Marine fauna sort at fine resolution in an ecotone of shifting wetland foundation species

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Abstract. Climate-driven global change is shifting the distribution and abundance of foundation species that form the base of ecosystems. The corresponding responses of inhabitant species to shifts in habitat-forming species are poorly understood, however we expect community responses to depend on how species perceive habitat patches and sort among them, particularly along range edges. We used the poleward shift of a mangrove–marsh ecotone to evaluate sorting of marine macrofauna (small fish and decapod crustaceans) among vegetation patches at a series of nested scales. Within the mangrove–marsh ecotone, we deployed retrievable panels of artificial vegetation structures mimicking a marsh grass and two mangrove species in patches dominated by each of these three foundation species. Over six months, we observed macrofaunal sorting by physical structure, isolated on panels, and by patch type, which included stand-level attributes such as production, shading, and chemical cues. We found multiscale partitioning of macrofaunal community composition by site (kilometer scale), vegetation type, and patch type with stand attributes (meters), and physical structure (centimeters). Differences in community composition between vegetation types at each scale indicated that mangroves and marsh grass differ as habitat for marine fauna and that wetland inhabitants can distinguish and sort among fine-grain habitat patches that co-occur within the ecotone. Such differences suggest that shifts in wetland vegetation are consequential for the protection and management of coastal populations. Studies that determine which habitat attributes shape inhabitant fauna associations can help reveal not just the spatial grain at which inhabitants associate with emerging frontier habitat but also how the redistribution of foundation species shapes the pace and resolution of broader community change.

Key words: climate change; coastal wetland; crustacean; dominant species; ecocline; mangrove–marsh ecotone; physical structure.

INTRODUCTION

Global climate change, manifest as increased mean and variability of temperatures and altered precipitation regimes, is driving changes in species phenology and geographic distributions (Yang and Rudolf 2010, IPCC 2013, Poloczanska et al. 2013). Some of the most marked effects of climate-driven global change arise from changes in the distribution and abundance of foundation species that form the base of ecosystems (Dayton 1972, Harley et al. 2006, Hoegh-Guldberg and Bruno 2010). Climate change has been linked to shifts in terrestrial, aquatic, and marine foundation species. Woody encroachment in savanna meadows is determined in part by changing precipitation regimes (Brown et al. 1997, Sankaran et al. 2005, Eamus and Palmer 2007, Haugo et al. 2011). Similarly, warming temperatures have been implicated in the spread of invasive encrusting marine species, shifts in Arctic algal production, and the displacement of kelp meadows, often by tropical reef species (Stachowicz et al. 2002, Smol et al. 2005, Kortsch et al. 2012, Vergés et al. 2014, Wernberg et al. 2016). Because ecosystems coalesce around foundation species, changes in the distribution of a small number of these key species are expected to alter associated communities and ecosystem function (Bruno et al. 2003, Ellison et al. 2005, Yang and Rudolf 2010). Indeed, facilitation can be so formative that the effects of changes in foundation species surpass the direct abiotic effects of climate change (Gedan and Bertness 2010).

The redistribution of foundation species results in landscape mosaics, or ecotones, where one set of dominant species is displaced by another. These range edge landscapes are characterized by habitat patchiness that is qualitatively different from the landscape at range centers (Arnot and Fisher 2007, Gastner et al. 2009, Thomas 2010, Osland et al. 2013). The impacts of foundation species range shifts, and associated habitat modification, on broader ecological communities will depend on how species assemble in patchy habitat of frontier landscapes. Indeed, inhabitants may respond to changes habitat attributes, especially physical structure, as much as to changes in vegetation type itself (MacArthur and MacArthur 1961). Especially where facilitative influences emerge at different scales, understanding which habitat attributes determine inhabitant fauna associations can help reveal the pace and spatial resolution at which shifting foundation species can stimulate changes in associated communities.

Globally along sheltered coastlines, subtropical mangroves are expanding poleward into temperate saltmarshes, forming wetland ecotones of contrasting woody and grassland habitat patches (Osland et al. 2013, 2017, Cavanaugh et al. 2014, Saintilan et al. 2014). The foundation plant species that compose the mangrove–marsh ecotone occup
comparable emergent intertidal zones exposed to saltwater inundation and available to mobile marine macrofauna, such as juvenile fish and decapod crustaceans. However, mangrove forests and saltmarshes differ in key attributes, including productivity, seasonality, shading, and growth form (Pennings and Bertness 2001, Hogarth 2015, Kelleway et al. 2017). Shifting wetland composition raises questions about ramifications for both transient and resident marine species that depend on wetland habitats. Habitat selection and use by marine fauna is shaped by a variety of cues from predators, conspecifics, physical structure, or production (Rittschof et al. 1998, Kingsford et al. 2002, Arvedlund and Kavanagh 2009). Habitat selection mechanisms are scale dependent: settling marine fauna orient toward suitable habitat using olfactory cues on broader scales of meters to kilometers, but are most attuned to visual cues at fine spatial scales (<1–10 m) to aid their perception of microhabitat suitability (Kingsford et al. 2002, Lecchini et al. 2005, Arvedlund and Kavanagh 2009).

To understand the pace and resolution at which marine macrofauna respond to shifting wetland composition, we need to determine the habitat attributes (and associated spatial grain) with which inhabitant fauna sort among habitat patches. Where mangrove patches emerge within the marsh landscape, microhabitat changes in physical structure (e.g., woody or herbaceous, branching, emergent, or overhanging) are spatially nested within changes in other attributes, such as export of primary production, that emerge at broader scales as patches expand. Habitat structural features arise at a fine spatial grain (centimeters to meters), beginning to form immediately upon the establishment of foundation species (Humphries et al. 2011). Once habitat patches surpass a critical size, emergent (e.g., shade) and late-breaking (e.g., flowering) habitat attributes differentiate patches functionally from the surrounding landscape, generating a suite of coarser grained (meters to kilometers) “stand-level” attributes (Lomolino and Weiser 2001, Bennett et al. 2006). Biomass production, for example, is tidally exported from mangroves and marshes, thus production of emerging small patches will be swamped by production from the surrounding vegetation matrix until patches become extensive (Lee 1995, Odum 2002). Sensitivity to fine-grain structural attributes should promote selective habitat associations at small scales and in nascent patches, whereas sorting based on emergent attributes should lead to habitat associations at coarser spatial resolution. Alternatively, species responses to both stand-level habitat attributes and fine-grain structural attributes could promote early community differentiation that develops in concert with habitat patch growth. Ultimately, inhabitant sensitivity to the habitat attributes that develop as foundation species establish should determine the spatial resolution of community responses in frontier landscapes.

Here, we evaluate marine macrofaunal sorting among habitat patches across nested spatial scales within a mangrove–marsh ecotone. We used a fully crossed manipulative field experiment to isolate the influences of vegetation structural form (<1-m² grain) from other stand-level attributes (>15-m² grain) at two geographical locations. We hypothesized (1) that each of two mangrove and one marsh vegetation types provides distinct habitat that is differentially inhabited by macrofauna and (2) that physical structure is among the suite of attributes that define habitat quality and, thus, faunal response to each vegetation type. Although structure is an important component of habitat, providing shelter, diversifying space, and increasing surface area for foraging, population dynamics and species distributions may be more closely linked to the presence of structure per se rather than to particular forms (Heck et al. 2003). If occupancy depends on the simple presence of structured vegetative habitat, then inhabitant communities should remain relatively unchanged by the shift from marsh to mangroves. However, if macrofaunal species respond to changes in structural form of vegetation patches, then mangrove expansion may shift inhabitant community composition. The early emergence of structural effects means that these changes could be detectable even where vegetation patches are rare and newly emergent along the range edge. We determined that communities differ between mangrove and marsh wetlands, due in part to differences in physical structure on a scale as small as 0.25 m². Broader patch-level attributes caused a comparable degree of sorting. Differences in macrofaunal community composition indicative of sensitivity to both structural and stand-level habitat attributes demonstrate that mangrove emergence among saltmarshes is altering wetland habitat, stimulating both early and fine-scale changes in marine community composition.

Methods

Study sites

We established a manipulative landscape-scale field experiment to quantify macrofauna (i.e., decapod crustacean and fish) habitat and structural associations along the Halifax and Matanzas Rivers to characterize patch use dynamics within the mangrove–marsh ecotone. The ecotone presently spans 2–3 degrees latitude from south of the St. John’s River inlet (30.27° N) to the south side of Cape Canaveral, Florida, USA (28.16° N). Both sites are characterized by interspersed monospecific patches of vegetation covering tens of square meters. The Halifax River site (29.09°, −80.94°) is a mangrove-dominated wetland north of Cape Canaveral, with small patches of Spartina alterniflora Loisel (smooth cordgrass) persisting along shallow, sandy banks. Seventy kilometers north, the Matanzas River site (29.67°, −81.24°) historically is an S. alterniflora-dominated saltmarsh south of St Augustine where mangroves have proliferated in recent decades (Zomlefer et al. 2006, Cavanaugh et al. 2014, Rodriguez et al. 2016). Avicennia germinans L. (black mangrove) were abundant and Rhizophora mangle L. (red mangrove) were still rare at the time of this study (Williams et al. 2014). Although Batis maritima L., Salicornia spp., Littoraria racemosa L., Distichlis spicata L., and associated species occur at both sites, our study focused on the three vegetation types with distinctive physical growth forms that dominate the intertidal ecotone landscape along the Atlantic Coast of Florida: S. alterniflora produces emergent shoots; A. germinans produces emergent pneumatophores (i.e., snorkel roots); R. mangle produces overhanging prop roots. Throughout the study, generic names refer to stand-level attributes; growth structures refer to physical structure type.
Experimental arrays were deployed adjacent to main waterways within 4.5 km of the inlet to minimize spatial variation in estuarine environmental attributes. During the study, sites had comparable salinity (29 ± 0.5 ppt [mean ± SE], Welch’s $t$, df = 145.78, $P = 0.95$) and water temperature (26°C ± 0.4°C, Welch’s $t$, df = 134.25, $P = 0.22$). Across sites, habitat patches were selected to provide a continuous channel-facing edge of a single vegetation type with a total patch area > 15 m$^2$. All patches had mixed sand, mud, and oyster substrates. An overall total of four patches per vegetation type were selected ($n = 12$ patches total), with six patches at each site allocated according to the natural abundance of each vegetation type (three Spartina, two Avicennia, and one Rhizophora patch at Matanzas; one Spartina, two Avicennia, and three Rhizophora patches at Halifax). To ensure comparable conditions, especially vegetation patch availability, between sites, the geography of inlets limited our study to two sites, with replication of experimental arrays within each site.

**Experimental design and sampling**

To characterize macrofaunal composition across habitat types and vegetation structures at nested spatial scales, we deployed 0.25-m$^2$ artificial vegetation panels along the periphery of >15-m$^2$ habitat patches in a balanced design across the pair of sites. Briefly, structure type was manipulated by fitting retrievable plywood panels with artificial vegetation mimics modeled on field measures of intertidal vegetation structures (details are provided in Johnston and Caretti [2017]). Panels were then deployed in triplicate, including one of each vegetation structure within each habitat type ($n = 36$ panels total or 12 per structure type across habitats and 12 within each habitat type; method as in Lindsey et al. [2006] and Pardo et al. [2007]; Fig. 1). We did not manipulate the specific attributes of complexity per se (e.g., diameter or density), but rather we isolated the effects of vegetation physical structure from other habitat attributes at the stand level. Control panels had structure that match their model habitat (e.g., grass shoot replicas within a Spartina patch, Fig. 1 and Appendix S1: Fig. S1). Manipulation panels were deployed “out of context” (i.e., in patches other than their model habitat), making them structurally distinct from their host patch (e.g., prop roots within a Spartina patch). Thus, panel treatment responses indicated the effects of physical structure alone, while productivity and other attributes were governed by the habitat patch at the stand level.

Panels were sampled and immediately redeployed every two weeks from mid-May through early November 2014 ($n = 13$ sampling events) within three days of full and new moons. We designed the retrieval method to capture nursery-stage individuals, primarily juvenile crustaceans and fish. Although the sampling design was not optimal for capturing large or fast-swimming individuals, finfish and swimming crabs were regularly captured, with specimens ranging in length from 0.5 to 100 mm. We identified individuals, primarily to genus or species based on morphology and limited in resolution by coarse field identification of live larval and juveniles stages, and immediately released macrofauna in the field to reduce artificial changes in community composition caused by destructive sampling (Williams 1984, Bullard 2003, Johnson et al. 2005, Kells and Carpenter 2011). Results are reported for samples collected from June through November 2014 ($n = 11$ sampling sessions). Samples grouped by panel structure, habitat type, or treatment (control or manipulation) allowed specific tests for differences in macrofaunal community composition across each predictor.

**Analysis**

Community analyses proceeded using morphospecies assignments, excluding data from morphospecies that occurred only once or twice in the total sample set. Community composition was tested as a function of stand type (Rhizophora, Avicennia, Spartina) and structure type (prop roots, pneumatophores, grass shoots) predictors. Although unreplicated, the effect of site was evaluated to account for landscape differences (i.e., mangrove or marsh dominated). All analyses were conducted within the program R version 3.2.3 (R Core Team 2015). Dispersion of community composition in ordination space was evaluated with Bray-Curtis distance metrics in the betadisper function in the vegan package in R (Oksanen et al. 2017). Dispersion was generally uneven between predictor levels (violating the PERMANOVA assumption of homogeneity of variances), thus we conducted all community analyses with generalized linear mixed effects models (GLMM) with species counts modeled with the Poisson distribution link function in the glmer function in the lme4 package in R (Bates et al. 2015). Within GLMMs, we used the random effect model structure “(% predictor|species)” to write random slopes models that allow changes in community composition via species-specific responses (Bolker et al. 2009, Johnson 2014). All models also included the predictor as a fixed effect to account for overall differences in abundance. Models with the stand type predictor also included a random effect of patch identity to account for pseudoreplication among duplicate manipulation panels (i.e., each of the two alternative structures). Model performance was optimized with the babyqa control function to adjust for over-conservatism in model convergence in later versions of lme4 (K. Edwards, personal communication). Diagnostics and model selection followed (Bolker et al. 2009). Specifically, the significance and explanatory contribution of each predictor was determined from likelihood ratio tests and changes in small sample-size corrected Akaike Information Criterion scores ($\text{AIC}_C$) between full and simplified models. We interpreted terms eliciting greater change in scores ($\Delta\text{AIC}_C$) as having more explanatory power.

We used the r.squaredGLMM function in the MuMIn package (Barton 2015) to calculate pseudo-$R^2$ values that represent the absolute value of goodness-of-fit for each model (Nakagawa and Schielzeth 2013, Johnson 2014); marginal $R^2_{\text{GLMM}}$ indicates the amount of total variation explained by the fixed effects, while conditional $R^2_{\text{GLMM}}$ indicates the combined explanatory power of fixed and random effects. The explanatory power of fixed effects was often very low, so here we do not report marginal $R^2_{\text{GLMM}}$ in cases where it fell below 0.01; in those instances fixed effects were negligible, so conditional $R^2_{\text{GLMM}}$ effectively measured random effects. Species contributing to significant groupings were identified by plotting modeled species-specific responses to each predictor.
For the study, (A) a series of retrievable panels outfitted with vegetation structural mimics representing *Spartina alterniflora* shoots (left), *Rhizophora mangle* prop roots (center), and *Avicennia germinans* pneumatophores (right) were deployed among habitat patches in the field. (B) The fully crossed design allowed the effects of structure type (shoot, prop root, pneumatophores) to be isolated from stand-level habitat attributes of *Spartina*, *Rhizophora*, and *Avicennia* based on various groupings of samples by stand and structure type; example groupings are delineated by dashed lines. Control panels that matched the background habitat patch were used to test (i) overall baseline differences in macrofaunal community composition by vegetation type, given all habitat cues. Manipulation panels were grouped to test effects of structure or stand-level attributes: (ii) composition by structure was evaluated by grouping individual panel types; (iii) stand-level community composition was evaluated by combining all manipulation panel types within a given patch type. Image credits for patch vegetation illustrations: T. Saxby and J. Thomas, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/image/library/).
We first checked for community differences by site, which would correspond to differences in the local species pools and any unvaluated environmental characteristics. To test whether community composition differed between mangrove and marsh vegetation types, we pooled data across sites to maintain the balanced sampling design. Control and manipulation panel treatments (Fig. 1B) were used to constrain data for hypothesis testing: community composition on control panels was used to test for baseline responses by vegetation type, given all possible cues; communities on manipulation panels (i.e., those deployed “out of context” in patches other than their model habitat) were used to test whether structure type and/or stand-level attributes alone were sufficient to stimulate faunal sorting. Among manipulation panel assemblies, community pattern by panel type indicated independent influences of structural form, while community pattern by patch type indicated independent influences of stand-level attributes.

For group visualization, community composition data were double Wisconsin transformed to control for large variation in abundance across species and samples. Data were then plotted with canonical analysis of principle coordinates (CAP) using the Bray-Curtis dissimilarity metric and the same predictors and data groups from model analysis in the vegan package in R. Thus, each plot directly corresponds to each hypothesis test (Table 1). All plotted CAP axes explain significant variation in the data.

Results

A total of 396 panel retrievals were sampled from June to November 2014, of which 383 were occupied by at least one organism. We ultimately sampled and characterized 1,920 individuals from Matanzas River and 1,122 individuals from Halifax River. Omitting singletons and doubletons, the final data included 24 taxonomic species and morphospecies, which were predominantly crabs, shrimp, and fish. Several taxa were at least one order of magnitude more abundant than all other species. At the taxonomic resolution identified, these abundant taxa were gobies (Gobiidae: Gobiinae and Gobionellinae), caridean shrimp (infraorder Caridea), penaeid shrimp (Penaeidae), Aratus pisonii (Sesarmidae), Callinectes spp. (Portunidae), and Gammarus amphipods (Gammaridae). Abundant isopods (order Isopoda) included members of Limnoriidae, but other families also may have been represented.

Contributing predictors

Macrofaunal community composition on retrievable panels (n = 383 repeated observations) was significantly distinguishable between sites, habitat patches, and structure types. Site had the strongest effect on macrofaunal composition (ΔAICc = 858; likelihood ratio test $\chi^2 = 1,122, df = 5, P < 0.0001$, conditional $R^2_{GLMM} = 0.22$; Appendix S1: Fig. S2A). Caridean shrimp and gobies were more strongly associated with the marsh-dominated site (Matanzas River), while Callinectes spp., isopods, and penaeid shrimp were associated with the mangrove-dominated site ( Halifax River; Appendix S1: Fig. S2B). Beyond differences in species composition between sites, macrofaunal composition responded significantly to stand-level attributes (ΔAICc = 213) and physical structure (ΔAICc = 219) at smaller scales.

Community differentiation: baseline assessment by vegetation type

To develop a baseline understanding of how macrofaunal communities differ by vegetation type within the ecotone, we first examined macrofaunal community composition by vegetation type on control panels, where physical structure matched the surrounding habitat patch, providing the full suite of habitat attributes (structural and stand-level). Significant differences in community composition across vegetation type control panels indicated that co-occurring mangrove and marsh vegetation types were inhabited by different suites of macrofauna (GLMM, $\chi^2 = 287.58, df = 9, P < 0.0001$, conditional $R^2_{GLMM} = 0.22, n = 44$ per vegetation type; Fig. 2A). Macrofaunal communities in Avicennia habitat fell intermediate in ordination space to those inhabiting Rhizophora and Spartina habitats. Composition differences were due primarily to the associations of caridean shrimp, amphipods, and panopeid crabs with Spartina shoots, penaeid shrimp with both mangrove species, A. pisonii with Spartina

<table>
<thead>
<tr>
<th>Test for community composition</th>
<th>Model</th>
<th>df</th>
<th>Likelihood ratio $\chi^2$</th>
<th>ΔAICc</th>
<th>Conditional $R^2_{GLMM}$</th>
<th>Figure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Do communities differ between vegetation types, given matching structural and stand-level cues?</td>
<td>Abundance ~ Habitat + (1 + Habitat</td>
<td>Species), Data = control</td>
<td>9</td>
<td>287.58</td>
<td>277.535</td>
<td>0.22</td>
</tr>
<tr>
<td>Are stand-level attributes sufficient to elicit differences in community composition?</td>
<td>Abundance ~ Habitat + (1 + Habitat</td>
<td>Species) + (1</td>
<td>PatchID)$\dagger$, Data = manipulation</td>
<td>10</td>
<td>344.32</td>
<td>334.293</td>
</tr>
<tr>
<td>Are structural attributes sufficient to elicit differences in community composition?</td>
<td>Abundance ~ Panel + (1</td>
<td>Panel</td>
<td>Species), Data = manipulation</td>
<td>9</td>
<td>125.53</td>
<td>115.511</td>
</tr>
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Notes: All models were superior to simplified versions, in which the random slopes model component was removed (italicized below); ΔAICc indicates the difference between the Akaike information criterion corrected for sample size for full and simplified models. For each model, “data = control” indicates communities modeled on panels deployed in their model habitat, where panel artificial structure matches the surrounding vegetation patch; “data = manipulation” indicates communities modeled on panels deployed in a patch that does not correspond to their artificial structure type, permitting the separation of structural and stand-level attributes. All models are significant at $P < 0.0001$.

$\dagger$A random effect of patch ID is included to account for replicated panels (n = 2) per habitat patch per sampling event.
shoots and *Rhizophora* prop roots, isopods, and hermit crabs with *Rhizophora* prop roots, and gobies and Mojarras with *Avicennia* pneumatophores (Fig. 2B).

**Community differentiation: contributory influences of stand-level attributes and physical structure**

Based on manipulation panel samples, those for which stand-level attributes are independent of physical structure, stand type elicited distinct community assemblages (GLMM, $\chi^2 = 344.32$, df = 10, $P < 0.0001$, conditional $R^2_{\text{GLMM}} = 0.24$, $n = 44$ per patch type; Fig. 3A). Caridean shrimp and gobies were associated with *Spartina*, penaeid shrimp and *Callinectes* spp. with *Rhizophora*, amphipods with *Avicennia*, and isopods and hermit crabs with mangrove habitat in general (Fig. 3B).

Similarly, manipulation panel samples revealed that vegetation physical structure alone also elicited distinct macrofaunal community assemblages (GLMM, $\chi^2 = 125.53$, df = 9, $P < 0.0001$, conditional $R^2_{\text{GLMM}} = 0.17$, $n = 88$ per structure; Fig. 4A). Amphipods, *Callinectes* spp., hermit crabs, isopods, and Mojarras (family: Gerreidae) were associated with both shoot and pneumatophore structure mimics; caridean shrimp associated with both shoot and pneumatophore structure mimics (Fig. 4B).
DISCUSSION

To understand how resident species will respond to shifting habitats, it helps to determine the scale(s) and attribute(s) that shape their associations. Experimentally separating physical structure from other habitat attributes within an ecotone landscape allowed us to test for macrofauna associations with shifting habitats based on specific vegetation attributes. Across sites, macrofaunal community composition differed between each mangrove and marsh vegetation type overall, with all associated attributes, and in response to their isolated structural and non-structural features. These association patterns emerged despite greater differences in macrofauna community composition between the study sites. Community differences by site suggest that mangrove- and marsh-dominated sites (Halifax and Matanzas, respectively), separated at the kilometers scale, host separate species pools, though this requires further investigation (Fahrig 2013). After accounting for responses to dominant vegetation at the site level, partitioning of macrofaunal community composition both by physical structure and stand type suggest that macrofauna are sensitive to a suite of habitat attributes that allow them to distinguish between and occupy mangrove and marsh patches at a fine-grained resolution.

General community sorting across vegetation types in the ecotone

In baseline assessments, community composition differed among all three vegetation types examined. Macrofaunal

![Graph](image)

Fig. 3. Marine macrofauna (A) community composition and (B) modeled abundances (per 0.25-m² panel) based on non-structural stand-level cues. Stand-level sorting was evaluated for manipulation panels grouped by patch type. In A, ellipses encircle 75% of the points.
community composition in *Spartina alterniflora*, the vegetation type displaced by expanding mangroves, differed more from macrofaunal communities in *Rhizophora mangle* than from those associated with *Avicennia germinans*. There are several possible explanations for this pattern. First, *A. germinans* is the pioneer mangrove species that extends farthest into the temperate marsh landscape (maximum latitude 30.48°) and likely has been intermixed the longest (Williams et al. 2014, Cavanaugh et al. 2015). *A. germinans* dominates mangrove cover in the ecotone landscape, providing a dynamic transition zone between *S. alterniflora* to the north and *R. mangle* to the south (maximum latitude 30.41°; Williams et al. 2014). As such, *A. germinans* may receive the most exposure to marine fauna that are common in both landscapes, leading to a hybrid and therefore less differentiated assemblage in the transitional *A. germinans* habitat (Kark 2013). Alternatively, pneumatophores may simply provide poor structural refuge and weak associated cues, leading to fewer species associations and weaker sorting into *A. germinans* habitat (Primavera 1997). Although we cannot resolve the origin of *A. germinans’* role in hosting intermediate community assemblages, the clear differences in macrofaunal composition among habitats can be attributed to species-specific responses to structural or stand-level attributes.

Sorting by specific attributes

Identifying the scales of habitat associations and their relation to particular habitat attributes can help us to understand how ecological communities are likely to respond to
changes in habitat availability and arrangement as climate change shifts the ranges of habitat-forming species (Loarie et al. 2009, Saintilan et al. 2014). When compared to overall associations by vegetation type as a baseline, responses to isolated structural or stand-level attributes reveal underlying drivers of individual species’ associations in the mangrove–marsh ecotone.

The association of isopods and hermit crabs with R. mangle habitat corresponded to their preference for mangrove stands independent of structural attributes. Marine isopods are broadly mangrove associated (Perry 1988), due at least in part to their dependence on woody substrate for boring. Explanations for this association are less clear for hermit crabs, which primarily occupy benthic habitats. Our experimental manipulation removed the influence of physical structure from stand-level responses, but stand-level associations could originate from sensitivity to a broad suite of stand-level attributes. Especially in tidally controlled systems, productivity and associated chemical cues are exported during outwelling, such that both are effectively controlled by stands of habitat (Oudem 2002). Some physical features, such as shading, may also depend on the presence of a threshold area of habitat and thus emerge at the patch level (Ellis and Bell 2004, Verweij et al. 2006). Each of these stand-level attributes affects marine communities, and any of them could be driving the differences in community composition at the stand scale in this study (Glasby 1999, de la Morinière et al. 2003, Ellis and Bell 2004, Verweij et al. 2006, Nagelkerken et al. 2008). Further experimentation will be needed to identify the specific attributes driving stand-level community sorting.

Physical structure alone also was sufficient to affect macrofaunal community composition when experimentally controlling for the surrounding stand type. Gammarid amphipods and Aratus pisonii (mangrove tree crab) habitat associations matched their responses to structure type, suggesting that structure provides the key cue that informs their associations with S. alterniflora shoots and R. mangle prop roots, respectively. A. pisonii depends on the woody structure of mangroves for foraging and refuge from predators (Wilson 1989, Sheridan 1992). Although A. pisonii also colonize Avicennia germinans, they generally inhabit the trunks and branches, which were not included in this study of intertidal structures. Of the elements structuring the low intertidal, only Rhizophora prop roots provide sufficient physical structure for A. pisonii. Explanations for the structural associations of gammarid amphipods are less clear. As epiphytic grazers and detritivores, they occupy and often find refuge within seaweeds and macroalgae (Zimmerman et al. 1979, Duffy and Hay 1991). Dense and structurally complex grass shoots may supply small spaces and high surface area that provide a superior combination of epiphyte food supply and refuge.

Callinectes spp. and penaeid shrimp demonstrated affinities based on structure type, but not for the same vegetation that they preferred overall. Both species were associated with Rhizophora stands, but Callinectes spp. were most abundant on grass shoots, while penaeid shrimp occupied pneumatophores. Both taxonomic groups may be drawn to Rhizophora attributes available at the stand level, such as primary production or shade, while preferring to occupy other, finer structure (Minello and Zimmerman 1985, Primavera 1997, Johnston and Lipcius 2012). In many biogenic habitats, one foundation species supports smaller foundation species that secondarily facilitate inhabitant fauna (a facilitation cascade; Bishop et al. 2013). Mangroves, especially R. mangle, often support epibionts such as oysters, sponges, and algae that form finer secondary structures that provide more effective refuge for inhabitant communities than the mangrove roots themselves (Bishop et al. 2013). Thus, the counterintuitive affinity for finely structured shoots and pneumatophores despite preference for Rhizophora stands might be explained by inhabitants’ use of secondary habitat structures, resolving the apparent discrepancy between stand preference and structural affinity.

The documented sensitivities to specific structure types is of particular interest given prior evidence that structure per se can be more influential than structure type (Primavera 1997, Heck et al. 2003, Ellis and Bell 2004, Nagelkerken et al. 2010, MacKenzie and Cormier 2012). Studies often use rough proxy substrates such as rocks vs. sand to examine responses to structured and unstructured habitat (Moksnes 2002, Lindsey et al. 2006). Others have examined effects of complexity by deploying sampling units on bare substrate, which can inflate settlement responses due to thigmotaxis within a barren landscape (Pallas et al. 2006, Paula et al. 2006, Pan et al. 2010). Both of these study approaches likely bias results toward highlighting the effects of structure per se over the effects of specific structural attributes. The added realism of structural mimics deployed within stands of vegetated habitat may have helped reveal the sensitivity to specific structural forms documented here. The importance of specific structural forms also may have been underestimated in prior studies if structural affinity is not always closely tied to structural refuge from predation, which has been most commonly studied (Minello and Zimmerman 1985, Primavera 1997, Kon et al. 2009, Johnston and Caretti 2017). As found here, structure may also be influential if it is necessary for basic behavior and functions, such as foraging by arboREAL crabs and epiphytic grazers (Laegdsgaard and Johnson 2001, this study).

Finally, sensitivity to habitat attributes was not always discordant or independent between scales capturing structural and non-structural effects: caridean shrimp strongly associated with marsh habitat, Spartina-dominated stands, and finely structured shoots and pneumatophores of S. alterniflora and A. germinans, respectively. Similarly, Penaeid shrimp associated with Rhizophora-dominated stands and pneumatophore structures of A. germinans, leading to an overall association with mangrove habitats. Gobies and Mojarra were associated with A. germinans vegetation overall, matching previously documented preferences (MacKenzie and Cormier 2012), but inconsistently associated with physical structure or stand-level attributes. However, they were more prevalent at the Matanzas River site, where A. germinans is abundant in the landscape. Many other species had nuanced responses to stand and structure type or demonstrated no sensitivity to either set of attributes. Species that did not sort by any attribute examined (n = 14 of 24 species recorded) may (1) not discriminate between the wetland types examined, (2) discriminate at a scale (or using a cue) not examined here, or (3) appear insensitive due solely to their rarity within our samples. Notably, the short sampling interval (two weeks)
and small grain size (50 cm²) of sampling units make our estimates of community sorting conservative. Nonetheless, we found quick and distinguishable macrofaunal sorting among co-occurring habitats. Inhabitants’ responses to stand type and vegetation structure indicate that the marine community is sensitive to fine-grained shifts in wetland composition, which should enable close associations even where patches emerge along the range edge.

CONCLUSIONS

Foundation species form critical habitats that facilitate biodiversity; thus, evaluating how species respond to changing foundation species can inform our expectations for subsequent, broader community change. The marine macrofauna community in a shifting mangrove–marsh wetland sorted among habitats at the finest grain tested (<1 m²), indicating fast and fine-resolution responses to changes in landscape composition. Sorting at multiple scales suggests that initial sorting among early patches strengthens as patches, and their suite of attributes, expand. Parallel studies of the resolution of resident species responsiveness to foundation species, and changes therein, can help us understand patterns of broader community change. Indeed, where resident species are at their own range edge, such studies could help reveal the differences between species that keep pace vs. those that lag the expansion of their preferred habitat; such species could be expected to have fine and coarse resolution sorting, respectively. Identifying the scale(s) of pattern characteristics used by organisms to distinguish habitats can help us understand not just the spatial resolution at which inhabitants associate with emerging frontier habitat but also how the redistribution of a few key species shapes the pace and resolution of broader community changes (Hoegh-Guldberg and Bruno 2010, Poloczanska et al. 2013).

ACKNOWLEDGMENTS

This research was supported by NSF EF-1065098, NASA Climate and Biological Response Program NNX11AO94G, and the Society of Wetland Scientists. Field assistance and logistical support were provided by J. Schefski, E. Steiber, D. Langley, E. Dark, M. Nathan, A. Forde, J. Baird, M. Edwards, L. Simpson, L. Duckett, M. Lehmann, W. Lee, S. Reed, H. Reichart, and volunteers of the Guana Tomolato Matanzas National Estuarine Research Reserve. Comments from the Gruner lab greatly improved this manuscript. This is contribution # 1094 from the Smithsonian Marine Station.

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