Eelgrass habitat structure affects epifaunal biodiversity and community composition but not the distribution of functional traits among taxa

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ABSTRACT: Habitat structure strongly influences faunal assemblages, but the relative roles of structural characteristics across different spatial scales in driving community structure and composition are not well understood. In this study, we extensively sampled a Southern California eelgrass *Zostera marina* L. seascape to determine which aspects of seagrass habitat structure exert the greatest influence on epifaunal density, diversity, community composition, and functional trait distribution. We use generalized linear models, generalized additive models, distance-based redundancy analysis, and fourth-corner analysis of trait distribution to model the relationships between epifaunal communities and features of eelgrass seascapes at microhabitat scales (e.g. shoot and epiphyte biomass) and patch scales (e.g. patch area, distance to edge, and percent eelgrass cover). We found that total epifaunal density and diversity were most strongly correlated with eelgrass shoot biomass and weakly correlated with patch area and eelgrass percent cover. Distance to the nearest patch edge explained very little of the variability in epifaunal density and diversity. In contrast, community taxonomic composition was most strongly driven by local shoot density and the availability of eelgrass habitat at larger scales as measured by the percent of eelgrass cover in the surrounding seascape. We found no evidence for effects of eelgrass habitat structure at any scale on epifaunal community functional composition. Our results demonstrate that epifaunal communities are influenced more by the amount of seagrass habitat than its configuration, but that the scale at which the amount of habitat is relevant depends on the community characteristic in question.

KEY WORDS: Habitat structure · Eelgrass · Epifauna · Functional traits · Community · Scale · Seascape

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1. INTRODUCTION

Habitat structure is among the most influential factors shaping ecological communities (Wilson et al. 2016). In terrestrial and marine ecosystems, structurally complex habitats provide refuge, food, and living space for organisms, thereby promoting biodiversity (Jones et al. 2021, Walter et al. 2021) and ecosystem function (Ishii et al. 2004, Voigt & Hovel 2019). Therefore, organismal density and diversity, community composition, and the relative abundance of organismal traits that drive ecosystem functions may strongly depend on various aspects of structural hab-

itat complexity, including the biomass, density, and surface area of structural elements at the scale of individual organisms (Stark et al. 2020). Likewise, the cover and configuration of habitats at landscape or seascape scales mediate species interactions, ecological functions, and patterns of community structure (McGarigal et al. 2016). For instance, habitat patchiness and connectivity as well as the size and shape of habitat patches influence prey vulnerability to predators (Hovel et al. 2021), organismal growth (Irlandi et al. 1995), and recruitment (Vozzo & Bishop 2019, Boström & Bonsdorff 2000). Quantifying the relative influence of landscape (or seascape) structure and

structural complexity on ecological patterns and processes is important because anthropogenic destruction, fragmentation, and degradation of habitats are leading causes of global biodiversity loss (Collinge 2009).

Despite decades of research focused on the effects of habitat structure on ecological processes, a great deal of uncertainty remains regarding the relative influence of different aspects of habitat structure on populations and communities. This may largely be due to a dearth of studies that simultaneously consider a variety of habitat metrics and ecological responses to determine which aspects of habitat and faunal community structure are most strongly correlated (McGarigal & Cushman 2002, Lindenmayer & Fischer 2007). In our study, we address this need by testing for correlations among multiple aspects of seagrass (eelgrass *Zostera marina* L.) habitat structure and the density, diversity, community composition, and functional traits of eelgrass epifauna.

Seagrass and associated epifauna form an ideal model system in which to study the effects of habitat structure on organisms across multiple scales. Seagrasses such as eelgrass often form monospecific seascapes consisting of discrete patches embedded within a relatively homogenous matrix of sand or mud (Boström et al. 2006, Irving et al. 2013, Pittman 2018, Yeager et al. 2020). Seagrass meadows also exhibit high variability in structural complexity within and among patches as well as a wide array of seascape configurations (Hovel & Lipcius 2001, Duarte et al. 2006). Moreover, seagrasses play outsized roles in global carbon sequestration, nutrient cycling, coastal biodiversity, and preventing erosion (Duarte 2002, Waycott et al. 2009, York et al. 2013, Röhr et al. 2018) but are widely degraded due to numerous anthropogenic stressors (Short & Wyllie-Echeverria 1996, van der Heide et al. 2011, Cabaço & Santos 2012). Eelgrass epifauna (i.e. small crustaceans and gastropods) play key roles in transferring energy and nutrients from primary producers (seagrasses and epiphytic algae) to higher trophic levels (Hemminga & Duarte 2000). Epifauna also are directly associated with seagrass blades and therefore may be more sensitive to seagrass configuration than benthic and infaunal invertebrates (Yamada et al. 2014) or larger-bodied, highly mobile organisms like fishes (Schultz et al. 2009, Yeager et al. 2016). Many epifaunal species engage in a key mutualism with seagrasses by consuming competitively superior algae that grow on seagrass leaves (Whalen et al. 2013, Reynolds et al. 2014, Duffy et al. 2015, Unsworth et al. 2015). Disruption of this stabilizing feedback mechanism between seagrasses and epifauna can lead to catastrophic regime shifts and ecosystem collapse (Maxwell et al. 2017, de Fouw et al. 2018).

The effects of habitat structure on seagrass epifauna have been heavily studied over the last few decades and a few general patterns have emerged. Seagrasses provide greater structural complexity than surrounding unvegetated habitats, thereby harboring more abundant and diverse communities than adjacent areas of unvegetated sediment (Orth et al. 1984, Hirst & Attrill 2008, Hu et al. 2022). Structurally complex seagrass patches (e.g. those with high shoot density, biomass, surface area, or epiphyte colonization) offer more food, living space, and predation refuge (Bologna & Heck 1999, Heck & Orth 2006), which can lead to a positive relationship between complexity and epifaunal abundance. Epifaunal abundance and community composition are also affected by the size, shape, and configuration of seagrass patches. Smaller patches lead to a greater proportion of edge habitat, and seagrass edges tend to harbor distinct communities with greater epifaunal densities (Tanner 2005, Pierri-Daunt & Tanaka 2014). More fragmented habitats contain greater heterogeneity of habitat types and resources and often support more abundant and diverse communities than continuous meadows of equal total seagrass area (Eggleston et al. 1999). However, faunal relationships with habitat structure can vary widely depending on interactions with other aspects of the environment across a range of scales (Hovel & Fonseca 2005, Nakaoka 2005, Cimon et al. 2021), and responses to any single metric of habitat structure are often species-specific or inconsistent across space and time (e.g. Hovel et al. 2002, Moore & Hovel 2010, Boström et al. 2011). Therefore, researchers trying to understand the complex interactions between multiple aspects of habitat structure and communities will benefit from simultaneously considering a suite of environmental metrics at different scales while also measuring multiple facets of communities.

In our study, we assessed how eelgrass habitat structure at multiple scales within a meadow affects not only univariate response variables like taxonomic richness and diversity but also community composition and epifaunal functional trait distribution. As any specific aspect of habitat structure is likely to benefit some species while having a negative effect on others (e.g. Moore & Hovel 2010), positive and negative responses of individual species often lead to species replacement, which can cause changes in community composition without any change to univariate community measures like faunal density and diversity (Eggleston et al. 1999, Boyé et al. 2017). However, this concept still does not directly address the biological

mechanisms behind organismal responses to habitat structure. To resolve this knowledge gap, we used existing information on eelgrass epifauna to categorize taxa according to a suite of functional categories (e.g. mobility or trophic guild) that represent important aspects of their biology and mediate how they interact with their environment (Mouillot et al. 2013, Martini et al. 2021).

Working throughout a Southern California eelgrass seascape, we quantified eelgrass structural complexity, patch-scale habitat configuration, and seascape cover and modeled their influence on the taxonomic and functional structure of eelgrass-associated invertebrate communities. This enabled us to address the following questions: (1) Which metrics of small-scale habitat structure exert the greatest influence on epifaunal communities? (2) To what degree are differences in epifaunal community structure driven by shifts in overall abundance and diversity versus compositional changes due to species replacement? (3) Do functional traits play an important role in mediating how species respond to habitat structure, and does overall functional composition vary with differences in habitat structure?

entrance of Mission Bay, San Diego, California (32° 45' 55'' N, 117° 14' 54'' W) (Fig. 1). We restricted our sampling to a single shallow basin to better isolate the effects of small-scale habitat structure by minimizing the potential influence of abiotic gradients. Areas like MB near the bay mouth experience less seasonal variation in abiotic conditions than the rest of Mission Bay (Elliott & Kaufmann 2007). Furthermore, MB has no natural freshwater inputs and is entirely ringed by a sandy shoreline, thereby avoiding any confounding influence due to differing proximity to other ecosystem types. We took samples in as small a temporal window as possible to reduce the influence of seasonal variation and chose months that did not coincide with extreme temperatures. MB contains approximately 3.5 ha of eelgrass exhibiting a wide range of morphologies and natural variation in small-scale habitat configurations, with eelgrass growth limited to the fringes of the basin between 0 and 5 m below mean lower low water (MLLW). At the time of our study in MB, eelgrass density varied from <100 to >3000 shoots m^{-2}, eelgrass height varied from <10 cm to >1 m tall, and eelgrass patches ranged from <0.01 to 17000 m^2 (Table 1).

2. MATERIALS AND METHODS

We collected all samples between 8 April and 9 June 2021 in Mariner's Basin (MB), a 1 km × 300 m tidally flushed embayment situated close to the

2.1. Eelgrass and epifauna sampling

We haphazardly selected sampling locations a minimum of 2 m apart within eelgrass cover throughout MB using SCUBA. At each sample location, we
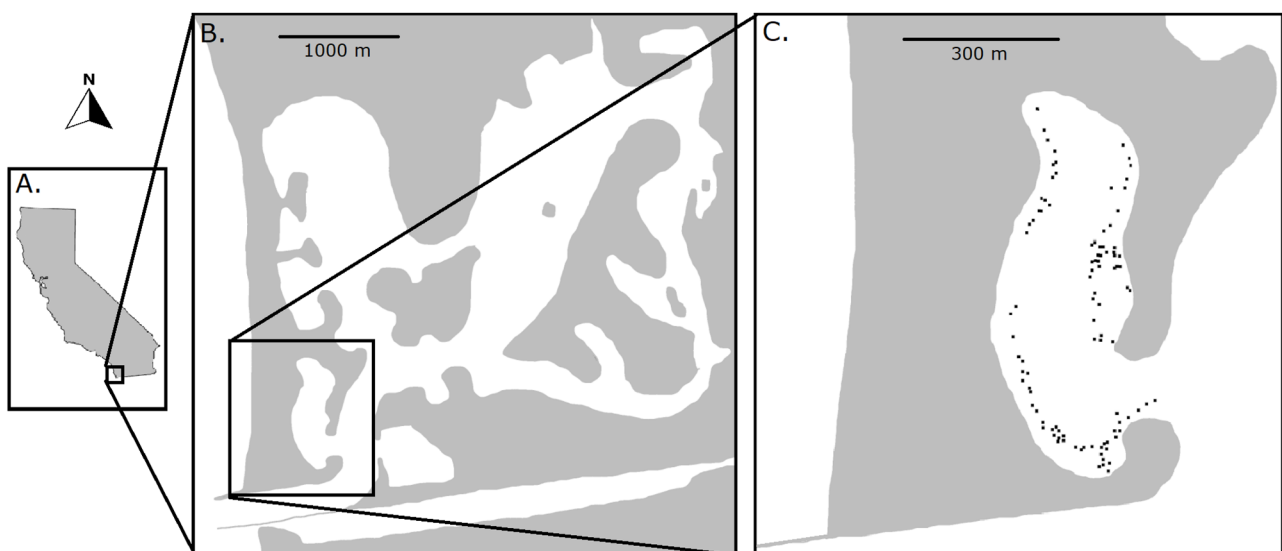

Fig. 1. Study site showing (A) Mission Bay within California and (B) Mariner's Basin (MB) near the mouth of Mission Bay. (C) A closer view of MB showing each sample location as a black dot. Our samples approximate the distribution of eelgrass in MB, which was restricted to the shallower margins of the basin

Table 1. Description and summary statistics of the habitat variables measured within the Mariners Basin eelgrass seascape in Mission Bay, Southern California

Environmental variable	Description	Mean	SD	Min.	Max.
Depth (m)	Depth of sample below mean lower low water	1.91	1.40	−0.15	4.74
Shoot density (no. m^{-2})	Shoot counts from 20 cm diameter drop trap samples	507.29	476.18	98.68	3320.61
Eelgrass biomass (g)	Dry weight of above-ground *Zostera marina* biomass per 20 cm diameter drop trap	3.53	2.75	0.39	11.88
Epiphyte biomass (g)	Dry weight of macroepiphytes per 20 cm diameter drop trap	0.41	1.66	0.00	13.40
Edge distance (m)	Distance to nearest patch edge	1.63	3.28	0.00	18.70
Average shoot surface area (cm^2)	Average surface area of 5 individual shoots adjacent to the sample	47.25	26.09	1.61	150.85
Patch size (m^2)	Patch area estimated as an ellipse using longest and shortest patch dimensions	4467.13	6803.59	0.001	17000
Local % cover (%)	Percent of eelgrass cover averaged across 25 quadrats within a 5 m radius of the sample	41.07	31.25	1.0	100

took samples of the epifaunal community and measured a suite of 8 environmental variables: water depth, eelgrass shoot density, average shoot surface area, eelgrass biomass, macroepiphyte biomass, distance to nearest patch edge, patch area, and percent eelgrass cover within a 5 m radius around the sample. To reduce disturbance to epifauna at each sampling event, we sampled epifauna before making measurements on eelgrass. We gathered epifaunal samples by gently lowering a 20 cm diameter PVC drop trap connected to a 500 μm mesh bag over the eelgrass, making sure that all eelgrass shoots within the footprint of the drop trap were contained within the bag. We then used scissors to quickly cut all eelgrass shoots just above the sediment surface. We counted the number of shoots within the 20 cm diameter drop trap to measure shoot density. We tied off the mesh bags containing drop trap samples and transported them back to the lab in a cooler for further processing. We used an additional 5 eelgrass shoots haphazardly collected within 25 cm of the drop trap to calculate the average surface area of individual shoots after measuring the length and width of each blade.

We used a GPS receiver carried on a surface float to record the time and location of each sampling event and used tide charts to standardize water depth to depth below MLLW. Next, we used a transect tape to measure the distance of each sample from the nearest edge where eelgrass bordered bare sediment. We visually estimated percent eelgrass cover within 1 m^2 quadrats each meter along five 5 m transects radiating outward from the drop trap sample. We averaged these 25 estimates of percent cover to calculate an estimate of total percent cover within a 5 m radius of the sample. Finally, we measured the longest and shortest lin-

ear dimensions of the eelgrass patch in which we were sampling and used these 2 measures to estimate the area of the patch using the equation for the area of an ellipse (area = π × length × width).

In the lab, we separated samples into eelgrass, epiphyte, and epifauna components by scraping each eelgrass leaf and rinsing all material through a 1 mm sieve. We picked out leftover epifauna from samples with large amounts of epiphytes or biofouling tubes using tweezers and a dissecting microscope. We recorded the dry biomass of both eelgrass and epiphytes from drop trap samples after drying them in an oven at 60°C for 48 h. We preserved epifauna in 70% ethanol and identified all individuals to the lowest taxonomic level possible using a dissecting microscope. We excluded calcareous tube worms (mostly Spirorbid worms) and anemones from community data because they often disintegrated during sample processing.

2.2. Functional traits

We characterized each taxon using 5 categorical functional traits: mobility, living habit (free living vs. sessile), feeding guild, larval development, and fertilization. We chose these traits because they describe functional aspects of an organism's biology that have been shown to influence how they respond to differences in their environment (Wong & Dowd 2015, Yeager et al. 2019, Hu et al. 2022). The scale at which an organism interacts with its habitat will depend on the range over which it moves during its lifetime. Species that are highly mobile, have planktonic larval development, and engage in broadcast spawning are

often more abundant than sedentary, direct developing, internally fertilized species in fragmented habitats where there is a greater amount of seagrass edge habitat for them to encounter during movement (Orth 1992, Boström et al. 2010, Lefcheck et al. 2016, Yeager et al. 2019, Murphy et al. 2021). Diet also plays a crucial role in determining an organism's habitat preferences. Suspension-feeding animals often prefer habitats with greater current velocities, such as edges, smaller patches, and lower shoot densities, while grazers often associate with denser and more continuous eelgrass, which provisions more primary production from both the macrophytes themselves and periphyton such as diatoms that coat their surfaces (Gullström et al. 2012, Lefcheck et al. 2016). Similarly, predators are often more prevalent along edges and in lower density eelgrass beds where they have an easier time locating and catching prey (Schultz et al. 2009, Wimp et al. 2011). In addition, these traits encompass how epifauna may contribute to overall ecosystem function. For example, increased grazer abundance can be important for preventing eelgrass shading by epiphytes (Duffy et al. 2003), whereas tube-building epifauna (such as some amphipods) can smother eelgrass (Lewis & Anderson 2012).

We determined these trait values using a broad array of peer-reviewed articles, databases, and identification resources (Table S1 in Section 1 of the Supplement at www.int-res.com/articles/suppl/m751 p037_supp.pdf). To avoid issues with collinear trait identities, we used the 'assocstats' function in the 'vcd' package in R (Meyer et al. 2022) to calculate the Cramer's V pairwise association of trait co-occurrence between all functional trait categories. All pairwise trait combinations had acceptable Cramer's V associations (>0.7).

2.3. Statistical analysis

2.3.1. Univariate metrics of community structure

We assessed the relationships between eelgrass habitat structure and univariate measures of (1) total epifaunal density, (2) taxonomic richness, (3) taxonomic diversity (Shannon Index), and (4) functional diversity. The eelgrass habitat structure variables used in all models are shown in Table 1. We $\log_{10}$ transformed epifaunal density, and prior to calculating diversity and community structure, we $\log_{10}$ transformed all individual species abundance data to more appropriately weight extremely abundant and very rare taxa. We also $\log_{10}$ transformed patch size and

$\log_{10}(x + 0.1)$ transformed edge distance because we sampled both of these variables across many orders of magnitude. We used the 'dbFD' function in the R package 'FD' (Laliberté et al. 2014) to calculate functional dispersion as an estimate of the diversity of functional traits in each sample. Functional dispersion accounts for both functional richness and evenness by calculating the average deviation from a community's center in trait space. Before constructing any models, we calculated Moran's I to test for spatial autocorrelation in each of the 4 univariate response metrics and found no significant autocorrelation (p > 0.1 for all 4 variables). Therefore, we did not adjust our univariate models to account for spatial autocorrelation.

Visualization of the relationships between community metrics and habitat structure revealed that trends were nonlinear, so we modeled their relationships using generalized additive models (GAMs) using the R package 'mgcv' (Wood 2011). Nonlinear relationships are common in faunal responses to habitat structure (Lannin & Hovel 2011, Yeager et al. 2016), and GAMs can outperform other methods such as generalized linear models (GLMs) at modeling species distributions (Chefaoui et al. 2016). We constructed a GAM for each community metric using all 8 habitat metrics and reduced the complexity of the model by following backward stepwise selection, removing non-significant terms from the models until we achieved a minimum Akaike's information criterion (AIC) value. We further simplified the models by changing splines with estimated degrees of freedom close to one into linear terms as long as doing so further reduced AIC. We also constructed GLMs of each community metric using bidirectional stepwise regression and found that the GAMs all had lower AIC values than their linear counterparts. Therefore, we did not further consider GLMs for univariate metrics. To investigate the relative importance of individual habitat metrics within each GAM, we constructed additional versions of each model in which one variable from the full model was left out. By subtracting the deviance of the full GAM from the deviance of a GAM built missing a given variable and dividing by the deviance of a null model, we were able to estimate the proportion of deviance explained by that variable on its own.

In addition to modeling univariate metrics, we constructed GLMs of the most abundant species representing major phylogenetic groups (gammarid amphipods, isopods, other crustaceans, gastropods, and polychaetes). We also modeled the abundance of the eelgrass limpet *Tectura depicta* because it is one of

the few local grazers known to consume eelgrass tissue directly and can have a profound negative impact on eelgrass growth and persistence (Zimmerman et al. 1996, Lewis & Anderson 2012). Individual species count data were zero-inflated and prone to overfitting by GAMs, so we modeled their abundance using negative binomial linear regression models and chose the best model using bidirectional stepwise model selection with AIC as the selection criterion (R package 'MASS'; Ripley et al. 2013). We calculated how much individual variables contributed to the variance of each model using the R package 'domin' (Luchman 2023).

2.3.2. Community composition

To test if community composition was spatially autocorrelated, we performed a Mantel test of the correlation between Bray-Curtis dissimilarity of $\log_{10}(n + 1)$-transformed species abundance data and a matrix of Euclidean distances between sample locations. This analysis revealed that community composition was spatially structured (Mantel test: $r^2 = 0.22$, $p = 0.001$), so we calculated distance-based Moran's eigenvector maps (dbMEMs), which capture spatial structure in samples across a variety of scales, using the R package 'adespatial' (Dray et al. 2016) to include as spatial variables in subsequent models.

We tested which aspects of habitat structure were driving overall differences in multivariate taxonomic community structure. First, we scaled all environmental variables by subtracting their mean and dividing by their standard deviation to account for the difference in scales measured in each variable. To disentangle the explanatory power of habitat structural versus spatial differences between samples as predictors of community composition, we performed variance partitioning using the 'varpart' function (Dray et al. 2016). We then used partial distance-based redundancy analysis (dbRDA) to model Bray-Curtis dissimilarity as a function of all habitat metrics. We included dbMEMs calculated using 8 nearest neighbors and a threshold distance of 355 m (which corresponded to the mean distance between any 2 random samples in our study) as covariates in the partial dbRDA, which revealed the effects of habitat structure on communities after accounting for the influence of spatial autocorrelation in the samples. We then used backward stepwise model selection by adjusted R^2 value to find a parsimonious version of the partial dbRDA model using the 'ordiR2step' function (R package 'vegan'; Oksanen et al. 2022). We then performed

further variance partitioning to test the contribution of each of the environmental variables included in this final model individually while accounting for spatial structure as dbMEMs. Since the 'varpart' function can only handle 4 factors at once, and we included spatial dbMEMs as one of those factors, we ran this variance partitioning twice; once with epiphyte and eelgrass biomass both included in a single table and again with shoot density and percent eelgrass cover combined. We performed all these analyses in R v.4.1.2 (R Core Team 2021).

We also created models to test whether the functional trait composition of the epifaunal communities was driven by similar aspects of the habitat as taxonomic community structure. We used dummy variables to encode all trait modalities as columns of binary values for each species and multiplied this by a matrix of $\log_{10}$-transformed species relative abundance, which gave us the relative abundance of each of the 15 trait modalities in each sample. We used this value to calculate a functional trait resemblance matrix using Gower distance. We used the 'RELATE' function with 999 permutations to test the relative strength of correlations between similarity matrices of taxonomic composition, functional composition, and the Euclidean environmental distance between samples. All multivariate trait analyses were done using PRIMER-E v.6 (Clarke & Gorley 2005).

2.3.3. Trait–environment relationships

Finally, we used an ordination-based 'rlq' function (R package 'ade4'; Dray & Dufour 2007) to perform a direct test of the overall significance of the fourth-corner interaction between traits and the environment in our data. The fourth corner is a matrix of interactions between individual trait modalities and environmental variables that can be used to model and predict species abundance as a function of their traits. The fourth corner is calculated using 3 other matrices: trait modalities per species, environmental variables per site, and species abundance per site. While some approaches to the fourth corner (e.g. Brown et al. 2014) test pairwise interactions between individual traits and habitat metrics, they do not provide a test for the overall significance of trait–habitat interactions. To assess the overall significance of the fourth corner, we used the 'model type 6' as proposed by Dray & Legendre (2008), which combines 2 separate tests. The first tests for a significant relationship between species composition and environmental conditions by permuting the environmental variables for

each sample to test if a model with real environmental data performs better than one with random environmental data. The second tests for a significant relationship between species abundance and traits by permuting species trait values to test if actual trait values explain significantly more variation in species composition than random ones. We used 49 999 permutations and the 'fdr' correction for multiple testing in both tests. We can only reject the overall null hypothesis that the relative abundance of traits is not related to the environment if we reject the null hypotheses of both tests.

3. RESULTS

3.1. Univariate metrics of community structure

We collected and processed a total of 70 751 individuals from 91 taxa. There was an average of 599 individuals from 17 taxa per 0.0314 m^2 drop trap but abundance ranged widely from 10 to 7477 individuals per sample (Table S2). Samples were heavily dominated by a few taxa, with the gammarid amphipod *Ericthonius brasiliensis* accounting for 52.5% of all organisms collected (Table S3). The 10 most abundant species accounted for >91% of all individuals collected and all but one of them were present in >70% of all samples. To simplify the data set, we removed all

taxa that comprised <1% of any one sample in the study (Clarke et al. 2014), which reduced the total number of taxa from 91 to 51. This amounted to the removal of only 121 individuals (0.171% of all individuals) from the study.

All habitat metrics other than distance from a patch edge were significant predictors in at least one of the GAMs of univariate community responses (Fig. 2, Table S4, Fig. S1 in Supplement Section 2). Epifaunal density, taxonomic richness, and taxonomic diversity were all influenced by a suite of habitat metrics that cumulatively explained more than 50% of their variation. Variance partitioning revealed that combinations of eelgrass biomass and epiphyte biomass jointly explained the majority of variation in models of total epifaunal density, taxonomic richness, and taxonomic diversity, suggesting that the amount of vegetation at the microhabitat scale had a greater influence on epifaunal communities than did habitat configuration. Eelgrass biomass was the strongest predictor in all 3 of these models and each shared a similar increasing curvilinear relationship. There was a steep increase in epifaunal density, richness, and diversity from low to intermediate values of eelgrass biomass but only a slight increase in these variables with eelgrass biomass above 3 g per 20 cm drop trap (95.5 g m^{-2}) (Fig. 3, Fig. S1). In contrast to the other 3 univariate community responses, functional diversity was not strongly correlated with eelgrass microhab-
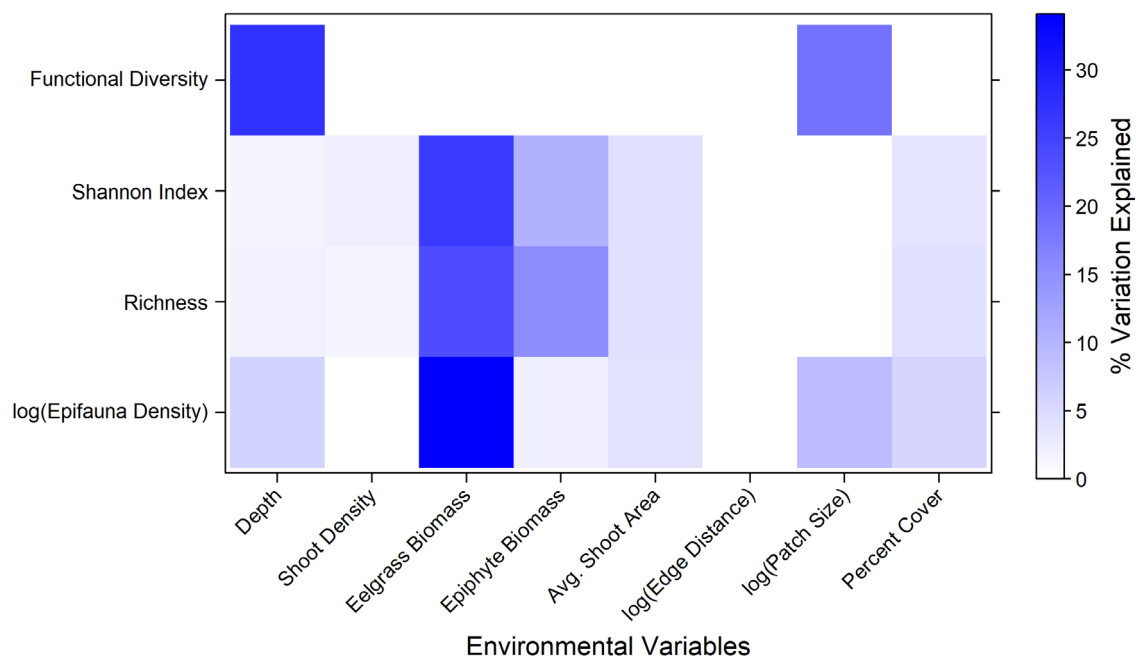

Fig. 2. Influence of environmental variables from the 4 final generalized additive models of univariate community structure; darker shading indicates stronger relationships. Color scale shows proportion of variance explained by a variable. See Table S4 and Fig. S1 for statistical results and a visualization of the form of all relationships

itat metrics but increased with depth and patch size (Table S4, Fig. S1).

Each of the individual species we modeled was related to a slightly different subset of environmental variables that explained between 11 and 30% of their density (Fig. 4, Table S5). Eelgrass biomass positively influenced the density of all species. No species' density was significantly correlated with shoot density, shoot area, or distance from an edge, which further suggests that species distribution was largely invariant with respect to differences in microhabitat-scale habitat structure. Depth and patch size had contrasting relationships with different species (Fig. 4).

3.2. Community composition

Initial variance partitioning between all combined environmental and spatial variables revealed a model that explained 24.2% (adjusted R^2) of Bray-Curtis dissimilarity, while spatial autocorrelation contributed 10.0% of explanatory power and habitat structure contributed 14.1%. The best partial dbRDA where spatial effects were used as covariates included percent eelgrass cover, shoot density, eelgrass biomass, and epiphyte biomass as environmental variables that cumulatively explained 14.9% of the variation in community structure (Table 2, Fig. 5). Further variance partitioning revealed that percent eelgrass cover contributed the most to the explanatory power of this model, followed by shoot density, eelgrass biomass, and epiphyte biomass respectively (Table 2, Fig. 6).

The epifaunal communities we sampled displayed a high degree of functional redundancy and were dominated by a small subset of traits. Samples contained a minimum of 11 trait modalities and most (76% of samples) contained representatives from at least 13 of the 15 trait modalities. Across all samples, each trait was represented by more than one taxon on average. Animals with a free-living habit, high mobility, herbivorous diet, direct development, and internal fertilization dominated trait abundance. The Gower distance between the multidimensional functional composition of samples revealed that functional community structure was fairly consistent throughout MB. All samples shared >67% functional similarity. Functional composition was closely related to taxonomic composition (Spearman's rho = 0.61, p < 0.001). Taxonomic composition was more closely related to the environment than functional composition (Spearman's rho = 0.39 vs. 0.25 respectively, p < 0.001 for both).
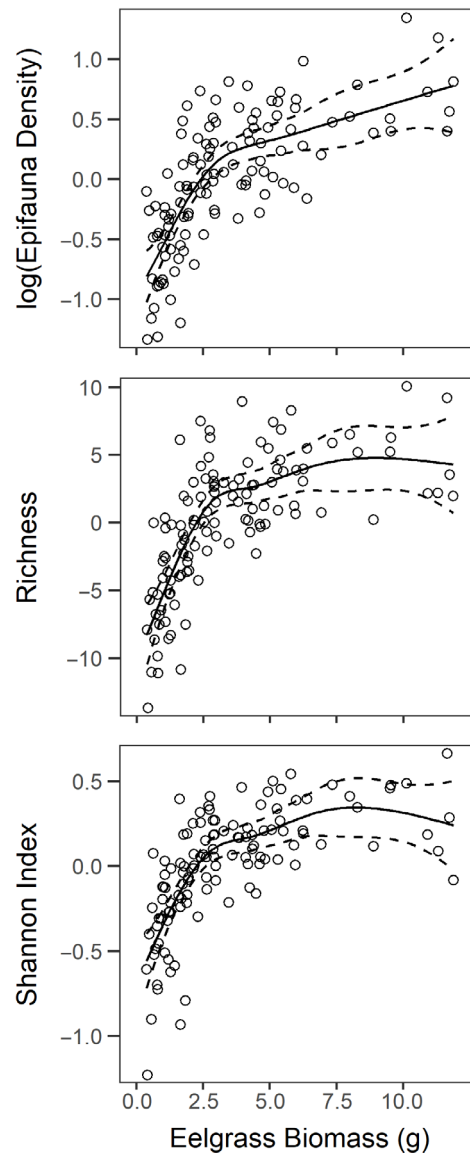

Fig. 3. Curvilinear relationships with eelgrass biomass predicted by generalized additive models of (A) $\log_{10}$-transformed total epifauna density, (B) richness, and (C) Shannon Index

3.3. Trait–environment relationships

Although the first test of trait–environment relationships revealed that species composition was significantly related to environmental variables (model type 2: p < 0.001), the second part of the test revealed that the traits we used did not predict species abundance significantly better than null models constructed by permuting species trait values (model type 4: p = 0.233). Thus, we found no evidence that the distribution of functional traits among samples was correlated with environmental variables.
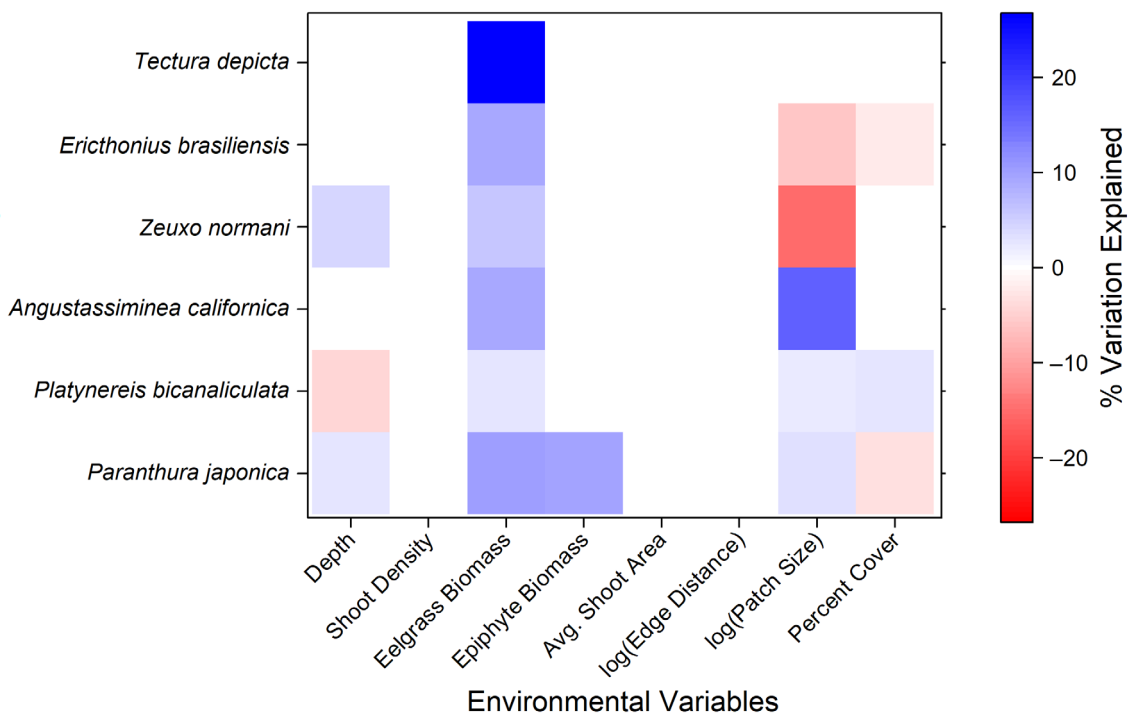
Fig. 4. Strength and sign of the influence of environmental variables from the 6 species abundance models. Red: negative; blue: positive; darker colors indicate stronger relationships. Color scale shows the percentage of variance explained by a variable. See Table S5 for statistical results

4. DISCUSSION

In this study, we examined the linkages between multiple characteristics of seagrass habitat structure and the density, diversity, taxonomic composition, and functional composition of epifaunal communities. We found that the density and diversity of epifauna were most closely (and positively) correlated with local-scale structural complexity in the form of eelgrass and epiphyte biomass. Though the best-

Table 2. Marginal test results of variables included in the best partial distance-based redundancy analysis model of Bray-Curtis community dissimilarity as a function of standardized environmental variables while accounting for spatial Moran's eigenvector maps (dbMEMs) as covariates (df = 111, adjusted r^2 = 0.15) (see Fig. 5). Variance contributed was calculated separately using variance partitioning including dbMEMs (see Fig. 6)

Environmental variable	Sum of squares	F	p	Variance contributed
Percent cover	0.76	4.58	0.001	0.046
Shoot density	0.84	5.04	0.001	0.038
Eelgrass biomass	0.46	2.76	0.003	0.028
Epiphyte biomass	0.44	2.66	0.003	0.011
Residual	17.87			

fitting models also included patch-scale variables (patch area) and seascape-scale variables (percent eelgrass cover), they contributed relatively little to the variability in epifaunal density and diversity. In
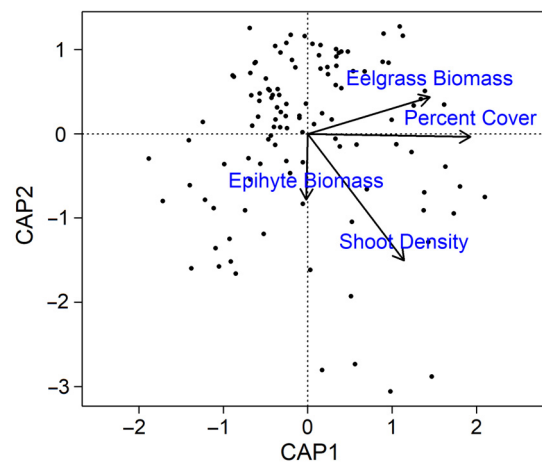

Fig. 5. Distance-based redundancy analysis of the relationship between taxonomic community structure and the 4 environmental variables retained in the final model after accounting for Moran's eigenvector maps as spatial covariates. The 2 axes encompass 80.3% of the variation explained by the model. Vectors represent the direction and magnitude of relationships between individual aspects of the environment and epifaunal community structure. See Table 2 for details

contrast, the strongest predictor of multivariate taxonomic composition was percent eelgrass cover, followed by aspects of structural complexity (shoot density and biomass). Functional composition was very similar throughout MB and did not change in response to variation in habitat structure. In aggregate, our results suggest that the density and diversity of epifauna respond most strongly to within-patch, local-scale eelgrass structure, but shifts in community composition are driven more by structure at larger spatial scales.

4.1. Univariate community density and diversity

The relationship between univariate community responses and environmental variables in our study clearly shows that microhabitat-scale habitat structural complexity influenced epifaunal communities. These relationships were primarily driven by differences in the total amount of habitat as measured by the biomass of eelgrass and epiphytes contained in each 20 cm diameter sample rather than other seagrass habitat features often found to be closely linked to epifaunal communities, such as shoot density. For

example, the distance a sample was taken from an edge had no significant effect on any univariate metric or species that we modeled. We observed that individual species responded uniquely to some metrics like patch size and depth, which suggests that some degree of species replacement occurred, but this effect was overshadowed by the ubiquitously positive influence of eelgrass and epiphyte biomass on total epifaunal density. Our results correspond with those of several other studies that directly compared the relative importance of multiple aspects of small-scale habitat structure within seagrass beds (Orth et al. 1984, Edgar & Robertson 1992, Attrill et al. 2000, Hovel et al. 2002, Yeager et al. 2019). Eelgrass biomass is intrinsically related to the density, height, and complexity of shoots, but of all the microhabitat-scale metrics of habitat structure, biomass is the most direct measure of the total amount of habitat available to epifauna. Conversely, larger scale measures of the area extent of eelgrass had only a small effect on total epifaunal density, richness, or diversity. In addition to providing space for epifauna themselves, more eelgrass translates into more space for the growth of periphyton on which many epifaunal organisms preferentially feed (Douglass et al. 2011).
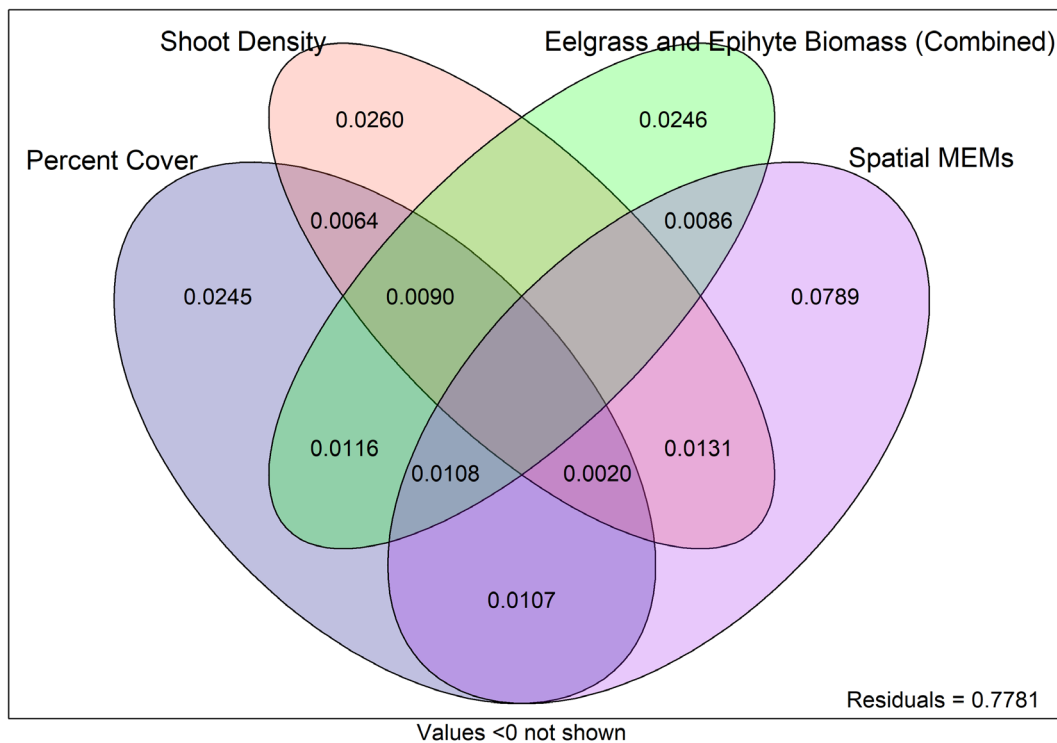

Fig. 6. Variance partitioning for community dissimilarity as a function of 4 environmental variables and 4 combined spatial distance based Moran' eigenvector maps (dbMEMs). Results from a model with eelgrass and epiphyte biomass treated as a single combined factor (see Table 2 for the variance contributed by each of these variables separately)

One commonality among many of the relationships we studied was that the effects of habitat structure on epifauna were nonlinear. Increases in structural complexity at low to moderate levels resulted in steep increases in epifaunal density or diversity, but this was not evident at moderate to high levels of structural complexity, where density or diversity plateaued. Increased eelgrass biomass represents a greater 2-dimensional area of eelgrass blades on which epifauna can live and so the saturating response of diversity to habitat complexity we observed may simply correspond to a species—area curve (Attrill et al. 2000). However, taxonomic richness and diversity co-varied with total epifaunal density, which displayed the same saturating response to habitat complexity. This indicates that at higher levels of eelgrass biomass, the density and diversity of epifauna became limited by the finite substrate area and seawater volume in which they were sampled. Sampling over a larger range of eelgrass habitat structure than most other studies enabled us to detect nonlinear responses that previous studies have alluded to (e.g. Hovel et al. 2002, Gullström et al. 2012) but have rarely been observed directly. These results highlight that the likelihood of observing a strong relationship between small-scale habitat structure and fauna will depend on the range of complexities that are considered in the study.

Epifaunal density, richness, taxonomic diversity, and functional diversity also increased with depth until around 3 m below MLLW. Micheli et al. (2008) found that even small (<1 m) differences in depth can drive differences in seagrass communities when habitat structure is held constant, and we sampled over a range of almost 5 m from the intertidal to the lower limit of eelgrass distribution at our site. Deeper patches tend to experience more stable temperature and hydrodynamic conditions, which could promote epifaunal abundance. We would expect lower primary productivity due to light attenuation at depth to have a negative influence on faunal density, but there is evidence that this effect can be mitigated by an increase in seagrass shoot height accompanied by a reduction in shoot density, which is commonly observed in deeper seagrass habitat (Collier et al. 2007) and is a feature of our study site.

Epifaunal abundance and diversity decreased with local percent cover, and richness was highest in intermediate sized patches within seascapes of 25—75% eelgrass cover (Fig. S1). These results suggest that continuous eelgrass meadows promote less abundant and diverse epifaunal communities than seascapes with some level of fragmentation. Some manipulative studies have found that larger patches harbor denser and more diverse epifaunal communities (Reed & Hovel 2006) while many others have found no difference in the communities of different sized patches (Hirst & Attrill 2008, Pierri-Daunt & Tanaka 2014) or degrees of seascape fragmentation (Lefcheck et al. 2016). Many of these manipulations occurred at ~1 m scales, which is relatively small in the scope of natural seagrass habitat variability (Boström et al. 2010). Species richness increased in our samples along with patch size at these smaller scales, and it was only in the largest patches (>5500 m^2), which are outside the scope of most studies (Boström et al. 2006), that richness began to decrease. This indicates that some level of fragmentation per se might benefit inhabitants by encompassing a more heterogeneous mixture of habitat types than continuous meadows.

4.2. Community composition

The majority of our epifaunal samples were numerically dominated by the same few taxa regardless of the environment, resulting in relatively consistent epifaunal community composition throughout MB. Thus, the large variability in density and diversity we observed did not translate into differences in community composition. Similarly, Carr et al. (2011) observed that seagrass epifauna community composition remained invariant despite orders-of-magnitude differences in abundance driven by microhabitat complexity. Habitat structure and spatial structure cumulatively explained 24.2% of multivariate community structure, which is comparable to other mensurative studies in seagrasses (e.g. Stark et al. 2020: $r^2 = 22\%$; Yeager et al. 2019: $r^2 = 20\%$; Murphy et al. 2021: $r^2 = 26\%$). Of the variation in multivariate community structure that was explained by the environment in our models (14.1%), the average percent cover of eelgrass within 5 m had the greatest influence. Both Yeager et al. (2019) and Murphy et al. (2021) also observed that epifaunal community composition was mostly driven by seagrass configuration within the surrounding seascape rather than structural complexity. We suggest that rapid epifaunal dispersal may explain why epifaunal community composition was fairly consistent despite high variability in microhabitat structural complexity and was more closely tied to larger-scale habitat structure (Boström et al. 2010, Carr et al. 2011, Lefcheck et al. 2016, McSkimming et al. 2016). Stark et al. (2020) explicitly tested the relative importance of the mechanisms of metacommunity assembly in structuring epifaunal metacommunities across eelgrass meadows separated

by up to 1000 km and found that the effects of dispersal limitation were overshadowed by niche filtering and biotic interactions even at such a large scale. While we did observe significant spatial structure in our community samples, this was manifested across a very small scale and is therefore unlikely to represent dispersal limitation. Even though the majority of epifaunal organisms are small and lack planktonic larvae, passive drifting (Brooks & Bell 2001) and active movements (Darcy 2003, Tanner 2003) allow rapid dispersal that can result in complete turnover at meter scales in less than a day (Howard 1985). This may create a stronger dependence on structure at the patch or seascape scale (e.g. the average shoot density throughout a patch or seascape) than on the microhabitat scale (e.g. the density of shoots present within a 20 cm drop trap) (Boyé et al. 2017). In accordance with this hypothesis, differences in eelgrass community composition are often driven by large-scale abiotic gradients (Hayduk et al. 2019, Morais et al. 2019, Namba et al. 2020, Stark et al. 2020) among seagrass seascapes separated by kilometers rather than within individual seascapes (Irlandi et al. 1995, Hovel et al. 2002, Dolbeth et al. 2013, Gross et al. 2017).

4.3. Functional composition

The fourth-corner analysis showed that there was no significant interaction between species' functional traits and the environment in our data. In contrast to our results, Piló et al. (2016), Iacarella et al. (2018), and Hu et al. (2019) all found significant interactions between functional traits and the environment; however, all 3 of these studies looked at large-scale abiotic gradients, which characteristically exert much stronger influences on epifaunal communities than small-scale habitat structure (Dolbeth et al. 2013, Yamada et al. 2014, Stark et al. 2020). Other studies using fourth-corner methods to relate measures of habitat structure to functional traits have not included statistical tests for overall significance, rendering conclusions drawn from their results dubious (ter Braak et al. 2017). The lack of a significant interaction between traits and the environment in our study was likely a consequence of high functional redundancy along with the relative constancy of taxonomic community composition due to rapid epifaunal dispersal over our small sampling area as we discussed above.

Functional diversity co-varies with taxonomic diversity but is typically less sensitive to environmental variables including habitat structure, especially where functional traits are represented by many different species (Gross et al. 2017). We observed a high degree of functional redundancy of traits across sampling: a group of free-living mobile grazers with direct development and internal fertilization dominated the abundance across all samples. High functional redundancy is a common property of seagrass epifaunal communities (Blake & Duffy 2010, Yamada et al. 2011, Lefcheck 2015). Seagrass epifaunal communities maintain high diversity and functional redundancy by subdividing relatively homogenous seagrass habitat into numerous microhabitats (Best & Stachowicz 2014). Epifaunal species that share similar functional traits often display a wide diversity of responses to environmental factors (Blake & Duffy 2010, Lurgi et al. 2016, Wong & Kay 2019). In addition, many epifaunal organisms display intraspecific trait variability by adapting their feeding mode or living habit in response to their surroundings (Dolbeth et al. 2013), and these labile organismal traits further dampen effects on community function (Liao et al. 2017). All these factors reduce the likelihood that species loss or replacement will translate to a change in ecosystem function (Villéger et al. 2008).

Functional redundancy and the resulting robustness that we observed in epifaunal communities have important ecological consequences. Epifauna have a vital role both as top-down grazers of epiphytic algae (Whalen et al. 2013, Duffy et al. 2015) and as a key intermediate step in transferring energy and nutrients from primary production of seagrasses and epiphytes to higher trophic levels (Hemminga and Duarte 2000). Robustness within this community contributes to rapid recovery of ecosystem function following seagrass restoration (McSkimming et al. 2016, Lefcheck et al. 2016, Orth et al. 2020) and maintains ecosystem health despite anthropogenic stressors (Tomas et al. 2015). Our results demonstrate that the functional composition of epifaunal communities is insensitive to changes in habitat structure; therefore, the overall ecological functions provisioned by epifauna are likely to scale simply with total epifaunal density.

4.4. Caveats

In this study, we were able to simultaneously account for numerous aspects of the environment at small scales but our ability to assess larger scale variation in habitat structure was limited. Our results indicate that large-scale habitat configuration plays a dominant role in determining community composi-

tion, but we were only able to characterize habitat cover within ~80 m^2 areas around each sample due to logistical limitations. It is plausible that our models would have explained more community variation if we had included aspects of seascape configuration such as connectivity between patches or percent cover within a larger radius of the sample. It would also be interesting to determine the distance at which measures of small-scale habitat structural complexity such as shoot density and eelgrass biomass stop being relevant to local epifaunal communities. Perhaps models of community structure that used the average shoot density in the area surrounding a sample would perform better than our models, which only measured structural complexity within 20 cm diameter drop traps. Our understanding of the upper limits at which habitat configuration affects local community composition would benefit greatly from more studies employing a hierarchical spatial design (Noda 2004).

We were also limited in our ability to define functional trait modalities for the taxa that comprised our samples both by the difficulty of finding traits that can be compared across various phyla and by the paucity of detailed information about the ecology and behavior of many epifaunal organisms. If there was more empirical information about the behavior, morphology, and reproduction of these organisms, future studies could create more accurate models of epifaunal functional responses by analyzing more traits and including some continuous traits like daily mobility or average fecundity.

4.5. Conclusions

In conclusion, we found that the amount of habitat at microhabitat scales as measured by eelgrass and epiphyte biomass had the strongest correlations with total epifaunal density, richness, and diversity, whereas community taxonomic composition was more closely linked to the amount of habitat available at larger scales as measured by the percent eelgrass cover in the surrounding seascape. These results demonstrate that the amount of habitat is more important than its configuration but that the scale at which measures of the amount of habitat are relevant depends on the ecological perspective in question. Differences in taxonomic composition did not translate into differences in functional composition, which indicates that species replacement by functionally redundant taxa made community function robust to differences in habitat structure. Overall, our study demonstrates the strengths of an integrative approach to seascape ecology. By accounting for numerous aspects of the environment and communities, we were able to capture many distinct and sometimes contrasting patterns of epifaunal responses to differences in their environment that would not be apparent from studies with a narrower scope.

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