. Additionally, we found that non-living roots (i.e. cut roots) quickly deteriorated and became shorter or were lost altogether (Fig. 2), and as a result, they had a reduced capacity to support a diverse community. We established an unmanipulated living mangrove root control (i.e. natural treatment) for comparison to scraped mangrove roots, and found that 14 mo, the fastest decay time among the treatments, was sufficient for the epibiont community to visually return to approximately its undisturbed state, in regard to percentage cover. However, that time period was not sufficient using the metric of biomass and greater taxonomic resolution. This provides both a timeline and criteria to determine whether the community recovers over that temporal scale. Further, we found that, overall, root mimics function similarly to living mangrove roots, although wood mimics were more similar to mangrove roots than PVC.

4.1. Are epibionts more likely to grow on living than on non-living mangrove roots?

We tested whether epibionts were more likely to grow on living scraped mangrove roots compared to non-living, cut mangrove roots. Although percent cover of broad taxonomic groups *in situ* failed to reveal significant differences in community composition, among treatments, the more detailed examination of the epibiont community through destructive sampling of the roots in the laboratory provided evidence to suggest that nutrient exchange or other such mechanisms may mediate epibiont community assemblage of mangrove roots (Table 1). These differences are partially due to the greater taxonomic resolution made possible in the laboratory, but are largely a consequence of the rapid deterioration of non-living mangrove roots (Fig. 2). This deterioration of non-living mangrove roots limits the ability to structurally support epibiont biomass. The correlation between root length and diversity implies a limited time following death during which roots serve as viable habitat for epibionts. Our study clearly shows high levels of root loss (10%) in healthy stands of mangroves, a pattern of loss that could potentially be amplified in stands under stress. Stress to mangrove stands is compounded in many regions of the world with increasing frequency and magnitude of hurricanes combined with urban and aquacultural/agricultural encroachment preventing mangroves from expanding landward to recover, and/or by altering hydrology of the area minimizing suitable refuge, which results in large stands of dead mangroves (Duke et al. 2017, Feller et al. 2017, Krauss et al. 2020, Radabaugh et al. 2020, Svejkovsky et al. 2020). Understanding the mechanisms influencing root length, including death and deterioration of roots, is important since root length determines the habitable area of roots, and length appeared to be the biggest difference between living and non-living roots in their influence on the biodiversity of epibiont communities. The sample size of non-living mangrove roots by the end of the study was limited, with only 6 roots remaining, and large variability within the cut root treatment makes it hard to determine whether there is a true non-effect, or whether it is an

artifact of the sample size and variability, warranting further exploration.

Given the roles that epibionts play in biofiltration, bioremediation, bioturbation, and habitat modification, and as food sources for fishes and humans (Ellison 2008, MacDonald et al. 2008, MacDonald & Weis 2013, Carrasquilla-Henao & Juanes 2017, Aguirre-Rubí et al. 2018, Seemann et al. 2018, Vaughn & Hoellein 2018), it is crucial for conservation and management purposes to understand how root damage/death affects the epibiont community. This is beneficial information for mangrove conservation and management because findings suggest that following death of mangrove trees, the roots and associated epibiont community may remain for months (Cintrón et al. 1978). However, new mangroves should be restored to the area as soon as possible given that the persistence of habitat provision function by mangroves is relatively temporary compared to the time required for mangrove regrowth.

4.2. Can root mimics offer suitable habitat for commonly found taxa, and does mimic type matter?

Given that living and non-living mangrove roots can be functionally similar, but non-living mangrove roots rapidly deteriorate, we directly compared root mimic treatments to one another to determine the usefulness of hard infrastructure as surrogates. One of the most commonly used root mimic materials in mangrove studies is PVC (Cocheret De La Moriniere et al. 2004, Nagelkerken et al. 2010, Hunting et al. 2013a, Janiak et al. 2018), despite there being few studies that have examined whether manufactured root mimics function similarly to living mangrove roots. Previous sponge studies found species-specific differences in growth on mangrove roots compared to PVC, with reef-associated sponge species growing faster when attached to PVC and mangrove-associate sponge species growing faster when attached to mangrove roots (Ellison et al. 1996, Wulff 2005). In the present study, we also found a difference in sponge richness and the types of sponge species growing on mangrove roots compared to root mimics. However, differences between root treatments varied depending on the taxonomic focus or resolution being examined. For example, when examining sessile community composition using *in situ* percent cover, we found PVC treatments were similar to scraped treatments. Yet, when using biomass data collected in the laboratory with higher taxonomic resolution, differences in the community composition were detected between PVC and scraped mangrove treatments. We also wanted to compare an organic root mimic (i.e. commercial wood) to living mangrove roots to determine whether the community of these mimics would better match that of the living mangrove roots than PVC. We detected no differences in any of our biodiversity metrics between scraped living mangrove roots and our wood treatment, suggesting that these treatments could be useful in both mangrove experiments and as a surrogate for real roots in temporary management interventions. Comparatively, PVC functioned similarly to scraped living mangrove roots except for overall epibiont biomass (Table 1). We found that PVC treatments had greater biomass than scraped mangrove roots. These results support the findings of Janiak et al. (2018), which showed higher epibiont percent cover, richness, and diversity on artificial structures (e.g. PVC colonization panels) compared to mangrove roots.

Although root mimics support general community patterns similar to those of live mangrove roots, we found differences in individual epibiont species and bias towards some taxa (e.g. barnacles), which warrants caution when describing species-level implications for mangroves if using root mimics. We found that both PVC and wood root mimics had greater abundance of barnacles, measured as both percent cover and biomass, and a smaller abundance of tunicates compared to living mangrove roots. Barnacles are common fouling species, especially on PVC (Janiak et al. 2018). These differences between treatments could be linked to chemical compounds emitted from the roots that could alter induction or inhibition settlement cues. A previous study by Guerra-Castro & Cruz-Motta (2014) using pine wood as an artificial root treatment found greater abundance of barnacles on the pine compared to mangrove roots. The authors hypothesized that the dominant oyster *Crassostrea rhizophorae* may outcompete barnacles on natural roots and/or that barnacle larvae select settlement habitats not previously colonized by oysters. Competitive exclusion is unlikely to be the cause of the lower abundance of barnacles on the mangrove treatments relative to root mimics in our study since mangrove roots had greater empty space than mimics, indicating that available space was not limited. Further, no relationship between barnacle and oyster biomass was detected. Extensive barnacle coverage of mangrove roots can be detrimental to the tree, as barnacles can interfere with root aeration and can reduce root growth by 30%, thus negatively impacting net production (Perry 1988). Therefore, the mangrove itself may release chemical cues to inhibit

barnacle settling, which could explain the lower abundance of barnacles on roots than mimics. Support for this potential explanation comes from the work of Hunting et al. (2010), who found a positive correlation between coverage and larval recruitment of sponges with tannin concentrations in *Rhizophora mangle* roots. Tannins affect the structure of the microbial biofilm of roots (e.g. chemical, textural, or structural), influencing larval settlement, and sponge colonization in turn increases the production of polyphenolic compounds and tannins, creating positive feedback for recruitment (Hunting et al. 2010).

The results of the present study suggest that non-living wood and PVC root mimics may be useful in sustaining epibionts when mangrove roots are not available (e.g. mangrove dieback) or in ecological experiments that require manipulation not possible with living roots. However, typical conditions of the mangrove environment (e.g. turbulent water, salinity, and UV radiation) increase leaching of harmful additives (e.g. BPA, phthalates) that threaten marine life from plasticized PVC into the marine environment (Suhrhoff & Scholz-Böttcher 2016). Therefore, plastic materials (e.g. PVC) should not be employed in large-scale programs.

4.3. Are ecologically and conservation-relevant time scales sufficient for the epibiont community to return to approximately its original state?

It is important for management and conservation purposes to know how long it takes epibiont communities to recover after being disturbed by storms, anoxic events, wave action, or pollution (e.g. oil spills) (Orihuela et al. 1991, Burns et al. 1993, Wulff 2012, 2013). In the present study, we tested whether the decay time of one of more treatments was sufficient for the epibiont community of scraped living mangrove roots to attain a community similar to that of unmanipulated roots. We found the decay time to be 14 mo due to the rapid deterioration of cut mangrove roots. Scraped living mangrove roots had similar sessile epibiont percent cover and bivalve richness to unmanipulated ('natural') mangrove roots by the end of the experiment. Still, the other measures of community structure, such as sessile biomass, mobile invertebrate richness, sponge richness, and bivalve biomass, did not converge with control epibiont communities on this temporal scale (Table 1). The discrepancies in community composition of these living mangrove roots may be due to a difference in the initial recruited epibiont community, which can determine patterns in epibiont distribution (Farnsworth & Ellison 1996). Although a final stage of community composition cannot be determined, Guerra-Castro & Cruz-Motta (2018) proposed that trajectories can be forecasted using broader taxonomic or functional groups. Their study of small-scale spatial variability in epibionts of mangrove roots found that roots are initially colonized by hydroids, bryozoans, and algae, followed by tunicates, oysters, and encrusting sponges at intermediate stages, with final stages of succession being dominated by massive sponges and more tunicates (Guerra-Castro & Cruz-Motta 2018). Given that bivalve richness is similar between scraped and natural mangrove roots in the present study, yet sponge biomass remains drastically different, this suggests that these roots are at an intermediate stage of community assembly.

4.4. Are there links between secondary foundation species and the mobile invertebrate community?

Despite the growing interest in facilitation cascades, few studies have examined the impact of secondary foundation species richness and abundance on inhabitant community richness and abundance. In our study, we observed overall positive relationships between secondary foundation species (e.g. sponge and bivalve) biomass and mobile community richness. Across treatments, sponge biomass was highly correlated with mobile richness in all treatments except PVC, and bivalve biomass was highly correlated with mobile richness in all treatments except cut mangrove roots. These results are consistent with previous work that observed positive relationships between sessile biomass and mobile fauna abundance in mangrove root communities of Florida (Janiak et al. 2020). We observed positive correlations between bivalve richness and mobile richness with natural and scraped mangrove roots and wood treatments, no relationship in the PVC treatment, and a negative correlation between bivalve richness and mobile richness in the cut treatment. Meanwhile, sponge richness was only positively correlated with mobile richness in scraped mangrove and wood treatments. The greater influence of secondary foundation species biomass than richness on mobile invertebrate richness may be due to the primary importance of structural complexity that massive sponges and bivalves offer as substrate. This apparent decoupling of sponge richness and mobile invertebrate richness may be due to 1 or 2 sponge species with complex morphology having a greater impact

on mobile invertebrate community structure than multiple less complex or encrusting sponge species. For example, sponge morphology has been shown to influence macrofaunal assemblages, with sponge volume and oscular diameter positively correlating with associated epi- and endo-fauna abundance and richness (Westinga & Hoetjes 1981, Ávila & Ortega-Bastida 2015, Chin et al. 2020).

In our study, we found that root treatment had significant effects on bivalve and sponge biomass and richness. These factors were correlated with the community structure of mobile epifauna, implying that root characteristics have an indirect effect on mobile organisms through a facilitation cascade. However, we did not directly manipulate sponge or bivalve richness or abundance on the roots, so we cannot conclusively establish the relative importance of primary (e.g. mangrove) versus secondary (e.g. sponge, bivalve) species on the mobile community. Given the known association of mobile invertebrates with structurally complex sponges and bivalve aggregations (Koukouras et al. 1992), and that many of the mobile species we documented are known to be obligately or commonly associated with those secondary foundation species, we suggest that mangrove root communities are a strong model system for further exploration of the facilitation cascade concept. Prior studies using mangrove ecosystems have found that traits of primary and secondary foundation species are important in facilitating cascades (Bishop et al. 2012, 2013, Schutte & Byers 2017), and our findings indicate that the diversity of secondary foundation species could be an important factor in mediating this relationship.

Analyzing *in situ* percent cover of broad epibiont groups (12 taxa) compared to biomass of higher resolution morphospecies (86 taxa) qualitatively gave the same outcome of treatment effects. Comparing the matrices created by both data sets, we found them to be highly correlated, but the higher resolution of biomass data revealed differences in pairwise comparisons not visible with *in situ* data. However, biomass data will also be biased towards heavier-bodied organisms (e.g. bivalves), and the variability within treatments was greater than between treatments, which should be taken into consideration. We suggest that the goals of the study should be carefully considered to determine whether destructive sampling is justified, since broad questions can be answered with *in situ* sampling techniques without damaging potentially sensitive ecosystems. To increase precision, we encourage future investigators to use *in situ* identification aided by photographs of epibiont communities to obtain percent cover of epibionts to further taxonomic resolution. For instance, the sponge group can be further resolved to morphospecies *in situ* with additional details of texture, shape, oscule size, etc.

4.5. Conclusions

This study has important conceptual and applied implications for mangrove management and biodiversity conservation by providing insights into how foundation species traits shape the community assemblage of associated organisms. By comparing living and non-living mangrove roots with root mimics, we were able to identify properties of mangrove roots needed to sustain driver communities of epibionts; and our results suggest that root mimics could be used to temporarily support mangrove-associated communities while mangrove stands recover. Further, anthropogenic perturbations can alter mangrove root traits (e.g. death and deterioration of roots) that affect epibionts, so it is important to understand and predict how these disturbances are likely to affect the structure of mangrove habitats and the complex communities that they support.

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