Latitudinal variation in local interactions and regional enrichment shape patterns of marine community diversity

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Abstract. While communities are shaped by both local interactions and enrichment from the regional species pool, we propose a hypothesis that the balance of these forces shifts with latitude, with regional enrichment dominating at high latitudes and local interactions dominating at low latitudes. To test this hypothesis, we conducted a latitudinal-scale experiment with marine epifaunal communities. In four regions of the North Atlantic Ocean and Caribbean Sea, we used mimics of ecosystem engineers to manipulate biogenic structural complexity. We iteratively evaluated diversity patterns of experimental communities up to one year after deployment. Additional data were also collected from one of our tropical sites 2.5 years after initial deployment. As hypothesized, we found a reciprocal latitudinal gradient in the effects of the structurally complex mimics and regional enrichment. In the tropics, local diversity was always higher in association with the mimics than in exposed areas that were more open to predation. This effect was consistent across two spatial scales and beyond the one-year timescale of the experiment. In temperate communities, no consistent effects of the mimics on diversity were observed. However, the proportion of species from the regional species pool that were present at the local scale increased from the tropics to the temperate zone, consistent with the hypothesis that higher-latitude communities may experience greater influence from the regional species pool than communities at low latitudes. This study represents the first large-scale experimental demonstration that suggests that the relative impact of local interactions and regional enrichment on community diversity may depend on latitude.

Key words: ecosystem engineers; fouling communities; latitude; marine epifauna; predation; regional enrichment; species interactions; structural complexity; temperate; tropic.

INTRODUCTION

While it has become well accepted that biodiversity patterns are shaped by both local interactions and regional and historic processes (Ricklefs and Schluter 1993), we still lack an integrated framework that predicts the balance of these synergistic forces. Regional species pools, created and maintained by climate, historical factors, speciation, and extinction rates, can augment local assemblages (Karlson et al. 2004, Freestone and Harrison 2006). Regional enrichment can occur in the face of weak species interactions that pose no upper limit to community richness, or when strong interactions are coupled with another coexistence mechanism such as disturbance (Tilman 2004) or mass effects (Leibold et al. 2004). However, the extent to which local communities are saturated, or in contrast, remain open to regional enrichment, is a hotly debated subject in both the terrestrial plant (Harrison 2008) and marine (Karlson et al. 2004, Russell et al. 2006) literature. While community saturation and the relevance of local interactions and regional enrichment have enjoyed much conceptual and theoretical attention, few studies have examined experimentally the relative importance of these processes in shaping community assemblages (Harrison and Cornell 2008).

The balance of local interactions and regional enrichment is dependent on scale (Rivadeneira et al. 2002, Russell et al. 2006, Schoch et al. 2006), habitat type and taxonomic resolution (Russell et al. 2006), and key environmental gradients (Huston 1999). In addition, an emerging pattern based on theoretical expectations and empirical observations suggests that this balance may also shift globally. The latitudinal diversity gradient, with species richness peaking at low latitudes, is one of the most robust patterns in ecology, affecting all major taxonomic groups (Hillebrand 2004*a*), including marine systems (Hillebrand 2004*b*, Witman et al. 2004). Even though this is one of the oldest documented patterns, the evolutionary drivers of this gradient continue to be in dispute (Mittelbach et al. 2007), and furthermore, we still lack a conceptual framework for how communities are shaped across latitude in ecological time. However, the "biotic interactions hypothesis," a leading evolutionary hypothesis for the latitudinal diversity gradient, suggests that species interactions are

stronger at lower latitudes, leading to higher rates of speciation and ultimately greater species diversity (reviewed in Mittelbach et al. 2007, Schemske et al. 2009). If local-scale interaction strength correlates with latitude, then this hypothesis clearly links both evolutionary and ecological patterns across the globe. Empirical studies are at the beginning stages of testing this hypothesis and are yielding promising support (Menge and Lubchenco 1981, Sanford and Bertness 2009, Schemske et al. 2009).

Additionally, recent empirical studies suggest that the importance of regional processes may also shift with latitude. Regional diversity generally shows a stronger relationship to latitude than local diversity (Rivadeneira et al. 2002, Hillebrand 2004a), thereby causing the ratio of local to regional diversity to have an inverse relationship to latitude, with higher ratios occurring at higher latitudes. Stated differently, local assemblages at high latitudes tend to be more representative of the regional species pool than at low latitudes, and this may imply that high-latitude communities are under greater regional control (Witman et al. 2004). Furthermore, if species interactions are weaker on average at higher latitudes, these communities would be expected to correlate more closely with regional species pool diversity. In contrast, stronger interactions at low latitudes may limit community membership thereby forcing independence between saturated local communities and regional species pool diversity.

From these theoretical and empirical advances, drawing from both evolutionary and ecological literature, an integrated concept emerges to understand how communities assemble over ecological time. We propose a hypothesis in which the relative importance of local interactions and regional enrichment hinges on latitude, with regional enrichment dominating at high latitudes, and local interactions dominating at low latitudes. To test this hypothesis, we conducted a latitudinal-scale experiment with marine epifaunal communities and evaluated the contributions of both local interactions and regional enrichment to community species richness. Very few studies have assessed the strength of local processes across latitude through direct in situ manipulations, but standardized experimental protocols replicated across large biogeographic scales are critical to understanding these dynamics.

While observed patterns of species diversity in coastal marine communities can be shaped by many different abiotic and biotic forces acting in concert (Schoch et al. 2006), we focused on the impacts of habitat-forming ecosystem engineers. This focus and our experimental approach enabled us to clearly define three key factors: (1) a taxonomic grouping of space-occupying fauna that are known to interact; (2) a biologically meaningful local scale at which the interactions are expected to occur, defined in this study as the area directly adjacent to the biogenic structure; and (3) a standardized habitat to reduce uncontrolled heterogeneity. Broad taxonomic groupings, larger spatial scales, and habitat differences are likely to conceal local scale effects and overestimate regional influences by incorporating habitat heterogeneity or noninteractive species (Huston 1999, Russell et al. 2006). Therefore, our focus on a clearly defined spatial scale and suite of interacting species provides an appropriate experimental environment.

Ecosystem engineers modify habitat for other species, and in epifaunal communities, this modification is often the creation of structural habitat for other species. Structural complexity created by ecosystem engineers can shape patterns of community diversity (Castilla et al. 2004) and can be created by a variety of species and growth forms such as mollusks (Gutierrez et al. 2003), tunicates (Castilla et al. 2004), and barnacles (Gosselin and Chia 1995). Structurally complex species can also serve as refuges from predation for other fauna, which can result in tight species associations and mutualisms (Stachowicz and Whitlatch 2005). Because marine ecosystem engineers are able to produce strong local effects in which the scale of interaction can be clearly defined and evaluated, this system is ideal for evaluating both local and regional contributions to observed community diversity patterns. Our investigation benefits from direct manipulations of these local interactions across a broad latitudinal gradient (25°).

To assess the influence of regional enrichment, we examined the relationship among local diversity, regional diversity, and latitude (Witman et al. 2004). Our use of standardized experimental habitats (see *Methods*), ecologically relevant local scales, and an iterative sampling design allowed us to empirically compile thorough and appropriate local and regional diversity estimates, thereby addressing several statistical concerns (e.g., pseudosaturation) that often hinder studies of diversity and scale (Harrison and Cornell 2008). Our specific hypothesis predicts that local interactions will be stronger at lower latitudes and communities will therefore be less open to enrichment from the regional species pool. In contrast, local interactions will be weaker at higher latitudes, and communities will therefore be more open to enrichment from the regional species pool.

METHODS

We tested this hypothesis using marine epifaunal invertebrates in the western North Atlantic Ocean and Caribbean Sea. These organisms are highly tractable for experiments given their global ubiquity and their rapid community development timescales. These communities occur naturally in the subtidal zone on any hard substrate, such as boulders or mangrove roots, and consist of a diverse array of sessile species including tunicates, sponges, bryozoans, tube-dwelling worms, bivalves, barnacles, hydroids, and anemones, among other groups.

We deployed 100-cm² experimental settlement panels in four regions along a latitudinal gradient: Connecticut
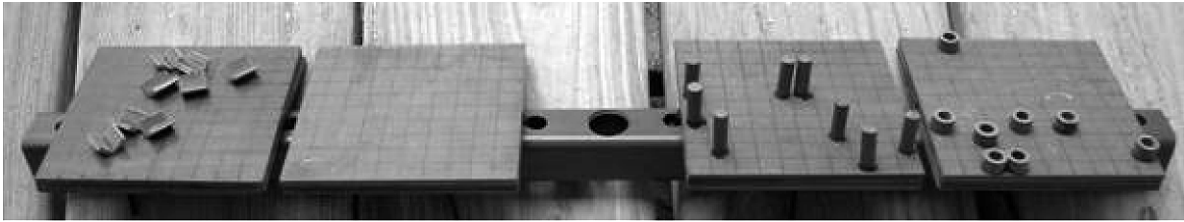
Fig. 1. Experimental array showing three types of structures (taxa). Shell mimics were approximately 13 mm long × 13 mm wide × 6 mm high; barnacle mimics were approximately 10 mm wide (outer wall) × 6 mm high; and upright structures were approximately 6 mm wide × 18 mm high. Panels are 100 cm². Total area was 127 cm² for shell mimic panels, 131 cm² for barnacle mimic panels, and 126 cm² for upright mimic panels.

(41° N), Virginia (37° N), Florida (27° N), and Belize (16° N). Settlement panels are commonly used in studies of epifaunal communities (Osman and Whitlatch 2004) and are an extremely tractable experimental analog to naturally occurring hard substrates. The use of settlement panels provides standard substrate material of a set area, while allowing recruitment and community development to proceed naturally. Three types of structural elements were designed to mimic structures that can be created by ecosystem engineers: bivalves (termed "shells"), barnacles, and any organism with an upright growth form (e.g., some bryozoans, hydroids, corals, or anemones). Each mimic was chosen to provide a unique type of structure. Shell mimics created habitat underneath overhanging ledges, barnacles created habitat inside a concentric wall, and the upright structure provided cylindrical vertical relief. Sizes of mimics were chosen to approximate average sizes of the focal natural organisms (Fig. 1). All substrates (panel and mimics) were made out of the same material (PVC type 1 gray) and were abraded to facilitate settlement by invertebrates.

Panels were assigned to one of four treatments. Three structurally complex treatments were made for the three focal taxa with eight mimics (one mimic type per panel) cemented in random arrays to each panel. The fourth treatment was a blank panel with no mimics. While all mimics provided equivalent surface areas (4.2 cm²), the footprint of each type of mimic was slightly different. Therefore, eight mimics were used per panel to ensure the least disparity in total panel area (<0.05%; Fig. 1).

Experimental panels were deployed at three sites in each of the four regions and were sampled at three intervals up to one year. Sites were 13.4 km apart on average. Low-salinity/estuarine areas were excluded, and all chosen localities maintained minimum salinities of greater than 20‰, and most commonly greater than 30‰ (see Appendix A for additional environmental characteristics of sites). At each site, four racks were deployed to a depth of 0.6 m below lowest low tide and at least 0.5 m above the bottom; each rack held one panel of each treatment, for a total of 48 panels per region and 192 in total. Panels were deployed between 8 July 2006 and 22 August 2006, which was early in the recruitment season for the northern, more seasonal latitudes. Panels in Connecticut, Virginia, and Florida were sampled at one-, three-, and 12-month post-deployment intervals. Panels in Belize were sampled at three-, six-, and 12-month intervals, which proved to be more appropriate for the slower community development timescales in the tropics. Because of feasibility constraints, 36 of the 48 panels were sampled in Connecticut, Virginia, and Florida at the one- and three-month sampling intervals, and all remaining panels (up to the 48; some were lost to tampering and/or storms) were sampled at 12 months. All panels were sampled in Belize during all intervals.

To evaluate the impact of the mimics on community diversity at the most biologically relevant local scale, invertebrate assemblages attached or directly adjacent to mimics were compared to assemblages on flat areas of the same panel. This scale, which is on par with other studies of structural heterogeneity and marine epifaunal communities (Lapointe and Bourget 1999), was chosen to best approximate the scale that natural dynamics of structure forming ecosystem engineers would occur and to provide enough surface area for numerous individuals to colonize. For example, while individuals in this community vary substantially in size, some never exceed a few millimeters in diameter, and during recruitment, up to 10 000 individuals can be observed on a 100-cm² panel (Freestone et al. 2009). Upon retrieval, panels remained in seawater while nondestructively sampled with a dissecting microscope and were returned to the field within two days of retrieval. On each panel, diversity was recorded for mimics as well as five randomly chosen quadrats of equivalent surface area (4.2 cm²) on the flat panel. Identifications were recorded for the lowest taxonomic grouping possible with the assistance of local experts and invertebrate keys. Where taxonomy was especially difficult and not well known, particularly in Belize, morphospecies diversity was recorded using common characteristics for differentiating groups. As an indication of sampling effort, 1742 mimics and quadrats were sampled during the 12-month sampling interval alone. Total panel diversity was also recorded for each panel, including species that were not recorded in any of the quadrat or mimic samples. Panel percent cover was estimated visually with the aid of a 10 × 10 cm grid (one cell is equivalent to 1% cover).

To evaluate the effect of structural complexity on diversity among latitudes, diversity at the scale of mimics and quadrats was analyzed using nested mixed models. Random effects were site (nested in region), rack (nested in site and region), and plate (nested in rack, site, and region). Fixed effects were region (Connecticut, Virginia, Florida, or Belize), taxa (shell, barnacle, upright), structural complexity (mimics or quadrats), and the interactions between structural complexity and taxa, structural complexity and region, taxa and region, and the three-way interaction. No qualitative difference in results occurred when interaction terms between fixed factors and nested random factors were included in the model; therefore these terms were not included in the final models. The critical element in these models is the interaction between structural complexity and region, as this will identify a latitudinal gradient in the effect of structure on diversity of the epifaunal communities. When examining mimics and quadrats in relation to the different types of structures (taxa), we focus here on the pairwise comparisons between mimics and quadrats on panels with the same type of structure (e.g., shell mimics vs. quadrats on panels with shell mimics). Three separate models were used for the three sampling intervals. For the "early" sampling interval, one-month data were used for Connecticut, Florida, and Virginia, and three-month data were used for Belize. For the "intermediate" sampling interval, three-month data were used for Connecticut, Virginia, and Florida, and six-month data were used for Belize (results are consistent even if three-month data for Belize are used in this analysis). For the "late" sampling interval, 12-month data were used for all sites.

To further explore if the effect of structurally complex mimics in Belize was (1) scale dependent and/or (2) consistent beyond the timescale of this experiment, two additional analyses were conducted. First, the effect of taxa (shell, barnacle, upright) on total panel diversity was modeled (ANOVA) to determine if the impacts of small-scale structural complexity were evident at a larger spatial scale. Second, to confirm that effects of the structures were robust to longer term community development in Belize, shell and blank panels were sampled again at one site in Belize 2.5 years after initial deployment and total panel diversity was compared.

Differences in community composition among spatial scales and experimental treatments at the 12-month sampling interval were also compared using a null-model approach. We calculated a similarity metric as the probability that the observed number of shared species between two samples differs from the null expectation of random community membership (Raup and Crick 1979, Vellend et al. 2007, Chase et al. 2009) using R 2.11 (R Development Core Team 2010). Because standard metrics of (dis)similarity, such as the Jaccard and Soreson indices, depend on the number of species occurring locally in the samples (alpha diversity), these

metrics cannot be used to test for differences in community composition (beta diversity) in isolation from differences in alpha diversity. However, the Raup-Crick metric removes this alpha dependence and is considered preferable to use when samples differ in alpha diversity, as observed in this study. We calculated the classic Raup-Crick (Raup and Crick 1979) metric with the exception that the probability of species being drawn from the species pool was set to be proportional to its among-site occupancy. These pairwise Raup-Crick similarity values were then analyzed using a permutational multivariate ANOVA (PERMANOVA, conducted in PRIMER 6.1 [PRIMER-E, Ivybridge, UK] with PERMANOVA add-on) to test for effects of site (random), rack (nested within site, random), taxa, structural complexity, and all interactions. Since species pools varied by region, and the Raup-Crick null model assumes a single species pool, it was necessary to conduct separate analyzes for each region. Additionally, data from Belize were also tested for differences in variability in community composition (multivariate dispersion) among experimental treatments (PERM-DISP, conducted in PRIMER 6.1 with PERMANOVA add-on).

To estimate regional enrichment along the latitudinal gradient, mean local diversity (panel diversity after twelve months) for each region was first divided by regional diversity to calculate overall ratios of local to regional diversity (Witman et al. 2004). Regional diversity was estimated by using the total number of species/morphospecies recorded in that region throughout the experiment. This provided the most conservative estimate of regional richness, including only those species that were known to occur during the experimental time period and could successfully colonize the settlement panels (see Russell et al. 2006 and *Discussion* for benefits of this approach). The ratio of local to regional diversity was then regressed against latitude. Analyses were completed in JMP 8.0 (SAS Institute, Cary, North Carolina, USA).

Results

A latitudinal gradient in the overall effect of structurally complex mimics on community diversity was observed at each of the three sampling intervals. All three mixed models yielded significant results (early, $R^2_{adj} = 0.72$, $N = 1405$; intermediate, $R^2_{adj} = 0.72$, $N = 1342$; late, $R^2_{adj} = 0.64$, $N = 1301$; Table 1), and the interaction between region and structural complexity was consistently significant in all models ($P < 0.05$, Table 1, Fig. 2). Structurally complex mimics in Belize always harbored more species than the flat quadrats (Fig. 2). No differences between mimics and quadrats were observed in any model for Florida or Virginia, and mimics were shown to harbor fewer species than quadrats in Connecticut during the intermediate sampling interval only (Fig. 2).

TABLE 1. Results of the mixed models for community diversity at each sampling interval.

Effects†	Early		Intermediate		Late	
	df or VC	F or SE	df or VC	F or SE	df or VC	F or SE
Fixed						
Region	3, 8.041	4.784*	3, 8.437	8.273**	3, 6.321	23.961**
Taxa	2, 68.6	11.096***	2, 101.4	8.754**	2, 80.92	1.793
Structural complexity	1, 1298	5.620*	1, 1297	0.080	1, 1239	3.868*
Taxa × structural complexity	2, 1326	12.221***	2, 1264	7.512**	2, 1257	10.622***
Region × structural complexity	3, 1297	14.834***	3, 1276	10.412***	3, 1230	3.442*
Taxa × region	6, 68.52	1.259	6, 83.92	0.733	6, 79.24	1.374
Taxa × region × structural complexity	6, 1321	2.448*	6, 1265	1.266	6, 1249	0.306
Random						
Site (region)	3.148	1.643	2.099	1.144	0.501	0.362
Rack (region, site)	0.083	0.225	0.373	0.189	−0.014	0.149
Plate (region, site, rack)	0.156	0.424	0.551	0.146	1.117	0.246
Residual	2.716	0.107	3.350	0.136	3.550	0.146

Note: Variance components (VC) were calculated using the restricted maximum likelihood (REML) method.

† For fixed effects, df and F values are presented. For random effects, VC and SE are presented. No qualitative difference in results occurred when interactions between fixed and nested random effects were used as error terms in the mixed models. These interactions were therefore excluded from the final models.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$.

The interaction between taxa and structural complexity was also significant in all models (Table 1). The focal comparisons were between mimics and quadrats on panels with the same type of structure (e.g., shell mimics vs. quadrats on panels with shell mimics), serving as paired comparisons. The shell mimics were the only type of structure to produce consistent effects, and mimics on shell panels always ranked highest in mean diversity. On panels with shell mimics, mimics harbored more species than quadrats at both the early and late sampling intervals ($P < 0.05$). While this difference was not significant at the intermediate sampling interval, shell mimics were still more diverse than all other combinations of taxa and structural complexity. At the intermediate sampling interval, upright mimics were less diverse than quadrats on panels with upright mimics. No other paired comparisons were significant ($P > 0.05$).

The three-way interaction between structural complexity, taxa, and region only served as a significant predictor of diversity beyond the two-way interactions at the early sampling interval (Table 1). The focal pairwise mean comparisons demonstrate a consistent pattern with the results reported above for the two-way interactions. There were no differences among these (or any) means in Virginia (Appendix B) or Florida (Appendix C) during any sampling interval. In Connecticut, upright mimics were less diverse than quadrats on upright panels, but only during the intermediate sampling interval (Appendix D). However, in Belize, shell mimics were always more diverse than quadrats on shell panels at all sampling intervals (Fig. 3). In addition, barnacle mimics were more diverse than quadrats on barnacle panels, but this effect only occurred at the early sampling interval and did not persist through time.

This consistent and positive effect of mimics on diversity in Belize also scaled from the smallest scale (e.g., individual mimics) to the larger panel scale and effects persisted beyond the completion of the one-year experiment. After 12 months, panels with shell mimics were more diverse than blank panels with no mimics (Appendix E; model $R^2_{adj} = 0.72$, $N = 48$; fixed effect of taxa $F_{3,33} = 2.82$, $P = 0.05$). While shell mimics on average harbored 1.42 ± 0.41 (mean $\pm$ SE) more species than flat areas on the same panel, this resulted in an average increase of 5 ± 1.71 species per panel when compared with blank panels. Shell and blank panels at one site in Belize were also sampled again 2.5 years after initial deployment, and panels with shell mimics were still more diverse than blank panels (one-way t test, $t = 2.29$, $P = 0.03$, $N = 8$; shell mimic, 23.3 ± 2.29 species per panel; bare, 14.5 ± 3.07 species per panel; Appendix E).

Diversity also varied among sites, particularly during the early and intermediate sampling intervals (early, 48% of total variance; intermediate, 33% of total variance; late, 10% of total variance; Table 1). Variance in species richness was negligible among racks at a site (up to 5.8% of total variation). Variance explained by the panel scale ranged from 6.5% at the early sampling interval to 22% at the late sampling interval. However, while our measured environmental characteristics (temperature, salinity, dissolved oxygen, chlorophyll, and clarity) did differ among sites within regions (as indicated by the variance explained by our random effect of site), no latitudinal clines with the exception of temperature were evident (Appendix A).

While rates of community development can vary with latitude, by the final sampling interval at 12 months, percent cover in all regions was fairly high (Connecticut, $97.6\% \pm 4.40\%$ [mean $\pm$ SD]; Virginia, $88.6\% \pm 18.9\%$; Florida, $92.5\% \pm 7.41\%$; Belize, $89.6\% \pm 11.9\%$).
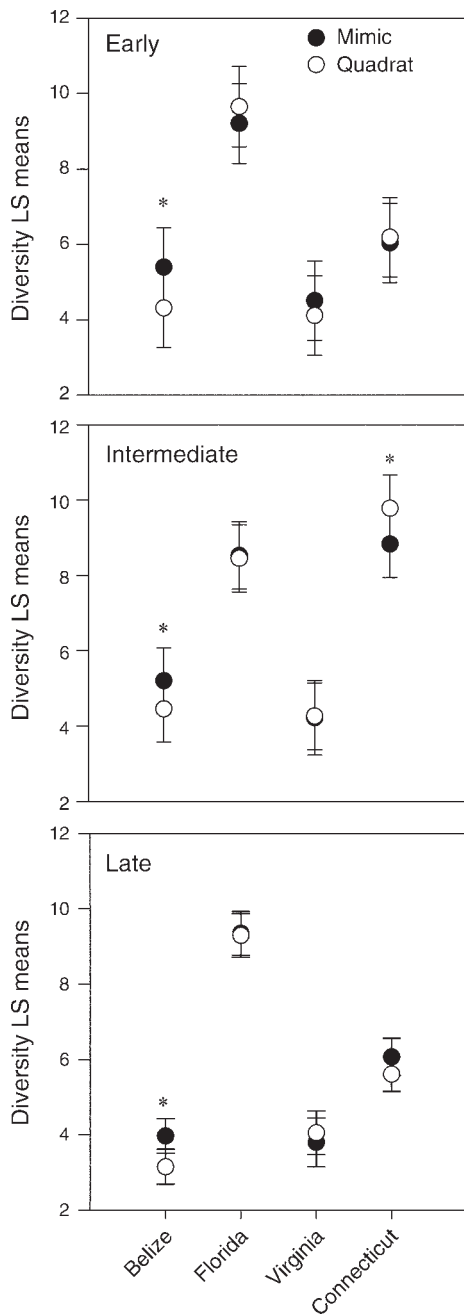
FIG. 2. Diversity least-squares (LS) means (±SE) are shown for the two types of structural complexity (mimic [complex] or quadrat [flat]) for each region at each sampling interval (early, intermediate, and late). This relationship corresponds to the structural complexity × region interaction in the mixed models (Table 1).

* Significant difference between mean diversity of mimics and quadrats at α = 0.05 (Tukey hsd).

FIG. 3. Diversity LS means (±SE) from the mixed models are shown for the two types of structural complexity (mimic [complex] or quadrat [flat]) for each taxon (shell, barnacle, upright). Values are shown for Belize only; see Appendices B–D for other regions.

* Significant difference between mean diversity of mimics and quadrats at α = 0.05 (Tukey hsd).

However, to confirm that systematic variation in percent cover of communities among latitudes did not bias the results, panel diversity at 12 months was modeled using a mixed model ANCOVA including random effects of site and rack (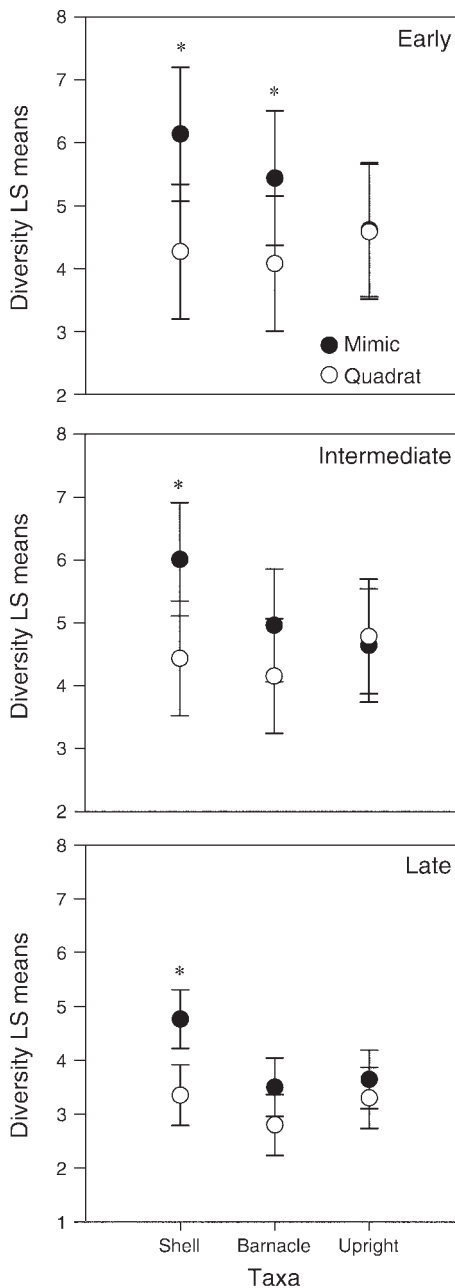nested in site) and the fixed effects of region and percent cover (arcsine transformed from percentage data). However, percent cover was not a significant predictor of panel diversity ($P > 0.05$).

Some differences in community composition were observed among treatments in Belize. While the experimental taxa and structural complexity treatments did not result in systematic shifts in community
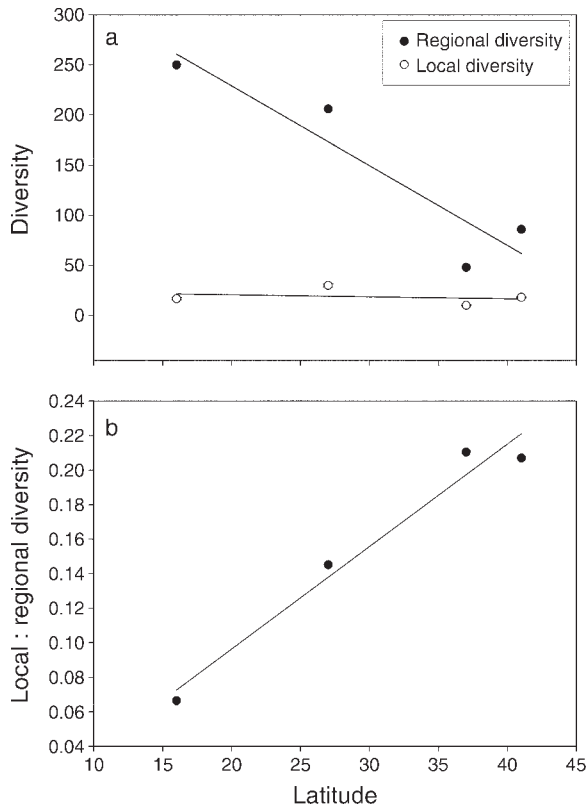
F<small>IG</small>. 4. (a) Local (panel) and regional diversity by latitude. Error bars for local diversity data are smaller than the symbols. (b) Relationship between the ratio of local to regional diversity and latitude.

composition in any of the three northern regions, a significant interaction between rack and taxa occurred in Belize (PERMANOVA, Appendix F), demonstrating spatial variation in the community response to the different types of structures. Community composition also varied among sites (in all regions) and among racks at each site (in Connecticut, Florida, and Belize). Furthermore, in Belize, community composition was more variable in association with mimics than quadrats for each taxa (e.g., PERMDISP, group factor; taxa and structural complexity combined, $F_{5, 456} = 64.9$, $P[\text{perm}] = 0.0001$, all focal pairwise comparisons $P < 0.05$). Community composition among panels with shell mimics was also more variable than either of the other two taxa (PERMDISP, group factor; taxa, $F_{2, 459} = 4.46$, $P[\text{perm}] = 0.012$). However, these differences were quite weak (mean distance to centroid among taxa and structural complexity groups = 69.723–69.999; among taxa groups = 70.088–70.13).

Correlative results are consistent with the hypothesis that higher-latitude communities may be more regionally enriched (Fig. 4). The local : regional diversity ratio increased from low to high latitudes (Fig. 4b; $R^2 = 0.97$, $P = 0.02$, $y = -0.022561 + 0.0059437x$), showing that high-latitude communities had proportionally more

species from the regional species pool present at the local scale than low-latitude communities.

Discussion

Our results are consistent with the hypothesis that there is a latitudinal shift in the relative importance of local interactions and regional enrichment with latitude. At the local scale, we found a latitudinal gradient in the effect of structurally complex mimics of ecosystem engineering species. After one year, only communities in our lowest-latitude region, Belize, showed a significant and positive effect of the mimics, particularly the shell mimic, on species diversity, which was evident at both the smallest sampling scale ($\sim$4 cm^2) as well as the larger panel scale ($\sim$100 cm^2). Shell mimic panels in Belize were an average of 35% more diverse than blank panels. While panels with shell mimics did have greater total surface area than the blank panels, if this was solely an area effect, then all panels with mimics would also have greater species richness than the blank panels, which was not the case. In comparison, panel diversity after 12 months did not statistically differ among types of structures (Taxa) in any other region. Furthermore, observations of naturally occurring oyster shells on panels in Belize (Appendix G) yielded qualitatively similar patterns of elevated local diversity, reinforcing our interpretations of the effects of the mimics. Longer term data further suggest that these patterns can persist through time in the tropics, even beyond the temporal extent of our one-year study. Our results are consistent with other studies that have found no effect of structural heterogeneity on subtidal epifaunal community diversity at higher latitudes (Bourget et al. 1994) and positive effects at tropical latitudes in intertidal systems (Menge and Lubchenco 1981, Castilla et al. 2004).

While no systematic shifts in community composition in response to our experimental structures occurred in the three northern regions, community composition did differ among taxa (shell, barnacle, upright structures) in Belize, although this effect was spatially variable among racks. Community composition was also slightly more variable in association with taxa mimics in Belize, demonstrating a small increase in beta diversity in addition to the increase in alpha diversity reported above. This beta diversity effect suggests that mimics did not consistently facilitate the same species; rather different individual mimics facilitated different suites of species. However, it's worth noting that the Raup-Crick metric, and in fact all pairwise measures of similarity, have little power to detect deviations from the null expectation when alpha is very low in comparison to the species pool. This limitation is certainly relevant for the data reported here, since alpha diversity for the mimics and quadrats ranged from 2 to 10 and species pools exceeded 200 species. This problem is inherent to these types of metrics (including Jaccard and Sorenson), and cannot be alleviated through quantitative approaches. Therefore, these results are conservative. Nonethe-

less, our results indicate that the structurally complex mimics impacted patterns of both species richness and composition in our lowest-latitude region, Belize.

While experimental results support the hypothesis that local interactions may be stronger at low latitudes, results may also suggest greater openness to regional enrichment at higher latitudes. Local diversity represented a greater proportion of regional diversity at higher latitudes (Fig. 4), consistent with the idea of greater regional enrichment (Witman et al. 2004). With potentially weaker local interactions that would otherwise limit community membership, these higher-latitude assemblages may be more open to augmentation from the regional species pool. Reciprocally, communities at low latitudes had proportionally fewer regional species present at the local scale, inferring that these tropical communities may be more limited in membership and thus more resistant to regional enrichment. Our correlative pattern is particularly strong considering our conservative estimates of regional richness. If our regional richness values underestimate true diversity the overall slope of the relationship is not likely to change. If diversity is underestimated more at lower latitudes, then local to regional diversity ratios for low-latitude regions would be even lower, further increasing the slope of the relationship. This latter scenario is the most likely, in that species accumulation curves for our 12-month sampling interval reached an asymptote at 50–60 species in Connecticut (using observed values and Chao2 and Jacknife 2 estimators), while in Belize, the species accumulation plots did not saturate. These patterns indicate that our temperate communities were well sampled, but our tropical species pool estimate is likely to be conservative. However, given the experimental effort within each region in our study, regional replication is, by necessity, low, and regression results should be viewed cautiously. Nonetheless, our correlative results are consistent with patterns demonstrated in previous studies with much greater regional replication (Witman et al. 2004).

Our results demonstrate a mechanism by which structure-providing species facilitate space-occupying species, possibly reflecting tighter niche partitioning and/or higher predation pressure. Our field observations support the latter explanation. While space is known to be the principle limiting resource in these communities, space generally was not limiting in the tropical environments. Panels were rarely completely covered, and often had visible scars from consumers (Appendix G). This space availability is also true for panels that were deployed at our sites in Belize over much longer timeframes (>4 years; A. Freestone and R. Osman, *personal observation*). This resource availability suggests predation rather than competitive dynamics may limit species abundances and ultimately diversity. This hypothesis is further supported by the observation that, despite the availability of space and the greater regional species pool in the tropics, panel diversity was fairly constant across the latitudinal gradient (Fig. 4). While Witman et al. (2004) suggested, among other hypotheses, that predation on competitive dominants at high latitudes could allow greater colonization from the regional species pool and thus greater regional enrichment, our study suggests that strong predation in the tropics could limit community membership, resulting in communities that are less open to regional enrichment. Habitat complexity has been shown to reduce predation on marine invertebrates in temperate (Russ 1980) and tropical (Menge et al. 1985) systems, and increased consumer pressure in the tropics (Menge and Lubchenco 1981) may further increase the importance of biogenic refuges from predation.

Although we found positive relationships in Belize between community diversity and the structurally complex mimics, particularly the shell mimic, we found one negative relationship in Connecticut: on panels with upright structures, diversity was lower on mimics than in quadrats at the intermediate sampling interval. Invertebrates did not attach as readily to the upright structures, but the negative effect disappeared by the late sampling interval, possibly as the basal community grew up around the mimics or colonized this less optimal habitat. This example highlights that no single effect resulted from an increase in structural complexity; rather community response is likely to be taxa dependent.

The regions also vary in their levels of seasonality. Recruitment in the northern regions peaks during summer and early fall and tapers off significantly in the winter months (Freestone et al. 2009), while recruitment in Belize is fairly slow and steady throughout the year (R. Osman, *personal observation*). Similarly, higher growth rates occur in the summer than in the winter in the northern regions, while growth occurs year-round in the tropics. We aimed to capture this variation in our iterative sampling design, speculating that the effects of the mimics would likely vary both in space and time. However, of the three northern regions and three sampling intervals, only the upright mimics had a (negative) effect on diversity at the intermediate sampling interval in Connecticut. There was no effect in any of the northern regions even after only one month, when one might expect relatively young and small individuals would have the strongest response to the small structures (Appendix H).

By employing standardized experimental protocols along a biogeographic transect, our study suggests that the relative importance of local interactions and regional enrichment may be latitude dependent. Regional enrichment should be thought of as ubiquitous, to the extent that communities are open to this augmentation. If species interactions are stronger in the tropics than elsewhere, then these tropical communities may be less open to enrichment than their higher-latitude counterparts. This conceptual framework can direct future studies that couple local scale experimental approaches to macroecological patterns (Connell and Irving 2009,

Sanford and Bertness 2009, Witman and Roy 2009) to gain a more integrated understanding of how communities assemble across the globe.

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APPENDIX A

Environmental data for sites (*Ecological Archives* E092-017-A1).

APPENDIX B

Diversity least-squares means for treatment combinations in Florida from mixed models (*Ecological Archives* E092-017-A2).

APPENDIX C

Diversity least-squares means for treatment combinations in Virginia from mixed models (*Ecological Archives* E092-017-A3).

APPENDIX D

Diversity least-squares means for treatment combinations in Connecticut from mixed models (*Ecological Archives* E092-017-A4).

APPENDIX E

Mean panel diversity by treatment in Belize after one year and 2.5 years (*Ecological Archives* E092-017-A5).

APPENDIX F

Results for permutational multivariate ANOVA (PERMANOVA) on beta diversity values for each region (*Ecological Archives* E092-017-A6).

APPENDIX G

Photographs of experimental panels in Belize with shell mimics and naturally occurring shells (*Ecological Archives* E092-017-A7).

APPENDIX H

Examples of panels with barnacle mimics from Connecticut and Belize at the early sampling interval (*Ecological Archives* E092-017-A8).