Trait sensitivities to seagrass fragmentation across spatial scales shape benthic community structure

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Abstract

1. The structure of local ecological communities is thought to be determined by a series of hierarchical abiotic and biotic filters which select for or against species based on their traits. Many human impacts, like fragmentation, serve to alter environmental conditions across a range of spatial scales and may impact trait–environment interactions.

2. We examined the effects of environmental variation associated with habitat fragmentation of seagrass habitat measured from microhabitat to landscape scales in controlling the taxonomic and trait-based community structure of benthic fauna.

3. We measured patterns in species abundance and biomass of seagrass epifauna and infauna sampled using sediment cores from 86 sites (across 21 meadows) in Back Sound, North Carolina, USA. We related local faunal community structure to environmental variation measured at three spatial scales (microhabitat, patch and landscape). Additionally, we tested the value of species traits in predicting species-specific responses to habitat fragmentation across scales.

4. While univariate measures of faunal communities (i.e. total density, biomass and species richness) were positively related to microhabitat-scale seagrass biomass only, overall community structure was predicted by environmental variation at the microhabitat, patch (i.e. patch size) and landscape (i.e. number of patches, landscape seagrass area) scales. Furthermore, fourth-corner analysis revealed that species traits explained as much variation in organismal densities as species identity. For example, species with planktonic-dispersing larvae and deposit-feeding trophic modes were more abundant in contiguous, high seagrass cover landscapes while suspension feeders favoured more fragmented landscapes.

5. We present quantitative evidence supporting hierarchal models of community assembly which predict that interactions between species traits and environmental variation across scales ultimately drive local community composition. Variable responses of individual traits to multiple environmental variables suggest that community assembly processes that act on species via traits related to dispersal, mobility and trophic mode will be altered under habitat fragmentation. Additionally, with increasing global temperatures, the tropical seagrass *Halodule wrightii* is predicted to replace the temperate *Zostera marina* as the dominate seagrass in our study region, therefore potentially favouring species with

planktonic-dispersing larva and weakening the strength of environmental control on community assembly.

1 | INTRODUCTION

Understanding the processes that regulate the structure of ecological communities is a central tenant of community ecology. Community assembly is thought to be determined by a series of stochastic, abiotic and biotic processes in which members are selected from a regional species pool (Cornell & Lawton, 1992; Keddy, 1992). Neutral models of community assembly predict variation in community structure across sites may be determined solely by stochastic processes coupled with dispersal (Hubbell, 1997, Bell, 2000). In contrast, deterministic models of community assembly measure the degree to which species traits are acted upon by abiotic or biotic factors to affect persistence within local communities. For example, environmental stress gradients may serve to preclude sensitive species, while biotic interactions, like competition, predation and facilitation, may further affect species persistence as well as relative abundance (de Bello et al., 2013; Cavender-Bares, Kozak, Fine, & Kembel, 2009; Hillebrand, Bennett, & Cadotte, 2008; Wiens, 1989). It is generally accepted that local communities are shaped by a combination of both stochastic and deterministic processes, although there is still much debate about the relative importance of various factors in controlling community structure across systems (McGill, 2010).

Inherent within the dynamics of community assembly is the tenant that these processes are hierarchical in nature with their relative importance being manifest at different spatial scales (Able & Fodrie, 2015; de Bello et al., 2009; Cavender-Bares et al., 2009; McGill, 2010). At the broadest spatial scales, dispersal will be important in bringing individuals from the regional species pool to an area. Apart from dispersal, it may be expected that abiotic factors will control community composition at large spatial scales (Jackson, Peres-Neto, & Olden, 2001) while biotic interactions will drive species abundances at small spatial scales (McGill, 2010; Pearson & Dawson, 2003; Whittaker, Willis, & Field, 2001). Thus, multi-scale approaches for assembly models are needed to capture the complex mechanisms by which local community structure is determined.

Trait-based approaches for analysing community structure are valuable in predicting species responses to both abiotic and biotic variables. These approaches capture the ecological role and habitat requirements of a given species within a discrete environment (Díaz & Cabido, 2001), while also revealing underlying mechanisms of coexistence (Chesson, 2000; Pacala & Tilman, 1994; Tilman, 1994). Trait-based approaches also allow for more generalizable models linking variations in community structure with environmental factors and therefore should improve predictions of biodiversity across systems (de Bello et al., 2013; Sydenham, Moe, Totland, & Eldegard, 2015).

Community assembly mechanisms may become altered under environmental change if fluctuating abiotic and biotic conditions modify selective pressure on species based on their traits. Specifically, habitat disturbances, like fragmentation, may alter habitat suitability for species by reducing habitat area and habitat connectivity (Fahrig, 2003) while changing abiotic conditions (Laurance, 1989; Levenson, 1981; Ng, 1983; Ranney, Bruner, & Levenson, 1981). For example, forest edges in fragmented landscapes may have substantially different microclimates than forest interiors due to increased light penetration, higher wind turbulence and greater desiccation. These differences have been shown to drive changes in species composition along edge habitats, selecting for species with hermaphroditic reproductive strategies and those that gain a competitive advantage under high nutrient and light conditions (Girão, Lopes, Tabarelli, & Bruna, 2007; Laurance, Delamônica, Laurance, Vasconcelos, & Lovejoy, 2000). Available evidence, largely based on studies of terrestrial plants, suggests that fragmentation may generally select for "pioneer" species with short life spans, fast growth rates and fast colonizing abilities (Laurance, 2006; Platt, Evans, & Rathbun, 1988). Models suited for consumer species, however, should incorporate additional traits related to resource acquisition, dispersal and reproduction, and explicitly incorporate scale-dependence in selection upon traits to help elucidate the complex processes by which fragmentation controls community assembly.

Seagrass ecosystems represent an ideal model system to explore the effects of habitat fragmentation on community assembly because they exhibit large gradients in natural and anthropogenic fragmentation. Previous work on fragmentation within seagrass habitats has generally focused on either landscape-scale or patch-scale responses, revealing that fragmentation may alter predator–prey dynamics along patch edges (Mahoney, Kenworthy, Geyer, Hovel, & Joel Fodrie, 2018) or decrease overall species diversity at landscape scales (Yeager, Keller, Burns, Pool, & Fodrie, 2016). In this study, we focused on responses of benthic macrofauna to habitat fragmentation, specifically examining effects of landscape, patch and microhabitat environmental gradients on organismal density, diversity and community structure. Additionally, we employed fourth-corner models to evaluate the predictive value of species traits in determining responses to environmental variables across scales to inform models of community assembly. As the current study focused on microhabitat to landscape scales, we were not able to parse out

community assembly processes happening at broad spatial scales (e.g. inter-estuary scales) at which factors like long-distance dispersal may be more important.

We expected to find that higher benthic faunal density and species richness would be associated with higher structural complexity at sub-metre scales and that fragmentation may have a negative effect on density and richness mediated through smaller seagrass patch sizes and lower overall habitat cover at the landscape scale. Furthermore, we expected that species would exhibit variable responses to environmental measurements associated with fragmentation across scales based on their traits. Specifically, we predicted that traits related to dispersal and reproductive mode would mediate responses to landscape-scale fragmentation metrics (e.g. patch number and landscape habitat area) while traits that mediate microhabitat use and biotic interactions (e.g. diet) would show the strongest interactions with changes in environmental variables at patch and microhabitat scales (e.g. decreasing patch size and seagrass biomass). Finally, we predicted that body size and mobility would also be important determinants of the scale of organismal response to fragmentation effects, with larger and more mobile species responding to environmental variation at larger scales.

2 | MATERIALS AND METHODS

2.1 | Study sites

We sampled 86 sites within seagrass habitats throughout Back Sound, North Carolina, USA (34°42′N to 34°39′N, 76°37′W to 76°31′W) (Appendix S1, Figure S1.1). Back Sound is a shallow (average depth = 2 m), well-mixed estuarine system with salinities ranging from 24 to 36 (Kenworthy, Zieman, & Thayer, 1982). This estuarine system lies at a critical interface between biogeographic ecoregions, thereby facilitating codominance of both the temperate species, *Zostera marina* (eelgrass), and the sub-tropical species, *Halodule wrightii* (shoalgrass). All sites were separated by at least 3 m.

Sampling sites were located across 21 seagrass "landscapes" which were defined by 200 m × 80 m rectangles (matching common bed size and shape within our system). These landscapes were previously selected to represent independent gradients in both total seagrass cover (260–11,764 m^2) and landscape patchiness (1–75 individual patches; Table 1; Yeager et al., 2016). Sampling sites in the current study were haphazardly placed across all 21 landscapes (3–7 sites per landscape), but always located within seagrass itself, and not the unvegetated matrix.

2.2 | Seagrass core sampling and laboratory processing

One core sample was taken from each sampling site to quantify both fine-scale seagrass structure and the benthic macrofaunal assemblage. The core (30-cm diameter) was gently placed by hand at each site and pushed down to a constant depth of 10 cm into the sediment. The core was gently rotated to break seagrass rhizomes, then dug out by hand, lifted and placed into a resealable 1.5-gallon plastic bag. The sample was transported back to the laboratory on ice. All cores were taken within 2 hr of low tide (within ~30 cm of minimum water depth), and the GPS location of each core was marked with a Garmin 72H handheld unit (Garmin International, Olathe, Kansas, USA). Low-tide depth was measured in situ at each site at the time of sampling to the nearest 10 cm. The shallowest sites (3/86) were exposed during low tide, and depth was recorded as 0 cm. This coring method samples both the above-ground seagrass habitat and top 10 cm of sediment.

In the laboratory, core samples were screened using a 500-µm sieve; benthic macrofauna were sorted from larger debris and seagrass tissue and transferred to a 70% ETOH solution for storage. These organisms were then identified to the lowest taxon possible, enumerated, dried (48 hr at 60°C) and weighed to the nearest 0.0001 g. Only polychaetes with intact anterior appendages were identified and counted for density estimates to prevent

TABLE 1 Summary of environmental variables

Scale	Environmental variable	Description	Mean	SD	Min	Max
Microhabitat	Depth (m)	Depth of the water column at low tide	0.56	0.22	0	0.9
Microhabitat	*Z. marina* biomass (g DW)	Above-ground biomass per 30-cm diameter core	1.63	1.46	0	5.2
Microhabitat	*H. wrightii* biomass (g DW)	Above-ground biomass per 30-cm diameter core	2.07	1.73	0	10.04
Patch	Patch area (m^2)	Area of seagrass patch within which the core was located, calculated in ArcGIS v 10.1	3,543.2	3,773.0	0.8	11,746.0
Landscape	Number of seagrass patches	Number of patches per landscape within which the core was located, calculated in FRAGSTATS v 4	12.2	17.0	1	75
Landscape	Landscape seagrass area (m^2)	Total seagrass area per landscape within which the core was located, calculated in FRAGSTATS v 4	4,476.6	3,547.6	260	11,764

TABLE 2 Functional trait categories for all invertebrate species classified along six axes

Trait category	Possible trait values	Hypothesized interactions with environmental drivers and spatial scale(s) of response
Primary trophic mode	Suspension feeding, deposit feeding, interface, carnivore, omnivore, parasite, herbivore	Responds to environmental variation that mediates biotic interactions (e.g. patch size, seagrass biomass) and food availability at patch to microhabitat scales; herbivores and suspension feeders should be favoured in smaller patches in contrast to deposit feeders and carnivores which should be favoured in larger patches; herbivores and omnivores should be favoured in higher seagrass biomass sites while other trophic modes will be favoured in lower seagrass biomass sites
Microhabitat use	Epifaunal, infaunal	Responds to environmental variation that affects habitat structure (e.g. depth, seagrass biomass) at microhabitat scales; epifauna should be favoured in deeper, higher seagrass biomass sites
Reproductive mode	Internal, external	Responds to environmental variation that affects habitat connectivity and dispersal (e.g. landscape seagrass area and fragmentation) at landscape scales; species with internal fertilization should be favoured in high seagrass area, contiguous landscapes
Larval development	Direct, planktonic	Responds to environmental variation that affects habitat connectivity and dispersal (e.g. landscape seagrass area and fragmentation) at landscape scales; species with direct development should be favoured in high seagrass area, contiguous landscapes
Post-settlement mobility	Mobile, sedentary, sessile	The scale of response to environmental variation will vary with species mobility; mobile species will respond to variation at larger scales than sessile or sedentary species
Body size	Range = 5.08–1,219.2 mm, median = 50.8 mm	The scale of response to environmental variation will vary with species body size; large species will respond to variation at coarser scales than smaller species

overestimation and because these are requisite features for accurate identification. Highly mobile and relatively large fishes were excluded from subsequent analysis as we did not feel their densities were well-sampled with the seagrass cores.

Seagrass tissue from the cores was separated and rinsed with clean freshwater. Seagrass was sorted by species (*Z. marina* and *H. wrightii*). All shoots were enumerated to assess species-specific density, and the first 20 shoots from each species were measured to assess maximum canopy height (rounded to the nearest mm). Seagrass was then sorted by above- and below-ground biomass; the above-ground biomass of each species was dried at 60°C for 48 hr and weighed to the nearest 0.01 g.

2.3 | Characterization of environmental variables across scales

We quantified relevant environmental variables at three spatial scales: microhabitat, patch and landscape. To assess microhabitat conditions, we evaluated fine-scale seagrass characteristics within our cores as well as local abiotic environment (low-tide water depth). Because above-ground seagrass biomass, shoot density and shoot height for each species were correlated within species across cores (Appendix S1, Table S1.1), we used above-ground biomass of each species (*Z. marina* and *H. wrightii*) as composite metrics of microhabitat-scale habitat complexity. Study sites ranged from those dominated entirely by *Z. marina*, *H. wrightii* or a mix of the two (Table 1).

Seagrass habitat was mapped within each seagrass landscape using ArcGIS v 10.1 based on orthorectified aerial photographs as described in Yeager et al. (2016). For our patch-scale environmental variables, we defined patch size (m²) using GPS locations from individual cores collected within each of our sites. Sites were located across 38 unique seagrass patches defined as areas of contiguous seagrass separated on all sides by unvegetated bottom, mapped at 1 m² resolution. In contiguous landscapes, sites may have been located within the same patch as the entire landscape was dominated by a single contiguous patch. In more fragmented landscapes, sites were typically located in separate patches.

To assess landscape-scale habitat fragmentation, we assessed both total seagrass habitat area within the landscape and number of discrete seagrass patches within the landscape (a measure of habitat fragmentation). Total seagrass area and number of seagrass patches were calculated using FragStats (v 4) (McGarigal, Cushman, & Ene, 2012; Table 1).

2.4 | Characterization of species traits

We identified six traits hypothesized to mediate a species' response to the environment and its functional role in the ecosystem; these traits included the following: primary trophic mode, microhabitat use, reproductive mode, larval development, mobility and maximum body size (Table 2). Body size was grouped into small (<10 mm), medium (10–99 mm) and large (≥100 mm) bins to conform with the requirements of categorical traits for the fourth-corner analysis. We assigned species trait values by compiling data from both peer-reviewed literature and web-based identification guides (Appendix S2, Table S2.1). For species with little or no available information, trait values were estimated using genus- or family-level information. We evaluated associations between traits across species using Cramer's V (which can be applied to categorical variables and ranges from 0 to 1) using the assocstats function in the vcd package in R (Meyer, Zeileis, & Hornik, 2017).

2.5 | Relative influence of environmental variables on univariate measures of faunal communities

We examined the relative influence of environmental variables at multiple spatial scales (microhabitat, patch and landscape) in predicting total faunal density, total faunal biomass and total species richness from our seagrass cores. We used multiple regression models to examine the effects of the six environmental variables on each faunal variable using the lm function in R (R Core Team, 2016). As a measure of effect size, we also report η^2 values which quantify the unique variation in a given response variable explained by an individual environmental variable. All environmental variables for all statistical tests were scaled and $\log_{10}(x + 1)$-transformed prior to analyses to improve normality. Total faunal density and biomass were also $\log_{10}(x + 1)$-transformed. Six sites were excluded from our analysis due to missing data for one or more variables. We excluded one apparent outlier from the model with Log faunal density as the response variable to improve model fit. To test for potentially confounding effects of collinearity among environmental predictors on model results, we quantified pairwise correlations among environmental variables and variance inflation factors (VIFs). Correlations among environmental variables retained for analyses were low (absolute value ≤0.40) except for patch- and landscape-scale seagrass area, which were moderately correlated (0.68) (Appendix S1, Table S1.1). However, VIFs for all environmental variables were reasonable (VIF ≤ 4.06) indicating that these moderate and low correlations should not be problematic for interpreting multiple regression results (Appendix S1, Table S1.2).

2.6 | Relative influence of environmental variables on faunal community structure

We tested if benthic community structure varied predictably along environmental gradients across scales. Bray–Curtis dissimilarity between each pair of sites was calculated based on square-root transformed species densities. We ran distance-based linear models (dist-LM function in PRIMER-E; Legendre & Anderson, 1999; McArdle & Anderson, 2001) to determine whether differences in community structure were predicted by environmental variables.

2.7 | Linking faunal density to environmental variables and species functional traits

We also evaluated whether species traits were important in predicting faunal responses to environmental gradients. These relationships are often inferred indirectly in a two-step process: first by examining species–habitat relationships and then by comparing trait distributions across species. The problem of measuring trait–environment relationships directly has been termed the fourth-corner problem (Legendre, Galzin, & Harmelin-Vivien, 1997) and can be conceptualized as a three-table problem, where ordination or matrix algebra can be used to quantify relations between environmental data, species abundance or occupancy data, and species trait data to infer trait by environment interactions (Dolédec, Chessel, ter Braak, & Champely, 1996; Dray & Legendre, 2008; Legendre et al., 1997). We employed a recently developed modelling approach to this fourth-corner problem inspired by species distribution modelling that estimates trait by environmental interaction terms and assesses the power of the model to predict observed species occurrence or abundance (Brown et al., 2014). Here, species abundance is modelled as a function of environmental variables, species traits and their interaction (hereafter referred to as the "trait*env" model). The response variable is the species abundance × site matrix, and the predictors are an environment × site matrix and a species × trait matrix. We used generalized linear models with species counts at each site modelled with a Poisson distribution. We used a model selection technique based on cross-validation and a least absolute shrinkage and selection operator (LASSO) penalty to determine which trait × environment interactions to include in the final model following (Hastie, Tibshirani, & Friedman, 2009) using code provided by Brown et al. (2014) in R. This technique allows weak, non-predictive trait–environment relationships to be dropped from the final model. We selected the model that minimized the LASSO penalty parameter, while cross-validation was based on leaving out 10% of study sites over 50 replicate runs to select the parameter. We report average per cent deviance explained (R^2_{test}) in the 10% hold-out sample averaged across the 50 replicate runs as a measure of effect size and predictive power of the model.

To determine how much of species-to-species variation in density across sites was due to trait responses to environmental parameters, we compared the "trait*env" model with a model fitting individual species responses to environmental variation across sites (as in species distribution modelling; "spp*env" model) following Brown et al. (2014). We fit a hybrid model which retained the trait*environment terms in the model, but also included a species x environment term to account for additional variation in species densities across sites not explained by variation in traits ("trait*env + spp*env" model). Again, we compared the predictive R^2_{test} values across models to evaluate model performance.

Finally, to ensure that our trait*env model results were robust to trait data used, we performed two sensitivity analyses. For some taxa, it was difficult to find detailed information on reproductive mode and larval development and individual trait values were assumed from higher-order taxonomic grouping (genus or family level). We therefore repeated our analysis dropping taxa for which we were less confident in species-specific trait values (denoted with an "*" in Appendix S2, Table S2.1) and re-ran the model results. We used body length as a measure of body size as this was the form of data available for most species, although length alone may not be representative of true space requirements or vulnerability to gape-limited predators. In particular, Annelid worms were typically classified as "large" in terms of body size due to their very elongate body form and dominated species in the largest size bin, but would presumably

represent less body mass than some other species with similar body length. Thus, we ran an additional model without Annelids to determine whether body size results were robust to their inclusion or not.

3 | RESULTS

3.1 | Relative influence of environmental variables on univariate measure of faunal communities

In total, we collected 1,549 individual animals belonging to 95 taxa. Environmental variables across scales explained between 18% and 24% of the total variance in univariate measures of faunal communities (faunal density, faunal biomass and species richness) across sites (Table 3). *Zostera marina* biomass at the microhabitat scales was the only important predictor of faunal density (η^2 = 0.13), faunal biomass (η^2 = 0.16) and species richness (η^2 = 0.11) being positively related to each (Figure 1). Our other estimates of environmental context, that is *H. wrightii* biomass, depth, patch area, number of patches and landscape area, were not important in predicting univariate faunal response variables (Table 3).

3.2 | Relative influence of environmental variables on faunal community structure

While only microhabitat variables were significant predictors of univariate measures of faunal communities, environmental variables measured at the microhabitat and landscape scales were important in predicting overall community structure (explaining 20% of total variation in community structure across sites; Table 4). Fragmentation at the landscape scale emerged as the strongest individual driver of variation in community structure across sites (total variation explained = 0.07), followed by *Z. marina* biomass at the microhabitat scale (0.04). Depth, seagrass area at the patch and landscape scales, and *H. wrightii* biomass each contributed to 3% or less of the explained variance in faunal community structure (Table 4).

3.3 | Role of species traits in mediating environment–community structure patterns

Species traits, environmental variation and their interaction explained 28% of the variation in organismal densities across sites within the 10% hold-out samples. Interestingly, we found evidence that all traits were sensitive to environmental variation at all three spatial scales considered: microhabitat, patch and landscape (Figure 2, Appendix S3, Table S3.1). While some traits showed moderate collinearity across species (e.g. Cramér's V for reproductive mode and trophic mode = 0.63; Appendix S2, Table S2.2), these traits showed variable responses to environmental variation.

The trait*env model (R^2_{test} = 0.28) performed similarly to the spp*env model (R^2_{test} = 0.27), indicating species traits are a similar (or better) predictor of individual responses to environmental variation

than species identity alone. The trait*env + spp*env (R^2_{test} = 0.28) model also performed similarly to the trait*env model, again indicating that species traits alone are able to predict as much variation in organismal density as species identity.

3.4 | Interactions between trophic mode and environmental variables

Contrary to our predictions (Table 2), interactions between trophic mode and environmental variation across all three scales were important in predicting organismal abundance (Figure 2, Appendix S3, Table S3.1). Herbivores were more abundant in shallow sites and high seagrass area landscapes, while omnivores and parasites showed only weak responses to measured environmental variables. Suspension feeders were most abundant in fragmented landscapes, while interface feeders were more abundant within large seagrass patches and high seagrass area landscapes. Deposit feeders were more numerous in shallow, contiguous sites with higher *Z. marina* biomass while carnivores showed the strongest response to landscape-scale seagrass area, with lower densities in high seagrass area beds.

3.5 | Interactions between microhabitat use and environmental variables

Interactions between microhabitat use and microhabitat variables (water depth and seagrass biomass) were most important in predicting organismal abundance relative to interactions with coarser-scaled environmental variation (Figure 2, Appendix S3, Table S3.1). Infaunal species (those that live within the sediment) exhibited higher densities within shallow sites while epifaunal species showed a stronger positive response to *Z. marina* biomass relative to infauna.

3.6 | Interactions between reproduction and larval dispersal and environmental variables

Larval dispersal mode showed sensitivity to environmental variation at the microhabitat and landscape scales. Organisms with planktonic larval dispersal were more abundant in high-area landscapes and in deeper microhabitats with high *H. wrightii* biomass (relative to species with direct developing larvae). Species with direct developing larvae showed a positive response to landscape fragmentation while species with planktonic larval dispersal did not respond to fragmentation (resulting in the negative model coefficient as direct development was the intercept value). Benthic fauna that displayed internal fertilization showed a moderate, negative response to both *H. wrightii* biomass and patch-scale seagrass area as compared to broadcast spawners. Responses of these two traits to environmental variation were also robust to the inclusion of species for which we have lower confidence in some assigned trait values (Appendix S3, Table S3.2, Figure S3.1).

TABLE 3 Results of general linear models for the effects of environmental variables measured at three spatial scales (microhabitat, patch and landscape) on total faunal density, total faunal biomass and total species richness from seagrass cores

Environmental variable	Sum Sq	df	F-value	p-value	η^2
Response variable: Log faunal density; R^2 = 0.24, F = 3.80, p = .002					
Log depth	0.36	1	3.75	.06	0.04
Log *Z. marina* biomass*	1.19	1	12.4195	.001	0.13
Log *H. wrightii* biomass	0.00	1	0.02	.9	<0.01
Log patch area	0.02	1	0.28	.6	<0.01
Log number of patches	0.13	1	1.32	.3	0.01
Log landscape seagrass area	0.06	1	0.64	.4	0.01
Residuals	6.90	72			0.76
Response variable: Log faunal biomass; R^2 = 0.23, F = 3.67, p = .003					
Log depth	0.14	1	0.83	.4	0.01
Log *Z. marina* biomass*	2.46	1	14.98	.0002	0.16
Log *H. wrightii* biomass	0.25	1	1.52	.2	0.02
Log patch area	0.08	1	0.50	.5	0.01
Log number of patches	0.10	1	0.61	.4	0.01
Log landscape seagrass area	0.10	1	0.59	.4	0.01
Residuals	11.98	73			0.77
Response variable: Species richness; R^2 = 0.18, F = 2.72, p = .02					
Log depth	38.19	1	2.08	.2	0.02
Log *Z. marina* biomass*	175.89	1	9.59	.003	0.11
Log *H. wrightii* biomass	1.29	1	0.07	.8	<0.01
Log patch area	27.50	1	1.50	.2	0.02
Log number of patches	2.79	1	0.15	.7	<0.01
Log landscape seagrass area	22.40	1	1.22	.3	0.01
Residuals	1,339.31	73			0.82

Note: η^2 = the unique variation in the response variable explained by each environmental variable. Environmental variables with a statistically significant effect on the response at α = .05 are denoted with an *.

3.7 | Interactions between body size and mobility and environmental variables

As hypothesized, the predictive power of trait by environment interactions across spatial scales for body size and mobility varied with trait value (Table 2). Mobile species responded most strongly to coarse-scale environmental variation, with their density being positively related to landscape seagrass area. Sedentary species responded to microhabitat variables, showing higher densities at shallow sites. Similar to predictions related to mobility, species with larger body sizes responded most strongly to landscape-scale variables; fragmentation had a strong negative effect and landscape seagrass area a weak negative effect on large-bodied species. The strong negative effect of fragmentation on large-bodied species appeared to be driven largely by a negative effect on Annelid worms, however, as the large body size*patch number model coefficient was much weaker in the full model when Annelids were excluded from the analysis (Appendix S3, Table S3.3, Figure S3.2). Conversely, small-bodied species responded most strongly to microhabitat variables, with higher densities in deep, low *Z. marina* biomass sites.
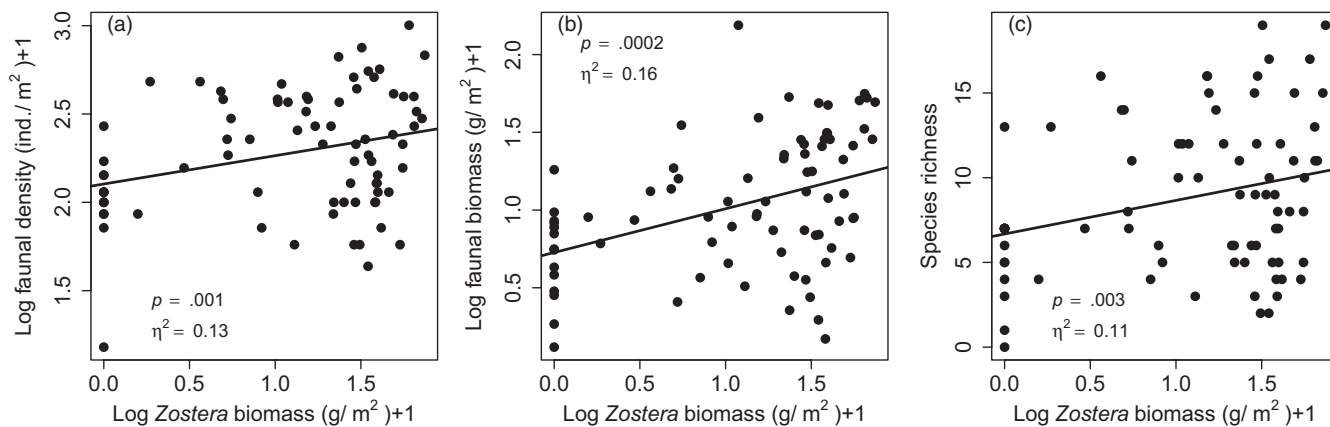
FIGURE 1 Univariate plots modelling the effects of *Zostera marina* biomass on total faunal density, total faunal biomass and total species richness from seagrass cores

TABLE 4 Results of marginal tests from distance-based linear models for the effects of environmental variables measured at three spatial scales (microhabitat, patch and landscape) on differences in community structure (measures as Bray–Curtis dissimilarity) across sites

Environmental variable	Sum of squares	Pseudo *F*-value	*p*-value	Proportion of variance explained
Total model R^2 = 0.20				
Log depth	5,952	2.13	.007	0.023
Log *Z. marina* biomass	10,795	3.77	.001	0.042
Log *H. wrightii* biomass	5,111	1.80	.02	0.020
Log patch area	3,119	1.05	.4	0.012
Log number of patches	18,707	6.30	.001	0.074
Log landscape seagrass area	6,891	2.17	.006	0.027

Note: The proportion of variance explained is the total variation explained by each environmental variable, not taking into account other environmental variables in the model.

4 | DISCUSSION

We observed predictable patterns in community structure of benthic seagrass fauna along fragmentation gradients, providing evidence for the importance of fragmentation in driving community assembly. As habitat fragmentation impacts environmental conditions at multiple scales (i.e. increasing patch number, decreasing patch size, shifts in fine-scale seagrass composition), using a multi-scale approach was necessary in our attempt to disentangle effects of various fragmentation processes. While univariate measures of community structure (e.g. faunal biomass, species richness) were only weakly predicted by microhabitat-scale environmental variables, overall community composition was predicted by variables measured at the landscape, patch and microhabitat scales. Incorporating information on species identity and relative abundance was therefore key in elucidating the role of fragmentation processes manifest at patch and landscape scales in driving community structure. Furthermore, results of the fourth-corner analysis revealed that species traits were as useful as species identity in predicting the distribution of individuals across sites, suggesting that species traits were the primary driver of species-specific patterns in density. Although the mediating effect of scale on shifts in community structure associated with fragmentation has been recognized, the scale-dependent responses of species based on their traits documented herein represent an important mechanistic link between the two.

While we predicted that some traits would be most strongly affected by environmental variation associated with fragmentation at a single scale (e.g. that dispersal and reproductive mode would respond primarily to landscape-scale variation), we instead found that every trait category considered was affected by environmental variation at two or three scales. These multi-scale responses of species based on traits to environmental variables reveal the numerous ways by which fragmentation may impact community assembly. For example, interactions between a single trait, trophic mode, with water depth, landscape-scale fragmentation and landscape-scale seagrass area appeared to have strong effects on organismal density. For herbivores, higher seagrass area within the landscape may confer higher total food availability if they consume seagrass or epiphytes directly, and thus, loss of landscape seagrass area associated with fragmentation may have driven negative
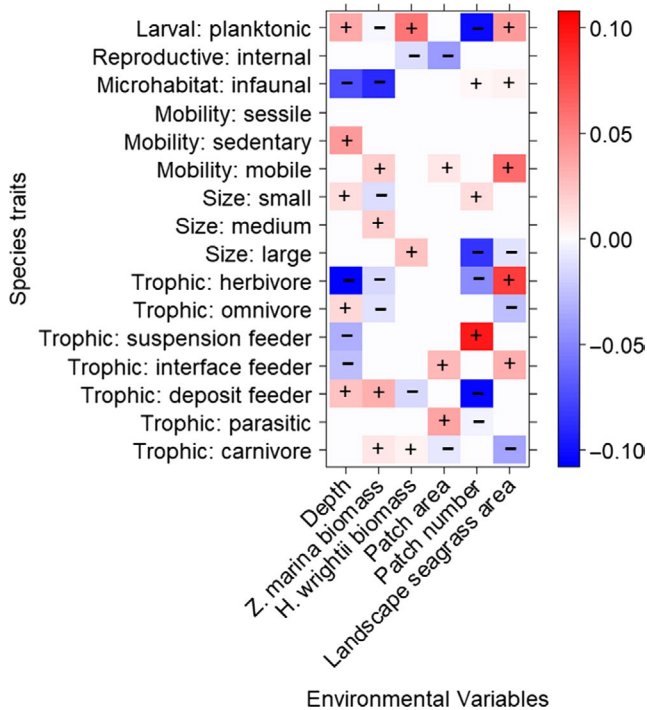
FIGURE 2 Results of fourth-corner analysis showing the sign and strength model coefficients for trait * environmental interactions retained in the final GLM-LASSO model used to predict species counts across sites

impacts on this guild. However, herbivore abundance may also be responding to the negative effect of landscape seagrass area on carnivores, their potential predators. These benthic carnivores and omnivores may in turn exhibit lower densities in high-area seagrass landscapes since high-area seagrass landscapes harbour higher densities of higher-order predators (Yeager et al., 2016). Thus, trophic cascades may be responsible for varying response of herbivores and carnivores/omnivores to seagrass landscape area. For example, many of the omnivores in our study were juvenile blue crabs (*Callinectes sapidus*) which have been previously shown to prefer smaller seagrass patches to avoid highly cannibalistic adult blue crabs (Hovel and Regan). In this way, declines in landscape-scale habitat cover resulting from fragmentation may shift food web structure and predator–prey interactions if trophic groups respond differently to this habitat modification.

The interplay between the biogenic habitat features and the hydrologic regime was likely another major environmental filter of benthic fauna in our system. Previous work has shown that wave/current energy appears to be a primary driver of landscape-scale habitat fragmentation in Back Sound and seagrass habitat structure should further modify water flow. Specifically, patchier seagrass landscapes are associated with higher flow regimes (Fonseca & Bell, 1998), with lower seagrass density often conferring reduced sediment stabilization (Fonseca & Fisher, 1986; Ginsberg & Lowenstam, 1958; Orth, 1977; Scoffin, 1970) concomitant with increased sediment transport and resuspension (Fonseca & Cahalan, 1992; Fonseca & Fisher, 1986; Ward, Kemp, & Boynton, 1984) at finer scales. Therefore,

suspension-feeding organisms, which filter plankton and organic matter from the water column, likely selected patchy habitats because higher flow supports greater food availability. Conversely, deposit feeders, which feed on settled organic matter, showed the opposite habitat preference, likely because slower water velocities increase deposition of organic matter onto the benthos.

Differences in flow rates among fragmented and contiguous seagrass beds may also explain the strong effect of landscape fragmentation on dispersal mode of organisms. The positive relationship between landscape-scale seagrass area and density of species with planktonic larvae may be explained by lower flow rates within larger, contiguous seagrass landscapes which may facilitate larval settlement as coarse particles filter through edge habitats and fine particles accumulate in the interior of seagrass beds (Ackerman & Okubo, 1993; Fonseca, Fisher, Zieman, & Thayer, 1982). At the microhabitat scale, the positive effect of *H. wrightii* biomass on species with planktonic dispersal could also be driven by decreased water velocities associated with higher seagrass structural complexity. Some previous studies have found that larval recruitment may be higher within seagrass edge habitats than seagrass interiors (Bologna & Heck, 2000; Carroll, Furman, Tettelbach, & Peterson, 2012). While we did not specifically compare edge to interior habitats in this study, we did not find a strong interaction between dispersal mode and seagrass patch size (with smaller patch sizes having higher edge to area ratios). Furthermore, there was a strong positive effect of fragmentation at the landscape scale on the density of species with direct developing larvae, which may indicate that patch-scale patterns regarding the importance of edge:area ratios do not necessarily "scale-up" to landscape-scale patterns. Moreover, in this study we were measuring densities of all benthic life stages and not measuring settlement, per se. Previous studies have found that post-settlement processes may reverse the relative value of edge and interior habitats as settlement versus juvenile/adult habitat (Carroll et al., 2012; Hovel & Lipcius, 2002).

Our observation that *Z. marina* biomass was a stronger predictor of community structure than *H. wrightii* suggests that the role of microhabitat variables in driving seagrass community composition in this region may be weakened under global change. Globally, increasing temperatures may force range shifts of many seagrass species (Short & Neckles, 1999) as well as shift biotic interactions and strengthen top-down control (Brodeur, 2015; Hernán et al., 2017). As North Carolina sits at a biogeographic boundary between sub-tropical and temperate ecoregions, effects of increasing global temperature on overall community structure will likely be dramatic. While we did not measure the effects of temperature on benthic seagrass fauna directly, the strong, differential responses of benthic fauna to seagrass species identity suggest that temperature-driven shifts in seagrass bed composition would have cascading effects on associated fauna. Specifically, it is predicted that increasing summer heat stress will result in more severe die-offs of *Z. marina* (Brodeur et al., 2015; Carr, D'Odorico, McGlathery, & Wiberg, 2012), potentially allowing *H. wrightii* to become the dominant seagrass species in the region. Our observed results of differences in benthic species

density, diversity and community composition associated with *Z. marina* dominated versus *H. wrightii* dominated seagrass beds support previous studies documenting distinct benthic communities associated with these two seagrass habitat types (Micheli, Bishop, Peterson, & Rivera, 2008). Furthermore, our observation that different traits were important in mediating the response of species to *Z. marina* or *H. wrightii* biomass indicates that climate change will alter the traits important in predicting community assembly near this range boundary. For example, epifaunal species with planktonic-dispersing larva may be favoured during community assembly if *H. wrightii* becomes more dominant within the system.

Our trait by environment models was successful in predicting up to 28% of the variation in species abundance across sites. While this predictive power is relatively good in comparison with similar empirical studies (e.g. Brown et al., 2014), there was still a large amount of variation in community structure unexplained. Neutral processes were likely important in driving some of this variation. We could presumably improve our models, however, by including other relevant environmental factors not considered in the current study. For example, below-ground seagrass structure or sediment characteristics like grain size or organic matter content may be particularly important for infauna (Honkoop, Berghuis, Holthuijsen, Lavaleye, & Piersma, 2008). Furthermore, our models were limited by the resolution and accuracy of trait data available, which is limited for many of the invertebrate species in our system. Life-history information like life span or growth rates are largely lacking for these species. While our sensitivity analysis indicated that our model results were largely robust to the inclusion of species traits in which we had lower confidence, many of our trait categories were necessarily coarse. Higher resolution data on mobility (e.g. average daily movement rates) or larval dispersal (e.g. pelagic larval duration) could help improve predictive power, particularly if extended over larger spatial extents. Additionally, fuzzy coding approaches may also help refine future models, especially for traits like diet where species may fall into more than one category (Chevenet, Dolédec, & Chessel, 1994). Relatedly, intraspecific variation in traits, although challenging to measure and not considered in our study design, could also improve future community assembly models as phenotypic plasticity can lead to variation in expressed traits and mediate individual responses to environmental variation (Bolnick et al., 2011).

Apart from understanding how fragmentation affects community assembly processes, the results of this study also contribute to growing empirical support for hierarchal community assembly models more broadly. While not excluding the importance of stochastic processes and large-scale dispersal in mediating community assembly at broad scales, our results support deterministic models of hierarchical community assembly whereby environmental variation at multiple scales acts upon species traits to control the persistence and relative abundance of species locally. In particular, the utility of species traits in explaining variation in species-specific responses to environmental variation is encouraging for creating more generalizable community assembly models and future comparisons across systems.

Our work extends previous studies documenting fragmentation effects on seagrass community composition which have generally focused on environmental effects on community structure at one or two scales (e.g. microhabitat and patch) (Hovel & Lipcius, 2002; Irlandi, 1995; Yeager et al., 2016) to reveal the complex, interacting processes by which fragmentation may affect ecological communities. Differential responses of fauna to fragmentation across scales based on species traits suggest that habitat fragmentation may alter community structure by shifting selective pressures on species traits during multiple community assembly stages. Similarly, a recent analysis of seagrass fish communities along the Pacific coast of Canada found distinct shifts in trait composition associated with human disturbance (Iacarella et al., 2018). Thus, we argue that multi-scale, trait-based approaches provide much future promise in continued efforts to disentangle the complex and interacting ways by which humans are altering biodiversity across systems.

CONFLICTS OF INTEREST

We have no conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

L.A.Y. and F.J.F. designed the study; L.A.Y. and J.K.G. collected and analysed the data; L.A.Y. and J.K.G. wrote first draft; and all authors edited the manuscript.

DATA AVAILABILITY STATEMENT

Faunal community data (Yeager, 2018a, 2018b), core seagrass biomass (Yeager, 2019a), environmental data (Yeager, 2019a) and trait data (Yeager, 2019b) are archived with the Biological and Chemical Oceanography Management Office.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.