



Area-Independent Effects of Water-Retaining Features on Intertidal Biodiversity on Eco-Engineered Seawalls in the Tropics

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Over the last decade there has been a global effort to eco-engineer urban artificial shorelines with the aim of increasing their biodiversity and extending their conservation value. One of the most common and viable eco-engineering approaches on seawalls is to use enhancement features that increase habitat structural complexity, including concrete tiles molded with complex designs and precast “flowerpots” that create artificial rock pools. Increases in species diversity in pits and pools due to microhabitat conditions (water retention, shade, protection from waves, and/or biotic refugia) are often reported, but these results can be confounded by differences in the surface area sampled. In this study, we fabricated three tile types ($n = 10$): covered tile (grooved tile with a cover to retain water), uncovered tile (same grooved tile but without a cover) and granite control. We tested the effects of these tile types on species richness (S), total individual abundance (N), and community composition. All tiles were installed at 0.5 m above chart datum along seawalls surrounding two island sites (Pulau Hantu and Kusu Island) south of Singapore mainland. The colonizing assemblages were sampled after 8 months. Consistent with previous studies, mean S was significantly greater on covered tiles compared to the uncovered and granite tiles. While it is implied in much of the eco-engineering literature that this pattern results from greater niche availability allotted by microhabitat conditions, we further investigated whether there was an underlying species-individual relationship to determine whether increases in S could have simply resulted from covered tiles supporting greater N (i.e., increasing the probability of detecting more species despite a constant area). The species-individual relationship was positive, suggesting that multiple mechanisms are at play, and that biodiversity enhancements may in some instances operate simply by increasing the

abundance of individuals, even when microhabitat availability is unchanged. This finding underscores the importance of testing mechanisms in eco-engineering studies and highlights ongoing mechanistic uncertainties that should be addressed to inform the design of more biodiverse seawalls and urban marine environments.

Keywords: habitat complexity, ecological engineering, urban marine ecology, species-area relationship, species-abundance relationship

INTRODUCTION

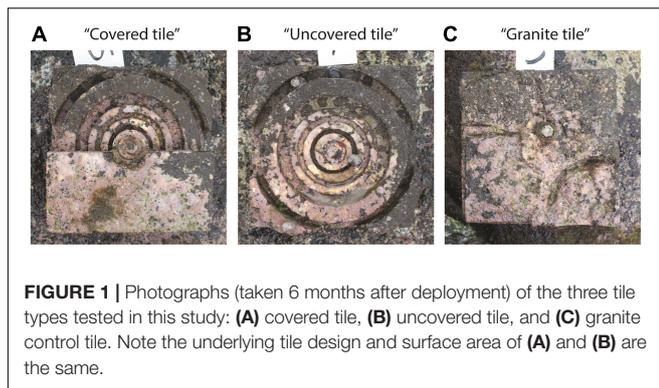
Growing coastal populations that are increasingly threatened by rising seas (Hinkel et al., 2014; Nicholls, 2015) are driving the construction of coastal defenses and flood protection, particularly in low-elevation coastal zones and vulnerable urban centers (Neumann et al., 2015). Ideally, coastal adaptation planning and defense systems should employ nature-based approaches, including “planned retreat” (pulling developments back from the present shoreline) and the creation or restoration of ecosystems that naturally protect against flooding, such as salt marshes and mangroves (Temmerman et al., 2013; Narayan et al., 2016). However, traditionally engineered artificial structures, such as seawalls, are pervasive, particularly in coastal cities, where sea level rise adaptation efforts primarily aim to protect the existing shoreline or advance the shoreline into adjacent marine habitats (Nicholls, 2011; Dafforn et al., 2015). These structures have considerable impacts on marine ecosystems (Bishop et al., 2017; Heery et al., 2017, 2018), yet are likely to remain a central component of coastal defense systems, either as the primary mode of flood protection or in combination with natural features (Bulleri and Chapman, 2009; Cheong et al., 2013). In response, there has been a global effort during the last decade to ecologically engineer hard artificial structures with the aim of improving their ecological value and alignment with conservation goals (Chapman and Underwood, 2011; Dyson and Yocom, 2015; Pioch et al., 2018). Ecological engineering solutions have already been applied to artificial shoreline projects in several cities, with various benefits to both marine ecosystems and human communities in urban areas (Arkema et al., 2017; Morris et al., 2018). Yet, for many of them, there have been few experimental studies that systematically explore precisely *how* they alter marine biota. A thorough understanding of the underpinning mechanisms through which ecological enhancements operate remains elusive.

Though ecological engineering of artificial structures can be used to meet a variety of objectives, its core environmental aims are often to enhance biodiversity and extend the conservation of native marine species to urban habitats that would otherwise be inhospitable (Loke et al., 2019). One of the most popular techniques for intertidal seawalls is to increase habitat structural complexity (Loke et al., 2014, 2017), for instance by removing pieces of the seawall to create recesses (Chapman and Blockley, 2009), drilling pits to form rock pools (Martins et al., 2010; Evans et al., 2016; Hall et al., 2018), and attaching “flower pots” and other concave enhancements (Browne and Chapman, 2011, 2014; Firth et al., 2016a; Waltham and Sheaves, 2018). These manipulations have repeatedly been shown to increase

the richness and abundance of benthic organisms on intertidal seawalls (reviewed by Loke et al., 2019), and their effectiveness is frequently attributed to increased shade and moisture (i.e., increased niche availability) allotted by structurally complex microhabitat features (Firth et al., 2014, 2016b; Perkol-Finkel et al., 2018; Strain et al., 2018), which can reduce temperature fluctuations, minimize desiccation stress, and facilitate the recruitment of sessile fauna (Metaxas and Scheibling, 1993; Blockley and Chapman, 2006; Seabra et al., 2011; Firth et al., 2013). To date, the majority of related experiments in this area have been conducted in temperate areas (e.g., Browne and Chapman, 2011; Evans et al., 2016; Hall et al., 2018). The deleterious effects of temperature and desiccation are potentially a greater threat to tropical intertidal assemblages, and hence more data are needed from low latitude countries.

Discerning between the mechanisms that explain why structurally complex features enhance intertidal diversity is essential for ensuring that ecological engineering achieves its objectives and that unintentional consequences are avoided, particularly as these features are now being “scaled-up” to meet growing commercial demand for ecological enhancements. As has been widely suggested in past literature, creating additional microhabitat features may indeed increase biodiversity primarily by increasing niche availability. However, this has rarely been tested explicitly and various other explanations are often feasible. For instance, greater surface area in structurally complex treatments will lead to greater species richness (due to basic species-area relationships, SAR) and prove misleading if not carefully accounted for in eco-engineering studies. Alternatively, even when surface area is accounted for, an increase in niche availability is just one of the possible mechanisms through which enhanced biodiversity can arise. For example, microhabitat conditions associated with structurally complex features may instead support greater abundances/densities of individual organisms, which in turn could increase species richness simply by increasing the probability that more species will be detected as more individuals are sampled (henceforth referred to as “species-individual relationship”; see Fisher et al., 1943).

In this study, we explored multiple alternative explanations for biodiversity increases that have been well-documented in response to structurally complex eco-engineering features and informally linked to increases in niche availability. To determine whether, in fact, changes in microhabitat conditions (e.g., combined effect of increased water retention, shade, protection from waves and/or refugia) provide a parsimonious explanation of increased species richness on structurally complex features, we accounted for the potentially confounding effect of surface area on species richness in our statistical analyses. Furthermore,



to discern whether microhabitat conditions primarily altered biodiversity by increasing the availability of niches, or whether other non-niche-related mechanisms are also important, we conducted an *a posteriori* analyses of the relationship between the number of individuals (N) and the number of species (S).

We deployed tiles of the same underlying tile design (and thus level of topographic complexity) to seawalls in Singapore—treatments differed only in whether they had water retaining features (i.e., had a cover). Consistent with previous findings, we hypothesized that: (1) Covered tiles would host greater species richness (S) compared to uncovered and granite (control) tiles; (2) Covered tiles would host a greater number of individuals (total abundance, N) compared to uncovered and granite tiles; and (3) Covered tiles would host assemblages that were compositionally different compared to uncovered and granite tiles. We additionally examined the species-individual relationship across treatments to assess whether there was evidence that microhabitat (niche) availability was likely the primary mechanism underlying these patterns. Note that by exploring the relationship between S and N , we did not explicitly test any mechanism *per se*, rather, we used this analysis to rule out the possibility that increases in S could be explained by increases in N , a pattern that would suggest that niche availability is not the only mechanism influencing biodiversity when surface area is held constant.

MATERIALS AND METHODS

Experimental Design, Tile Fabrication and Deployment

We fabricated three tile types: “covered” tile (grooved tile with a concrete cover plate to retain water, **Figure 1A**), “uncovered” tile (same grooved tile but without a cover, **Figure 1B**) and “granite” tile (**Figure 1C**). The concrete cover plate served to trap water and provide shade and protection from waves and predators in the “covered” tile treatment, but these components were not disentangled by our study. All tiles measured $200 \times 200 \times 60$ mm (width \times length \times depth). The covered and uncovered tiles were made of concrete following the “complex-groove quarter tile” design used in Loke and Todd (2016) and were cast from silicone rubber molds using a 1:3 Portland cement to sand mix. Granite

tiles, which served as a control, were made of broken granite slabs cemented onto a concrete base to mimic the surface of the surrounding granite seawall (for more details on how the tiles were constructed please refer to Loke and Todd, 2016). This was a procedural control and provided an idea of what the background seawall would support within the same timeframe given the same mounting system as the concrete tiles.

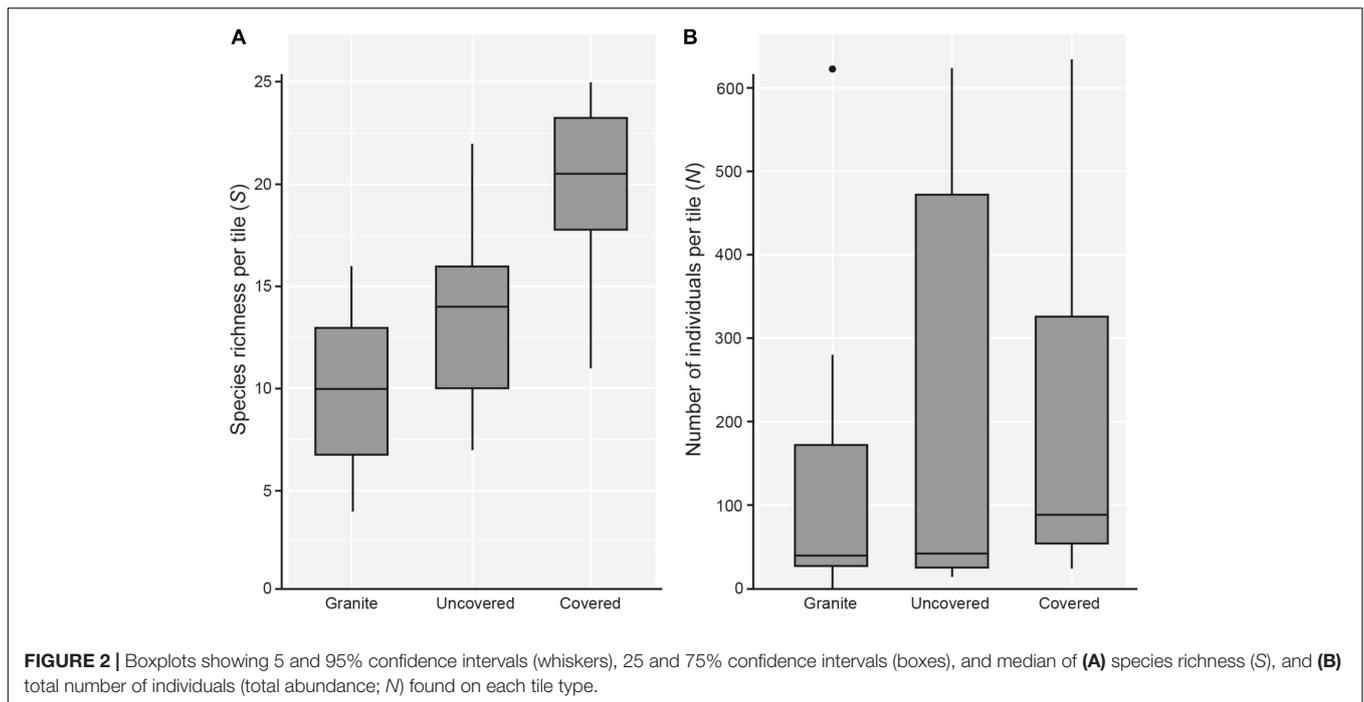
The tiles were deployed during low tides on 9–10 August 2010 along un-grouted, sloping ($\approx 30^\circ$), granite rip-rap seawalls at two sites south of Singapore’s mainland: Pulau Hantu ($1^\circ 13' 34''$ N, $103^\circ 45' 0''$ E) and Kusu Island ($1^\circ 13' 22''$ N, $103^\circ 51' 40''$ E). Ten replicates of each tile type were attached onto the seawalls in random order using M8 stainless steel bolts (**Figure 1**). All tiles were installed flat along the sloping seawall (see **Figure 1**) 0.5 m above chart datum and spaced at least 2.0 m apart. Hence, there was a total of 60 tiles with “tile type” as a fixed factor and “site” as a random factor; i.e., 2 sites \times 3 tile types \times 10 replicates.

Field Sampling and Laboratory Procedures

The tiles were retrieved after 8 months. The colonizing benthic assemblage on the tiles was sampled; organisms on tile surfaces were scraped into trays immediately after retrieval. Benthic organisms colonizing the outside of the concrete cover plate on the covered tiles were not included, but those on the underside were. Even though the concrete plates provided additional substrate where they covered the grooves of the underlying tile, they also removed habitable area where they were in contact with the top of the ridges. The overall effect was that the covered tiles had slightly less surface area (60 cm^2) available for colonization than the uncovered tiles. This amounts to a 6.9% difference that was accounted for in our statistical models (see section “Statistical Analyses”). Note that, although water retained by the covered tiles presumably provided greater three-dimensional habitat for suspended organisms, these organisms were lost when covers were removed and thus were not among the organisms sampled. All specimens were stored in 70% ethanol until they were manually sorted, counted and identified to species or morphospecies level (within known genera) except for polychaetes and amphipods, which were identified to family level, and algae, which were identified to functional group level following Loke et al. (2016).

TABLE 1 | Estimated parameters, standard errors, z-values, and p-values for the negative binomial mixed effects models; significant p-values are in bold.

Models	Estimate	SE	z-value	p-value
<u>Species richness (S)</u>				
Intercept	3.52	0.09	38.49	<0.001
Uncovered tile	-2.09	0.10	-20.35	<0.001
Covered tile	-0.50	0.10	-5.25	<0.001
<u>Number of individuals (N)</u>				
Intercept	5.68	0.85	6.72	<0.001
Uncovered tile	-2.02	0.17	-11.87	<0.001
Covered tile	-0.49	0.17	-2.85	<0.01



Statistical Analyses

As some tiles were lost due to wave action, there were six covered tiles, seven uncovered tiles and six granite tiles remaining at Kusu Island, resulting in an unbalanced ANOVA design (no tiles were lost at Pulau Hantu). To avoid removing a large number of replicates to run a balanced analysis, we modeled species richness (S) and number of individuals (N) as counts using mixed effects models with negative binomial error terms to test for differences in S and N among tile types (Hypotheses 1 and 2, respectively). We selected the negative binomial error structure due to overdispersion in the Poisson models and included surface area as an offset in the model (Zuur et al., 2009). All models were constructed in R version 3.3.0 (R Development Core Team, 2016) with tile type as a fixed effect and site as a random effect. We then explored the potential species-individual relationship (i.e., relation between S and N) via simple linear regression [$lm()$ function in R]. Following the protocols outlined in Zuur et al. (2010), prior to our analyses we examined the data for overdispersion, non-linearity, heteroscedasticity, and presence of outliers.

To test for differences in community composition between tile types (Hypothesis 3), we used permutational distance-based multivariate analysis of variance (PERMANOVA; Anderson, 2001) to analyze the full resemblance matrix calculated on Bray-Curtis similarities from log-transformed abundances with site as a random factor and tile type as a fixed factor. Due to highly significant differences between the communities among the sites, we then ran separate PERMANOVAs for each site. P -values were generated using 9999 unrestricted random permutations of residuals. Canonical analysis of principal coordinates (CAP) was applied to examine whether the communities on the three tile types could be separated and to explore the potential

relationships between the individual species found and the canonical axes. The significance of the canonical relationship in each combination was tested using 9999 unrestricted random permutations of the transformed community data (Anderson et al., 2008). All multivariate analyses were performed using the PERMANOVA+ add-on for PRIMER v6 (Anderson et al., 2008).

RESULTS

A total of 8925 individuals representing 52 different faunal species and six algal functional groups were recorded. None of these species are unique to seawalls in Singapore (i.e., they are also found on natural rocky shores in Singapore; Lai et al., 2018) and none are known to be non-native (Jaafar et al., 2012; Tan et al., 2018).

As hypothesized, covered tiles hosted significantly greater S ($\chi^2 = 504.61$, $df = 2$, $p < 0.001$) and N ($\chi^2 = 153.65$, $df = 2$, $p < 0.001$) compared to uncovered and granite tiles (Table 1 and Figure 2). We also found that the variability in N was due primarily to the dominance by a single species: *Siphonaria guamensis* at Kusu island (Figure 3). *S. guamensis* (the false limpet) was generally absent on tiles at Pulau Hantu (only a single individual recorded) but present in disproportionately large numbers at Kusu Island (319.1 ± 154.8 individuals per tile; mean \pm SD) (Figure 3).

A plot of the abundance of *S. guamensis* alone revealed a similar trend to the plot of total individual abundance summarizing the whole dataset (i.e., Figure 3A vs. Figure 2B). On removing *S. guamensis*, the N pattern resembled the S pattern, with the greatest number of individuals found on covered

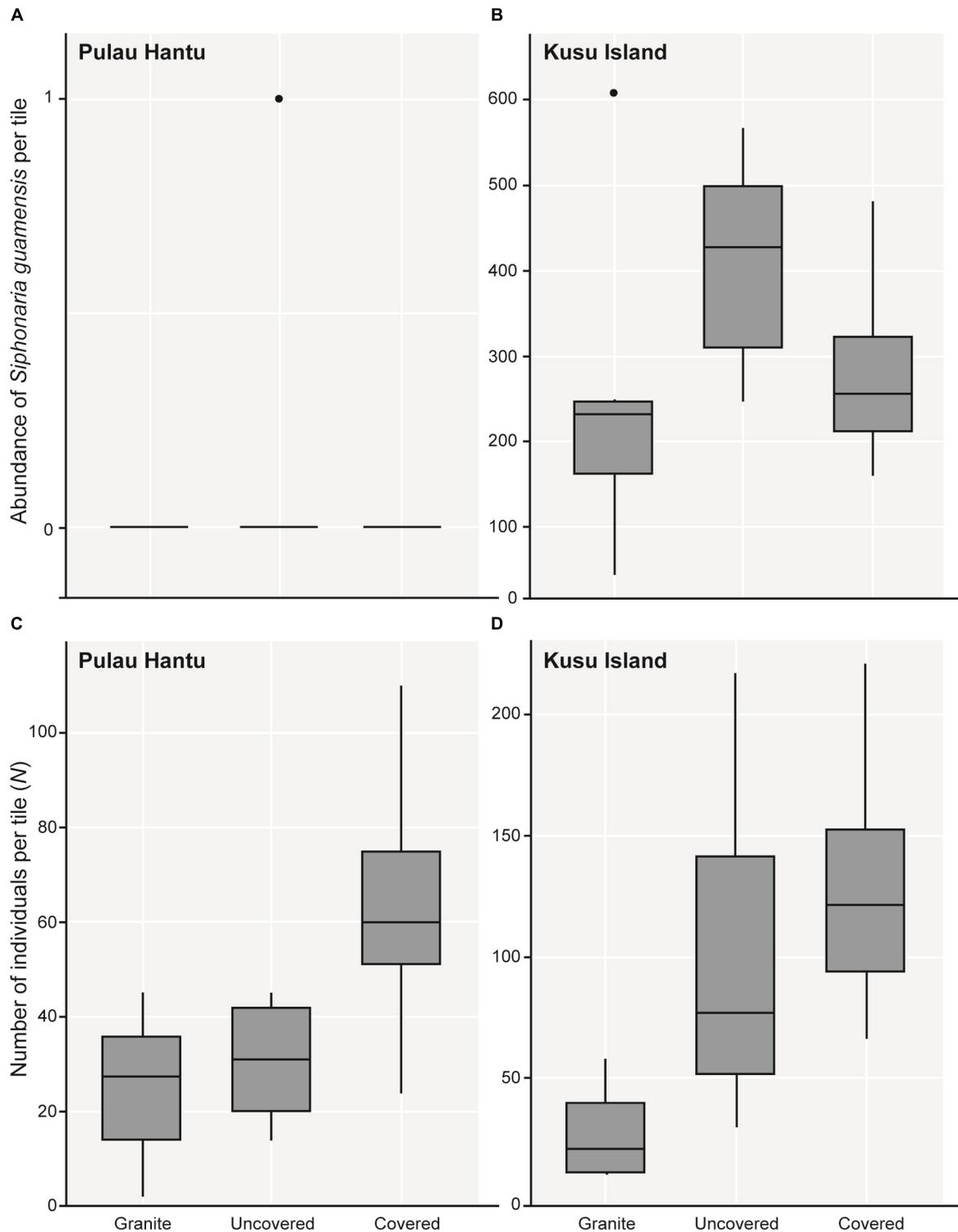


FIGURE 3 | Boxplots showing 5 and 95% confidence intervals (whiskers), 25 and 75% confidence intervals (boxes), and median of the total abundance of **(A)** *Siphonaria guamensis* in each tile treatment at Pulau Hantu and **(B)** Kusu Island; **(C)** the total number of individuals (N) of all 51 species in each tile treatment at Pulau Hantu and **(D)** Kusu Island after removing *S. guamensis*.

tiles, followed by uncovered and granite tiles (Figures 3B–C vs. Figure 2A).

The simple linear regression between *S* and *N* revealed an overall significant positive relationship although the trend at each site differed, and was apparently non-linear at Kusu Island, again due to the disproportionately large abundances of *S. guamensis* (Figures 4A–B). As with the mixed effects model for total abundance, the removal of *S. guamensis* revealed highly significant positive linear relationships between *S* and *N* at both sites (Figures 4C–D).

Due to significant community differences between the assemblages at Pulau Hantu and Kusu Island (PERMANOVA; *df* = 1, 43, *MS* = 34172, *Pseudo-F* = 26.3, *P* (perm) < 0.001) we performed separate PERMANOVAs for each site. Results revealed that community composition differed significantly among the tile types at each site except between “uncovered” and “granite” tiles at Pulau Hantu (Table 2). The CAP analysis also showed a significant separation between the tile types at each site (*p* < 0.05; Figure 5). Species commonly found under rocks, such as *Barbatia amygdalumtostum* and *Isognomon legumen*, characterized covered tiles.

DISCUSSION

Many of the ecological engineering efforts to improve biodiversity on urban structures have employed the use of water-retaining features (Firth et al., 2016a), but these features often differ in surface area from less structurally complex controls, and could be influencing species numbers. Without controlling for area, it is difficult to attribute increases in *S* solely

to changes in microhabitat conditions—e.g., water retention, shade, protection from waves and/or biotic refugia—as species-area effects can dominate, as has been shown across nearly all systems and scales (Fahrig, 2013). Our study demonstrates experimentally that increased *S* from water-retaining features is indeed a function of microhabitat provisioning (i.e., niche availability) to some extent, and this effect is independent of surface area. In fact, even though covered tiles had 6.9% less surface area than uncovered tiles, they supported greatest *S*. By ruling out surface area as the driver of enhanced biodiversity, this finding adds an essential piece to the mechanistic puzzle underpinning ecological enhancements of shorelines, and strengthens the foundation of ecological engineering as a discipline, ultimately aiding in its advancement.

We ruled out surface area as the driver of diversity patterns by comparing covered and uncovered tile treatments that offered the same structurally complex substrate for benthic organisms. As in previous studies, structurally complex tiles (both covered and uncovered tile treatments) were found to increase abundance and species richness compared to the less complex substrata that characterize seawalls (Loke and Todd, 2016). However, the added value from this study is exemplified by the differences observed between covered versus uncovered treatments. We observed higher *S* on covered tiles compared with uncovered tiles. Covered tiles also supported greater *N*, and this effect was especially pronounced when the disproportionately abundant false limpet, *S. guamensis*, was removed (discussed further below). These findings are consistent with past studies (e.g., Chapman and Blockley, 2009; Browne and Chapman, 2011; Waltham and Sheaves, 2018), and suggest that incorporating additional microhabitats (e.g., shade and water retaining features) may be an effective strategy for biodiversity enhancement. More broadly, the findings lend weight to the idea that enhancing habitat (niche) complexity can and does play an important role in supporting more diverse communities on seawalls.

Water-retaining features are thought to enhance the diversity of intertidal biota through multiple mechanisms. Pits/pools are continually submerged, eliminating desiccation stress and other risks associated with emersion during low tide (Connell, 1972), and are rapidly colonized by a suite of taxa (Underwood and Jernakoff, 1984). They also provide greater shade than emergent surfaces, which dampens temperature variability (Seabra et al., 2011), reduces thermal stress (Williams, 1994; Bertness et al., 1999), and provides highly localized refugia for temperature-sensitive taxa, such as gastropods (Garrity, 1984) and newly recruited sessile invertebrates (Blockley and Chapman, 2006; Chapman and Blockley, 2009). This can lead to net increases in diversity (Blockley, 2007), even though reduced irradiance is limiting for some taxa, particularly primary producers (Goldberg and Foster, 2002). Mediated desiccation and temperature stress act in combination with a complex suite of additional abiotic and biotic variables (e.g., dissolved gas accumulation and decreasing pH during low tide, Huggett and Griffiths, 1986) to influence the composition of organisms in pits/pools, and community response to water-retaining features is therefore highly variable (Bugnot et al., 2018). The addition of a cover plate may also

TABLE 2 | PERMANOVA results based on Bray–Curtis dissimilarities of the relative abundances (pre-treated with log[X + 1] transformation) of 56 different species in response to the tile type treatments.

Source	df	MS	Pseudo-F	<i>p</i> (perm)	Unique perms
<i>Pulau Hantu</i>					
Tile type	2	3666	2.1274	0.0084	9913
Residual	27	1723.2			
Total	29				
<i>Kusu Island</i>					
Tile type	2	2176.6	3.7061	0.0001	9923
Residual	16	587.3			
Total	18				
Groups	<i>t</i>	<i>p</i> (perm)	Unique perms		
<i>Pulau Hantu</i>					
Covered, uncovered	1.7646	0.0085	9418		
Covered, granite	1.779	0.0027	9402		
Uncovered, granite	0.66005	0.9666	9384		
<i>Kusu Island</i>					
Covered, uncovered	1.4639	0.0023	460		
Covered, granite	2.2765	0.001	1708		
Uncovered, granite	1.8583	0.0085	9418		

Significant *p* (perm) values are highlighted in bold.

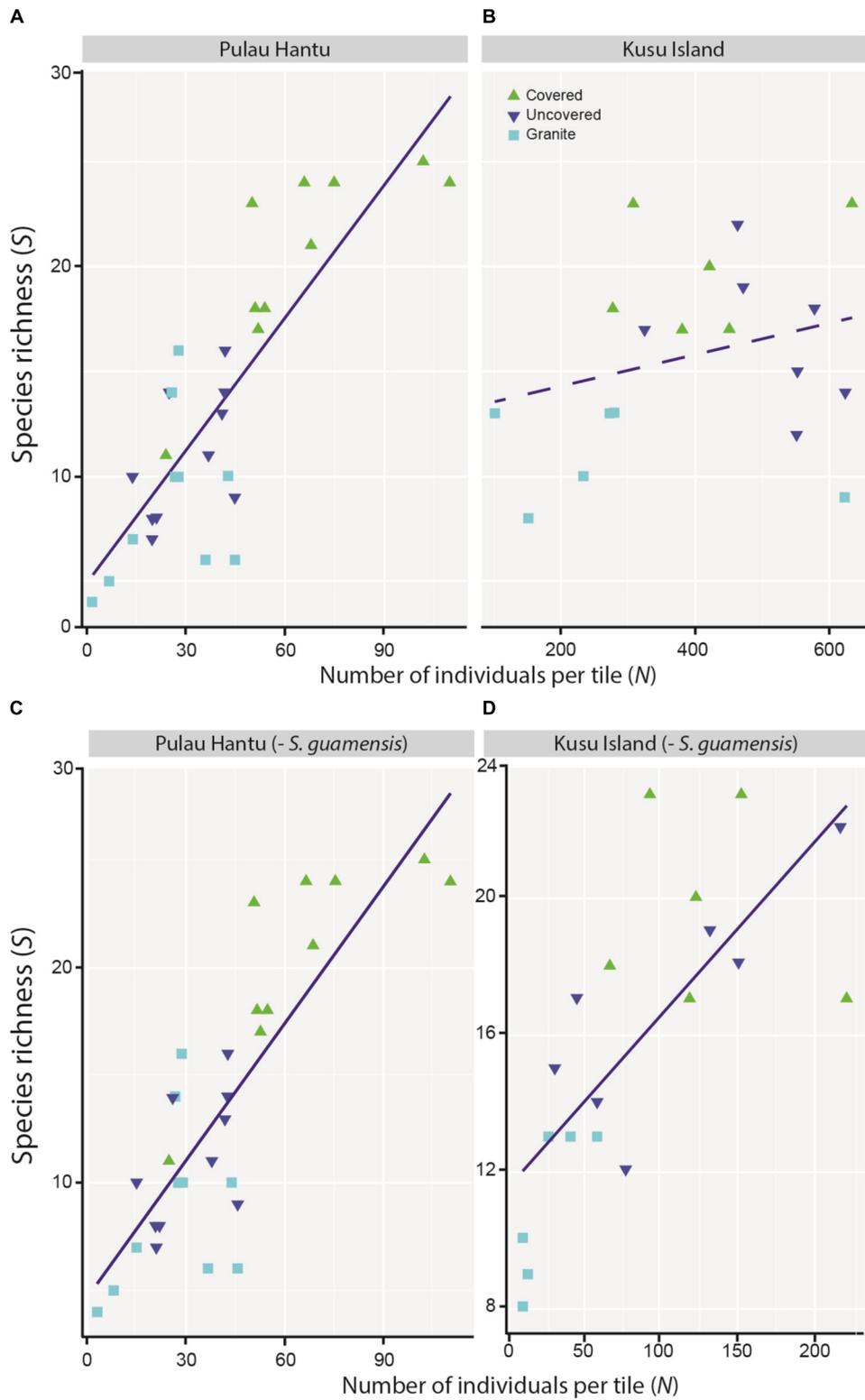
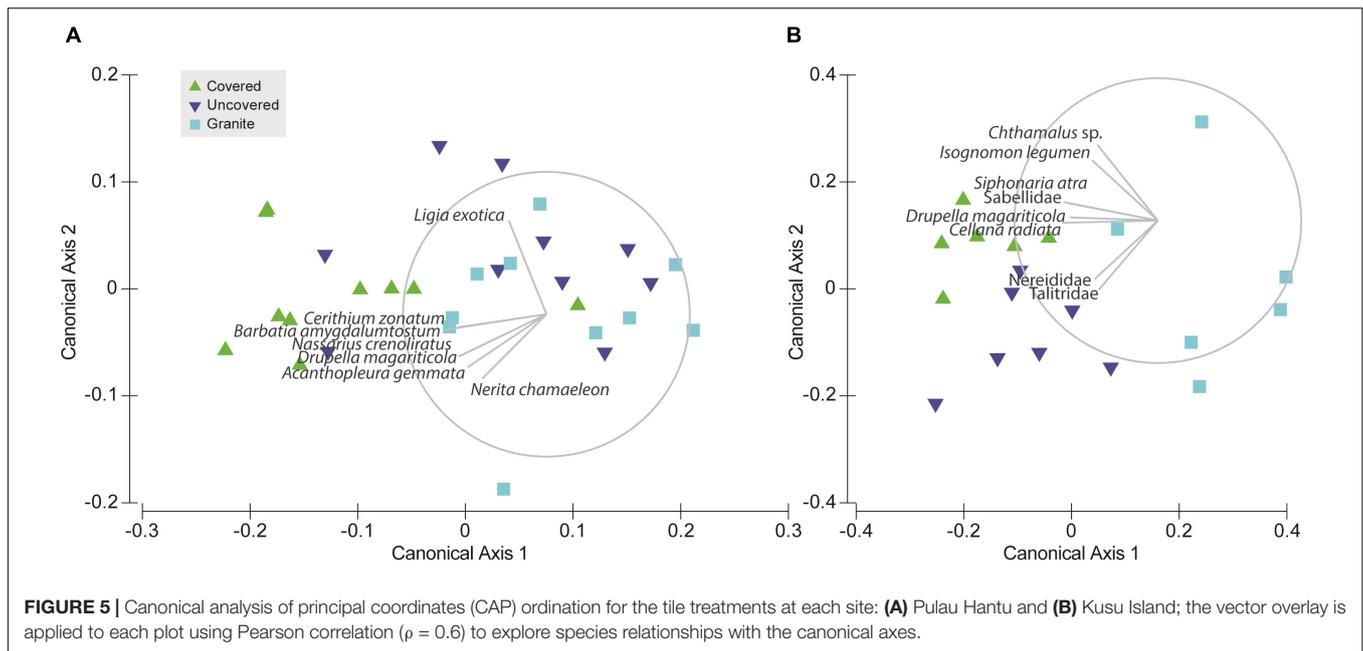


FIGURE 4 | Simple linear regression between species richness (*S*) and total number of individuals (*N*) at **(A)** Pulau Hantu ($r^2 = 0.68, p = 0.000$), and **(B)** Kusu Island ($r^2 = 0.19, p = 0.262$), and after removing *S. guamensis* at **(C)** Pulau Hantu ($r^2 = 0.54, p < 0.001$), and **(D)** Kusu Island ($r^2 = 0.66, p < 0.001$).



afford organisms greater shelter from wave action and water movement—potentially a critical resource at sites with higher wave energy such as Kusu Island (Loke and Todd, 2016)—and possibly additional protection from predators.

Although discerning specific niche mechanisms was beyond the scope of this study, differential responses to tile treatments observed among intertidal fauna provides some insights into key abiotic differences between our treatments. For instance, *S. guamensis*, which was primarily found on uncovered tiles at Kusu Island, was 1–2 orders of magnitude more abundant than all other faunal species. This species tends to dominate exposed flat surfaces (Amnuaypon and Wangkulangkul, 2018; Loke pers. obs.), which may explain why uncovered tiles hosted a greater abundance of *S. guamensis* than the covered tiles (Figure 3A); uncovered tiles had a greater amount of “exposed area.” *S. guamensis* was found to contribute significantly to the site differences in community structure but not to differences in species composition among tile types (Figure 4). This suggests *S. guamensis* has no strong preference for particular topographical features or substrate material compared to the other gastropods we found at Kusu Island. Conversely, *Drupella magariticola*, *Cellana radiata*, and *S. atra*, were found to be driving the community differences between the concrete tiles (both covered and uncovered tiles) and the granite tiles. This could be due to differences in both substrate material and topographic complexity. Covered and uncovered tiles at Kusu Island were distinguished along the second CAP axis by the pod tree oyster, *I. legumen*, which usually occurred in clumps on the face beneath the cover (Loke pers. obs.). At Pulau Hantu, assemblages colonizing the uncovered and granite tiles were not compositionally distinguishable (Figure 5 and Table 2) but it was evident that covered tiles were distinct from the granite tiles. This is mainly due to *Cerithium zonatum* and *B. amygdalumtostum* (bearded ark clams); the latter are usually found on the underside

of rocks and boulders on natural shores. Thus, our study shows that, even by adding one more habitat niche (thereby increasing “informational complexity,” *sensu* Loke et al., 2015), we can increase the number of species by providing habitat for specialist species with narrower niche breadths.

While our study demonstrates biodiversity increases from water-retaining features irrespective of surface area, these increases are probably not due to microhabitat differences (niche effects) alone. This is evidenced by the strong positive relationship we observed between the total number of individuals (N) and species richness (S), particularly after accounting for *S. guamensis*. Had the covered tiles captured a greater species richness but not greater individual abundance compared to the uncovered and granite tiles, it would have shown that the improved richness was due solely to the niche effects provided by the covered tile. Instead, the consistent relationship between S and N suggests that in addition to the niche effects, treatment differences might have simply resulted in the capture of more individuals, which in turn increased the likelihood of capturing more species. While this does not take away from the fact that microhabitat properties such as water retention play an important role in improving species richness, it underscores the importance of accounting for the possible influence of N on S when interpreting results from eco-engineering studies.

CONCLUSION

In conclusion, water-retaining features combined with complex topography can enhance biodiversity on existing seawalls independently of area through mechanisms that act directly via niche effects, and possibly indirectly via total individual abundance. Until we are able to discern the relative importance of these mechanisms, we suggest that they be explored

empirically (for instance, by examining species-area relationships (SARs) and/or species-individual relationships) as alternative explanations for the results of future eco-engineering studies. Such efforts are needed to ensure that claims regarding the efficacy of eco-engineering solutions to increase species diversity are justified and well supported.

AUTHOR CONTRIBUTIONS

LL, TB, and PT designed the experiments. LL conducted the experiment and collected the data. LL and EH analyzed the data. LL wrote the first draft of the manuscript. All authors contributed to the revisions.

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