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ORIGINAL RESEARCH ARTICLE

Habitat Characteristics and Plant Community Dynamics Impact the Diversity, Composition, and Co-occurrence of Sediment Fungal Communities

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Abstract
Habitat edge effects can have profound impacts on biodiversity throughout terrestrial and aquatic biomes. Yet, few studies have examined how habitat edge effects impact the spatial patterning of sediment properties and microbial communities, especially in coastal ecosystems. Coastal salt marshes throughout the world are being transformed by sea level rise; high-marsh, flood-intolerant species, such as *Spartina patens*, are being fragmented and replaced by low-marsh, flood-tolerant species, such as *Spartina alterniflora.* The consequences of these habitat transformations on fungal communities remain unclear. Thus, we sought to identify how habitat edge effects, alongside changing plant community dynamics, impact the spatial patterning of fungal communities associated with ubiquitous *Spartina* species. We analyzed 26 *Spartina patens* patches: 13 pure monocultures and 13 mixed patches with *Spartina alterniflora* infiltration. We measured patch characteristics, plant characteristics, sediment physicochemical properties, and sediment fungal communities. We found that habitat edge effects structured sediment and plant properties in both pure and mixed patches. However, habitat edge effects only structured fungal community composition in mixed patches, counter to expectations. These results indicate that changing plant community dynamics driven by sea level rise can exacerbate habitat edge effects in coastal ecosystems. Least discriminant analysis and co-occurrence networks further revealed unique taxa and network structures between pure and mixed patches and between interiors and edges. In sum, we found that habitat transformation of coastal salt marshes driven by global change impacts the spatial dynamics of sediment and fungal properties.

Keywords Habitat fragmentation · Habitat edge effects · Microbial ecology · *Spartina patens* · Mycobiome · Sea level rise

Introduction

Habitat loss, habitat fragmentation, and habitat edge effects can have profoundly negative impacts on biodiversity throughout the world (Fahrig 2003, Fletcher et al. 2018, Püttker et al. 2020). While numerous studies have examined individual animal species or community responses to habitat edges (Ries et al. 2017; Wimp and Murphy 2021), fewer studies have examined how habitat edge effects impact the spatial patterning of fungal communities. Indeed, most studies specifically avoid edge habitats when identifying microbial communities or calculating critical ecosystem parameters (Rippel et al. 2020). Further, it remains unknown how other global change factors associated with habitat fragmentation, such as shifts in foundation plant species, concurrently impact microbial communities (Rillig et al. 2019; Perrault and Laforest-Lapointe 2022). Thus, we sought to determine the impacts of habitat edge effects, as well as changing plant community dynamics, on the spatial patterning of fungal communities in a fragmented coastal ecosystem.

Coastal ecosystems are valuable model ecosystems for studying habitat fragmentation because they typically contain foundational plant species growing in patchy

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monocultures shaped by a variety of physical, chemical, and biological interactions (Boström et al. 2011, Wimp and Murphy 2021). Recent studies have revealed habitat edge effects on ecosystem processes and microbial communities in seagrasses and mangroves (Jiang et al. 2013; Carroll et al. 2019; Yeager et al. 2020). However, fewer studies have examined the spatial patterning of microbial communities in salt marshes, which are increasingly impacted by sea level rise, species loss, and habitat fragmentation (Campbell and Wang 2020; Vinent et al. 2021, Rippel and Minsavage-Davis et al. 2023). In coastal salt marshes along the United States' eastern coast, tide-intolerant *Spartina patens* (also known as *Sporobolus pumulis*) often occurs in the high marsh and while tide-tolerant *Spartina alterniflora* (also known as *Sporobolus alterniflorus)* dominates the low marsh (Denno 1977; Bertness 1991). In the Mid-Atlantic region, these two species can form concomitant monocultures, wherein *S. patens* patches are isolated from one another through a mosaic of *S. alterniflora*. However, pure stands of *S. patens* patches are being lost, fragmented, and/or transformed at an alarming rate, often being replaced or infiltrated by *S. alterniflora* (Watson et al. 2016, Rippel and Minsavage-Davis et al. 2023). Although these plant species have unique sediment microbial assemblages (Kearns et al. 2019), no studies to our knowledge have investigated the impact of salt marsh transformation or habitat edge effects on sediment fungal communities, despite their importance for nutrient cycling, plant community dynamics, and carbon storage.

Fungal communities play a regulatory role in carbon cycling and plant nutrient dynamics in marine and coastal ecosystems, including salt marshes (reviewed in Raghukumar 2017 and Calabon et al. 2021). Fungi play a dominant role in the decomposition of above-ground biomass in coastal salt marshes (Newell et al. 1996; Buchan et al. 2002, 2003), and greater appreciation has recently been given to their role in the decomposition of soil organic matter (Kearns et al. 2019). Symbiotic mycorrhizal associations also occur in coastal salt marshes, particularly for high marsh species, such as *S. patens* (Burke et al. 2002, 2003; Welsh et al. 2010). The question of which fungi correspond with healthy salt marshes was raised in d'Entremont et al. (2021), who alluded to the presence of certain mycorrhizal species, such as *Funneliformis geosporum*, as fundamental to a stable ecosystem, despite their relatively low abundance and root colonization rates for *S. alterniflora* (Burke et al. 2003; Welsh et al. 2010; d'Entremont et al. 2018). However, the analysis of fungal communities as a whole, including co-occurrence network analysis, may also provide useful metrics determining the resilience and functioning of fungal communities (Faust et al. 2012; Berry and Widder 2014; Wang et al. 2022). Although researchers debate which metrics of soil fungal communities best measure wetland ecosystem health (Wu et al. 2015; Ramírez-Viga et al. 2018; Onufrak et al. 2020), robust microbiome data must be gathered from vulnerable ecosystems before they are fragmented, lost, or degraded.

Here, we sought to determine whether fungal communities varied with sediment properties and habitat characteristics associated with *S. patens* patches. We examined whether *S. patens* patches with infiltrating *S. alterniflora* (mixed patches) differed from monocultures of *S. patens* (pure patches) in sediment and microbial properties. We also assessed whether the interiors of *S. patens* patches differed from the edges, as edge effects are key to understanding the impacts of habitat fragmentation (Grilli et al. 2017; Yeager et al. 2020). Thus, we asked the following questions: (1) Do habitat edge effects impact the spatial patterning of fungal communities and physicochemical sediment properties? (2) Does the infiltration of *S. alterniflora* into *S. patens* patches impact fungal communities and/or ecosystem properties? We hypothesize that habitat edge effects will influence sediment physicochemical soil properties in all *S. patens* patches. Further, we predict that these differences in sediment properties, along with changes in plant community dynamics, will result in differences in fungal communities between patch types (mixed vs. pure) and patch locations (edge vs. interior). Lastly, we hypothesize that the interior of *S. patens* monocultures (pure patches) will have the most distinct fungal communities, due to a complete lack of influence from *S. alterniflora.*

Materials and Methods

Experimental Design and Plot Selection

In 2021, we sampled 26 *Spartina patens* patches of varying size and shapes in a vast intertidal salt marsh on the Tuckerton Peninsula in the Jacques Cousteau National Estuarine Research Reserve, which lies in the Great Bay–Mullica River Estuary near Tuckerton, New Jersey (Fig. 1). Half of the patches were pure monoculture stands of *Spartina patens* ("Pure Patches") while the other half consisted of *S. patens* with infiltrating *Spartina alterniflora* ("Mixed Patches"). We selected mixed patches using a percent cover threshold, with patches needing to have > 25% cover of *S. alterniflora* (Table 1). Patches were chosen haphazardly but we attempted to capture the range in patch size and morphology present at this location. We set up two plots (0.25 × 0.25 m) in each patch (n = 52): one in the center of the patch (interior) and one at the border of the patch (edge).

Elevation and Patch Characteristics

To evaluate elevation and patch characteristics, we georeferenced each plot with a Garmin GPSMAP 64sx (Garmin Ltd.,

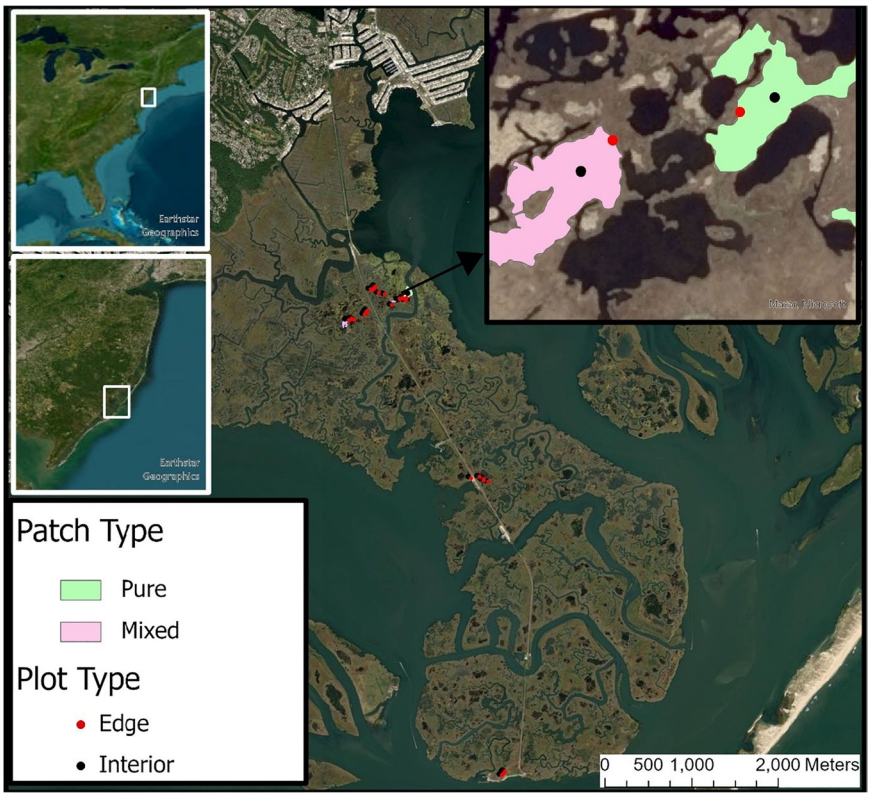

Fig. 1 Location of *S. patens* patches and plots in Jacques Cousteau National Estuarine Research Reserve (39°33′09.5″N 74°20′09.1″W)

Table 1 Plant and sediment properties for each plot type (mean ± standard error)

	Plot Type			
	Pure Interior	Pure Edge	Mixed Interior	Mixed Edge
Total Live Biomass (g)	46.8 ± 6.7	27.4 ± 1.4	36.5 ± 4.5	22.7 ± 2.1
Patens Live Biomass (g)	46.8 ± 6.7	26.6 ± 1.5	27.8 ± 4.9	14.5 ± 2.5
Alterniflora Live Biomass (g)	0 ± 0	0.8 ± 0.6	8.7	8.2 ± 1.6
Alterniflora % Cover	0 ± 0	0 ± 0	34.0 ± 4.1	36.8 ± 4.0
Elevation (m)	0.67 ± 0.03	0.61 ± 0.021	0.64 ± 0.015	0.61 ± 0.018
Sediment Carbon (%)	8.9 ± 0.99	9.7 ± 0.65	7.8 ± 0.66	7.6 ± 0.84
Sediment Nitrogen (%)	0.6 ± 0.056	0.68 ± 0.044	0.54 ± 0.04	0.54 ± 0.059
Sediment C:N Ratio	14.6 ± 0.33	14.3 ± 0.26	14.5 ± 0.22	14.3 ± 0.12
Sediment Salinity	20.4 ± 2.3	29.4 ± 1.96	19.3 ± 1.7	23.1 ± 2.0
Sediment pH	5.6 ± 0.12	5.9 ± 0.056	5.7 ± 0.12	5.7 ± 0.09
Root Density (g / cm^3)	0.036 ± 0.004	0.051 ± 0.0044	0.034 ± 0.0055	0.047 ± 0.0064

Olathe, Kansas, USA) and uploaded the data to ArcPro 2.3 (ESRI, Redlands, CA, USA), where all subsequent analyses were performed. We digitized all plots as well as the patches in which they occurred. We acquired 3 m digital elevation models through the New Jersey Department of Environmental Protection (NJDEP 2022), and we assigned an average elevation to each plot using the *Zonal Statistics (Spatial Analyst)* tool. Patch area, patch perimeter, patch perimeter-to-area ratio, and distance between plots were calculated with the attribute table and then log-transformed to fit a normal distribution for all subsequent analyses.

Primary Production and Dead Biomass

We removed all biomass from plots at the end of the growing season in 2021. We first separated live *S. patens*, dead *S. patens*, live *S. alterniflora*, and dead *S. alterniflora.* We counted the number of culms of each species and measured

culm length of 15 representative *S. patens* culms, using the mean of these measurements to represent culm length for the plot. We dried biomass at ~60 °C and weighed each biomass group separately.

Sediment and Root Characteristics

We collected sediment samples with a soil corer (7.5 × 15 cm) after aboveground biomass collections. We immediately opened cores and subsampled 3 g of a mixture of sediment and fine roots from the center of cores for later microbial analysis. All samples were placed on ice for transport and subsequently stored at -20ºC for soil cores and − 80ºC for microbial samples. We separated sediment cores into roots and sediment using 2 mm sieves. Roots and sediment were dried separately at ~60ºC and weighed to calculate root biomass and sediment bulk density. We measured sediment pH and salinity using a Hanna Edge Multiparameter (Hanna Instruments, Rhode Island, United States) with pH (HI11311) and EC/TDS/salinity (HI763100) probes, respectively, after mixing 10 g of dried, sieved soil with 25 mL of water (1:2.5 ratio) and shaking for 20 min. We sent subsamples of dried sediment to Cornell Stable Isotope Laboratory (Cornell University, Ithaca, USA) to determine carbon and nitrogen concentrations.

Fungal DNA Extraction and Sequencing

We extracted DNA from 40 mg of field-moist root-sediment mixture using Qiagen DNeasy Plant Mini Kits (Hilden, Germany). We lysed cells with a Qiagen TissueLyser II (Hilden, Germany) and followed manufacturers extraction protocols for the remainder of the extraction. We used a Qubit 2.0 fluorometer (Invitrogen, Eugene, OR, USA) to quantify extracted DNA. To confirm the presence of fungi, extracted DNA was amplified using ITS86(F)/ITS4(R) primer sets (Forward: GTGAATCATCGAATCTTTGAA, Reverse: TCCTCCGCT TATTGATATGC). Once fungal DNA was confirmed, we sent 10 µg of genomic DNA to the Integrated Microbiome Resource at Dalhousie University for paired-end sequencing of the ITS2 amplicon (same primers as before) using the Illumina MiSeq platform. Of the 52 samples sent, 45 had sufficient read depth for subsequent analyses (a natural break occurred between samples at ~6100 reads).

Microbial DNA Processing and Classification

We followed the *QIIME 2* pipeline for ITS2 sequence assembly and comparison (Kuczynski et al. 2012; Kõljalg et al. 2013). We trimmed and denoised sequences, removed extremely rare species (< 20 reads), constructed phylogenies, and taxonomically assigned amplicon sequence variants (ASV) (Caporaso et al. 2010; Bolyen et al. 2019). After these steps, we retained 644,522 reads, containing 492 unique ASVs with an average sampling depth of 14,322 per sample. We examined several metrics of fungal alpha diversity and community composition to assess differences in fungal communities among plots. We calculated species richness (ASV richness), Pielou's evenness (species equitability), and Shannon's diversity index for each plot. To control for different sequencing depths among samples, we used the *alpha-rarefaction* function in *QIIME2* to rarify samples to 6,100 reads (minimum sequencing depth).

To assess the differences in fungal community composition between plots, we used Jaccard (Jaccard 1912; Chung et al. 2019) and Bray-Curtis dissimilarity (Faith et al. 1987) indices to test for differences in species presence and abundance, respectively. We generated Jaccard and Bray-Curtis dissimilarity metrics for statistical analysis using the *core-metrics-phylogenetics* function in *QIIME 2*. ASVs were taxonomically assigned using a pre-trained naïve Bayes classifier (Fungal UNITE database, 99% similarity) with the *fit-classifier-naive-bayes* function (Nilsson et al. 2019).

Statistical Analyses

Edge Effect Sizes for Pure and Mixed Patches

We analyzed "habitat edge effects" using log response ratios (LRR) that compared the sediment and plant characteristics of interior plots to edge plots. We calculated the LRR of variables within a patch as $LRR = ln\left(\underline{E_i}\right) - ln\left(\underline{I_i}\right)$, where $ln\left(\underline{E_i}\right)$ is the average natural log of the variable measured in the edge of a patch and $ln\left(\underline{I_i}\right)$ is the natural log of the variable measured in the interior. We assessed the significance (based on an alpha value of 0.01) of edge effect sizes by comparing the effect sizes of each variable to 0 using the *ttest* function in R (Version 4.0.5 for all analyses) (Team 2021). Percent change is derived from LRRs with the following equation: $Percent\ Change = 100 * (e^{LRR} - 1)$.

Fungal Alpha Diversity across Plot Types

We compared fungal alpha diversity metrics (ASV Richness, Pielou's evenness, Shannon's Diversity) across the four plot types (pure interior, pure edge, mixed interior, mixed edge) using pairwise comparisons. We used pairwise comparisons due to the specific blocking structure of this experimental design (blocks apply within pure and mixed patches separately). When comparing plots that were within a patch type (i.e., pure interior vs. pure edge), we used linear mixed models (*lme4* package) with block as the random effect and plot type as the fixed effect (Bates et al. 2015). Linear mixed

models were used as it allows for unbalanced random effects. When comparing plots from different patch types (i.e., pure edge vs. mixed interior), we used simple t-tests. We used an adjusted alpha value of 0.01 to account for multiple comparisons associated with pairwise analysis.

Fungal Community Composition Across Plot Types

To assess differences in fungal community composition among plot types, we ran PERMANOVA on all pairwise comparisons using the *vegan* (Oksanen et al. 2013) and *pairwiseAdonis* (github.com/pmartinezarbizu/pairwiseAdonis*)* packages in R (Oksanen et al. 2013). We used PERMANOVA to test for both differences in species presence/absence (Jaccard Index) and species abundance (Bray-Curtis dissimilarity). Similar to the previous section, we included block as a random effect when comparing plots within a patch type (i.e., pure-edge vs. pure-interior), and no random effect when comparing plots across patch types (i.e. mixed-edge vs. pure-interior). We constructed NMDS plots depicted as Euclidean Distances using the *vegan* package in R (Oksanen et al. 2013). We produced three separate NMDS plots (all patches, pure patches, and mixed patches) for Bray-Curtis dissimilarity and Jaccard distances, respectively. Pairwise comparisons were Bonferroni corrected. We used the *envfit* function in the *vegan* package for vector analysis, which regressed plant and sediment properties with the Euclidean Distances of the Bray-Curtis dissimilarity and Jaccard matrices. Only significant ($P < 0.01$) vectors are shown in NMDS plots, which are interpreted with R^2 values.

To assess which species drove the differences between plot types, we implemented similarity percentage analysis (SIMPER) on pairwise Bray-Curtis dissimilarity matrices and species presence/absence matrices with 1000 permutations each using the *simper* function in the *vegan* package in R (Clarke 1993; Oksanen et al. 2013). Finally, we utilized the linear discriminant analysis (LDA) effect size (LEfSE) method using the *microbiomeMarker* package in R (Cao et al. 2022). This analysis identifies which clades are unique to each plot type relative to all other types. We used default parameters of the package with a selection criteria of $P < 0.01$ and LDA > 2.5.

Co-occurrence Network Analyses

For each plot type, we created co-occurrence networks by computing Spearman correlation matrices using the *phylosmith* package in R (Smith 2019). Our analysis was based on the relative abundances of 10 rarefied samples per plot type; only fungal ASVs with relative abundances above 0.1% were considered. We only included correlations that were considered robust (Spearman's correlation coefficient (rho) > 0.7 and $P < 0.01$). The resulting matrices were imported into the Cytoscape platform (version 3.9.1) to identify nodes and calculate network statistics (Su et al. 2014). We analyzed networks for network size (total number of nodes (ASVs), total number of edges (number of robust correlations between ASVs), network density (proportion of potential edges that exist in the network), average degree (average number of edges per node), clustering coefficient (the tendency for a node's connections to also be connected), degree heterogeneity (the variation in degree across nodes in a network), the number of modules, and modularity (the strength of connectivity within modules compared to between modules). Modules and modularity were generated using the Glay community clustering algorithm in Cytoscape (Su et al. 2014). Networks were visualized with the *phylosmith* package.

Results

Edge Effect Sizes for Pure and Mixed Patches

As predicted, habitat edges and habitat interiors differed significantly in sediment properties (Fig. 2, Table S1, S2). Within patches, we found that the difference in elevation between interior and edge plots was greater for pure patches (edge plots were 7% (14 cm) lower than interior) than for mixed patches (edge plots were 4% (8 cm) lower than interior). However, these differences within a patch did not appear to correspond to overall differences in elevation between mixed and pure patches (range in mean elevation across treatments: 0.61–0.67 m; Table 1). Lower elevations at habitat edges are likely what led to significant differences in sediment physicochemical properties between interior and edge samples. In pure patches, sediment at the edges was 38% more saline and 5% more basic in pH than sediment in the interior. Further, sediment at the edge of mixed patches was 19% less dense and 20% more saline than habitat interiors. In pure patches, edge plots had 48% less total live biomass and 59% less total dead biomass than interior plots, showing that edges have sufficiently less primary production overall and *S. alterniflora* does not make up for the reduction in *S. patens*. In mixed patches, edges had 64% less total live biomass and 53% less total dead biomass compared with habitat interiors.

Fungal Alpha Diversity Across Plot Types

Of the three alpha diversity metrics analyzed (fungal species richness, Pielou's evenness, Shannon's Diversity), we only found trending differences in species richness (Fig. 3A, Table S3). Through pairwise comparisons, we determined that edge plots in mixed patches were nearly distinct from mixed-interior ($df = 12$, $F = 5.49$, $P = 0.047$), pure-edge ($df = 18$, $t = 2.16$, $P = 0.037$), and pure-interior

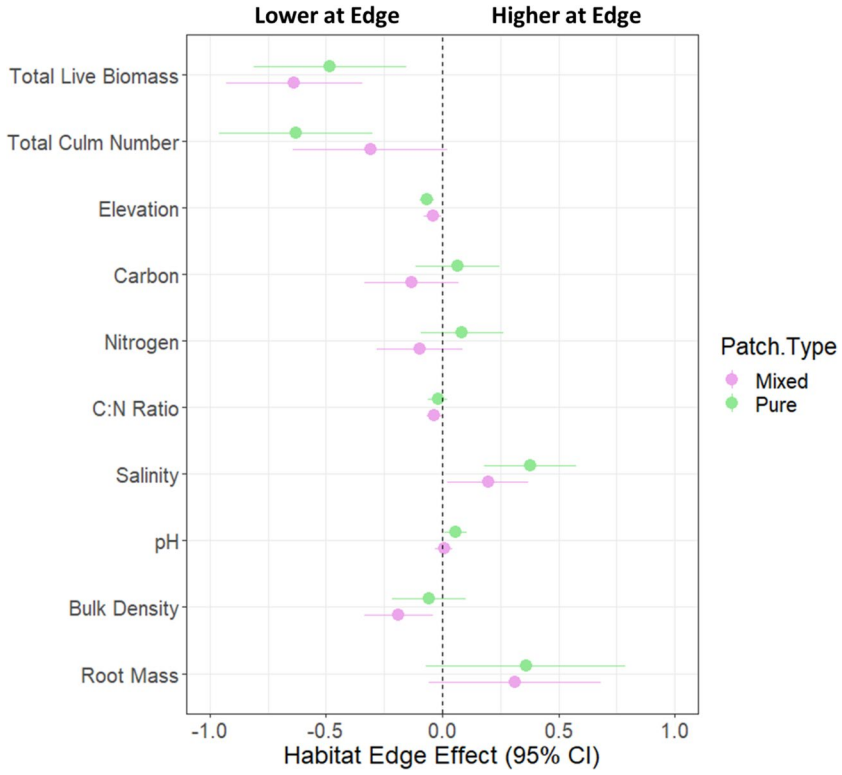

Fig. 2 Results from habit edge effect size showing the average effect size (log response ratio) of properties at the edge of *S. patens* relative to the interior. Effects are significant if 95% confidence intervals do not overlap with 0

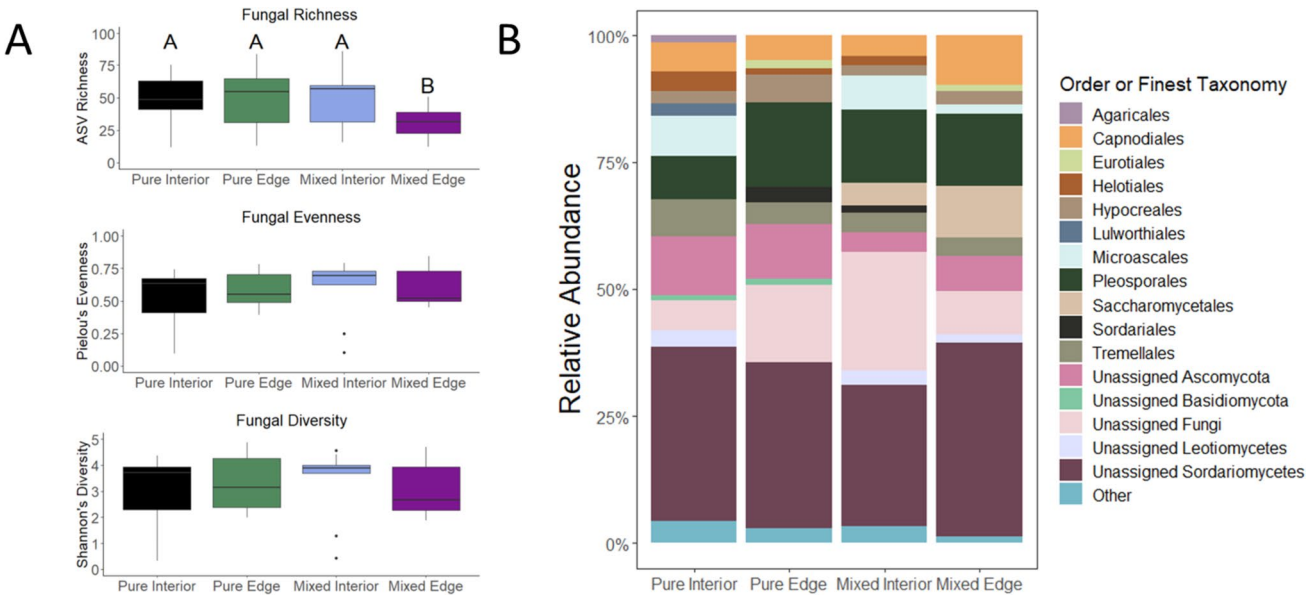

Fig. 3 **A** Comparisons of ASV richness, evenness, and diversity among our four plot types. Letters indicate that plot types were nearly significantly ($P < 0.05$) different from one another. Box plots display medians and interquartile ranges. **B** Average taxonomic composition of sediment fungal communities among plot types

plots (df = 18, t = 2.05, $P = 0.046$). Sediment taken from mixed edge plots contained ~ 31 fungal species, while all other plots contained ~ 49 fungal species.

Taxonomic Composition

In all plots, sediment fungal communities were dominated by the phylum Ascomycota (80.2%), with smaller contributions from Basidiomycota (6.7%), Glomermycota (0.05%), and Mucoromycota (0.003%). Additionally, 13.1% of sequences were unable to be classified to the phylum level. Across all of our plots, Sordariomycetes (42.9%) [Orders: Unassigned (30.8%), Hypocreales (3.2%), Microascales (4.1%)], Dothideomycetes (19.7%) [Orders: Pleosporales (13.5%), Capnodiales (6.1%)], and the Basidiomycota class Tremellomycetes (4.9%) [Order: Tremellales (4.8%)] dominated the fungal communities (Fig. 3B). Although these groups generally dominated throughout the marsh, fungal community composition differed between plot types at multiple taxonomic levels, as explained below.

Fungal Community Composition Across Plot Types

Of the six pairwise comparisons of the presence/absence of fungal species (Jaccard Index), three pair significantly differed from one another and one pair trended towards differences (Fig. 4, Table S4). Mixed-edge plots were distinct from mixed-interior, pure-edge, and pure-interior plots in the presence/absence of fungal species, and pure-edge and mixed-interior plots were nearly distinct from one another. The most robust difference in species presence/absence occurred between sediment from pure-interior plots and that from mixed-edge plots ($F_{1,21} = 3.59$, $R^2 = 0.15$, $P < 0.001$). SIMPER analysis revealed that the presence/absence of 2 species were significantly different between pure-interior vs. mixed interior plots, 14 species for pure-interior vs. mixed-edge plots, 4 for pure-edge

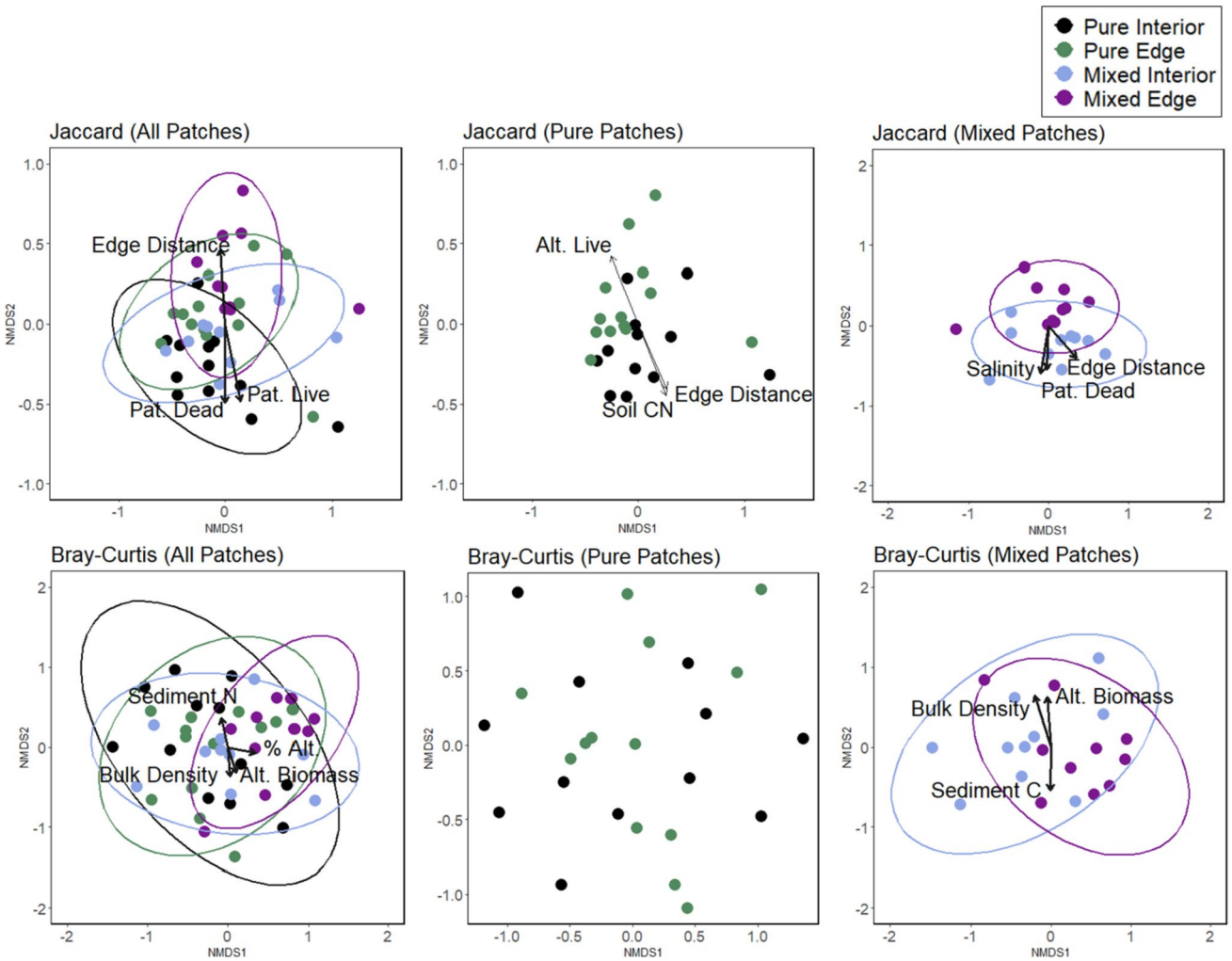

Fig. 4 NMDS ordinations based on Jaccard Index (top row) and Bray-Curtis (bottom row) distance metrics. Separate ordinations were constructed for all patches, pure patches, and mixed patches to better show compositional distinctions between plot types. Ellipses are shown if there were significant ($P < 0.01$) differences between plot types. Vectors represent significant correlations ($P < 0.01$) between environmental variables and fungal community composition

vs. mixed-interior plots, 7 for pure-edge vs. mixed-edge plots, and 2 species for mixed-interior vs. mixed edge plots (Table S5). Notably, mixed-edge plots differed from other plots by the complete absence of several species that were found in the other plot types. Using vector analysis, we found that the distance between plots (distance from edge; df = 51, $R^2 = 0.32$, $P < 0.01$), *S. patens* live biomass (df = 51, $R^2 = 0.24$, $P < 0.01$), and *S. patens* dead biomass (df = 51, $R^2 = 0.29$, $P < 0.01$) corresponded with changes in the presence/absence of fungal species between all plot types. When pure patches were analyzed separately, *S. alterniflora* live biomass (df = 25, $R^2 = 0.24$, $P < 0.01$), soil C:N ratio (df = 25, $R^2 = 0.23$, $P < 0.01$), and distance from edge (df = 25, $R^2 = 0.26$, $P < 0.01$) corresponded with species presence and absence. For mixed patches, salinity (df = 25, $R^2 = 0.22$, $P < 0.01$), distance from edge (df = 25, $R^2 = 0.13$, $P < 0.01$), and *S. patens* dead biomass (df = 25, $R^2 = 0.13$, $P < 0.01$) all corresponded with changes in the presence and absence of fungal species.

For the relative abundances of fungal ASVs, as represented by Bray-Curtis dissimilarity, mixed-edge plots differed from pure-interior ($P < 0.01$), and nearly so for mixed-interior plots ($P = 0.02$) and pure-edge plots ($P = 0.03$) (Fig. 4, Table S4). Considering no other differences occurred between other plot types, we can conclude that sediment from mixed-edge plots contained unique abundances of fungal communities. Mixed-edge plots had enriched abundances of *Candida gosingica*, *Phaesohaeria halima*, Teratosphaericeae *sp.*, and *Neodevriesia sp.* as well as reductions in *Lulwoana uniseptata, Acidomelania panicicola*, and *Bulleribasidium variabile* (Table S6). Using vector analysis, we found that sediment nitrogen (df = 51, $R^2 = 0.13$, $P < 0.01$) sediment bulk density (df = 51, $R^2 = 0.14$, $P < 0.01$), percent *S. alterniflora* (df = 51, $R^2 = 0.14$, $P < 0.01$), and live *S. alterniflora* biomass (df = 51, $R^2 = 0.14$, $P < 0.01$) corresponded with changes in fungal community composition when all patches were analyzed together. Pure patches did not have any environmental vectors that corresponded with changes in community composition. Mixed patches, however, had similar results to the analysis of all patches, as *S. alterniflora* live biomass (df = 25, $R^2 = 0.34$, $P < 0.01$) and sediment bulk density (df = 25, $R^2 = 0.29$, $P < 0.01$) corresponded with species composition differences.

LDA analysis confirmed several species that were detected in SIMPER analyses but included several that were not detected (Fig. 5). Pure-interior plots were differentiated from other plots by unclassified Basidiomycetes, Lulworthiaceae spp., and Polyporales spp. Pure-edge plots were differentiated by species from Sordiales and Xylariales. Mixed-interior plots were differentiated by *Kluyveromyces aestuarii, Myrothecium gramineum, Niesslia indica*, and *Bulleribasidium variable.* Mixed edge plots were differentiated by *Phaeospharia halima.*

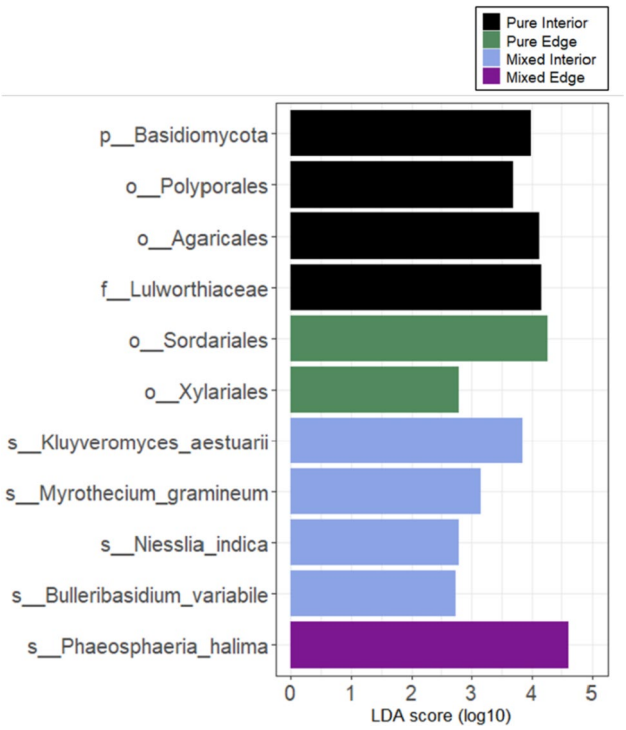

Fig. 5 Linear discriminant analysis effect sizes for taxa underlying plot type differences, where p = phylum, c = class, o = order, f = family, g = genus, and s = species. Species displayed are unique to their respective plot type

Co-occurrence Network Analyses

The four co-occurrence networks we constructed for each plot type differed in node- and network-scale properties (Table 2; Fig. 6). For pure patches, interior plots had higher average number of nodes (343), edges (5306), and average degree (30.9), relative to habitat edges (# of nodes: 334, # of edge: 3592, average degree: 21.5), indicating a higher network connectivity. Pure-interior plots also had higher density (0.09) clustering (0.64), and modularity (0.70) relative to pure-edge plots (density: 0.064, clustering coefficient: 0.23, modularity: 0.66). Similarly, for mixed patches, interior plots had a higher number of nodes (292), edges (4003), and average degrees (27.4) than edge plots (# of nodes: 179, # of edge: 1574, average degree: 18.0). Mixed-edge plots had higher density (0.11), clustering (0.766), and modularity (0.77) than mixed-interior plots (density: 0.094, clustering coefficient: 0.74, modularity: 0.72). Finally, all four networks appeared to be modular (all above 0.68 modularity), containing between 5 and 8 modules.

Table 2 Attributes of co-occurrence networks of different plot types

Plot Type	Nodes	Edges	Density	Average Degree	Clustering Coefficient	Degree of Heterogeneity	Modules	Modularity
Pure Interior	343	5306	0.09	30.93	0.643	0.473	6	0.698
Pure Edge	334	3592	0.064	21.45	0.233	0.628	5	0.666
Mixed Interior	292	4003	0.094	27.42	0.741	0.614	8	0.718
Mixed Edge	179	1574	0.11	17.98	0.766	0.593	7	0.768

Discussion

Our experiment revealed stark differences in fungal communities and their co-occurrence networks between *S. patens* monocultures and mixed *S. patens* patches containing *S. alterniflora*. We found that the spatial patterning of fungal communities in coastal ecosystems are impacted by habitat edge effects and plant community dynamics, akin to forested ecosystems (Grilli et al. 2012, 2015; Kiesewetter and Afkhami 2021; Su et al. 2022). Our results indicate that the infiltration of *S. alterniflora* may disrupt the assemblages of fungal communities present in *S. patens*, similar to its influence as an invasive species in other parts of the world (Yang et al. 2019; Zhang et al. 2021). We also found differences in fungal communities between the interiors and edges of mixed patches, suggesting that patches with *S. alterniflora* had habitat edge effects that structured fungal communities. Although sediment physicochemical properties were altered by habitat edge effects in both patch types, fungal communities were only structured by habitat edge effects in mixed patches, but not in pure *S. patens* monocultures. Notably, mixed-edge plots appeared to be especially divergent in fungal alpha diversity, community composition, and co-occurrence networks, indicating a large transformation of fungal communities in these areas. Thus, we provide evidence that plant dynamics and habitat edge effects alter sediment fungal communities in coastal salt marshes.

Consistent with our hypothesis that habitat edge effects will influence sediment physicochemical soil properties in all *S. patens* patches, we found that both pure and mixed patches had disparate sediment and plant properties at their edges relative to their interiors. These results support past studies that have shown the impact of habitat edge effects on soil and plant properties in terrestrial systems (Lippok et al. 2014; Ruwanza 2018; Su et al. 2022). Mixed patches had lower sediment bulk densities at the edge, pure patches had high sediment pH values at the edge, and both patch types had lower elevations, higher salinities, and lower total above-ground biomass at the edge. Although Rippel et al. (2020) reported no differences in above-ground biomass between interiors and edges, we found a 56% reduction in total live biomass at edges relative to interiors. This discrepancy is likely driven by a difference in plot selection; Rippel et al. (2020) measured edge biomass 0.5 m into a patch, whereas our study took measurements at the absolute edge of a patch where *S. patens* and *S. alterniflora* form a border with one another. This discrepancy between studies supports findings that edge effects can exist at a range of spatial scales (Laurance et al. 2007; Ries et al. 2017). The reduction in live biomass at edges may lead to enhanced degradation of *S. patens* patches, as live biomass regulates sedimentation and accretion rates (Chen et al. 2018; Cahoon et al. 2021; Bass et al. 2022) and moderates soil conditions (Pennings et al. 2003). Notably, plant and physicochemical soil properties, including those impacted by habitat edge effects, were found to correlate with variation in the composition of fungal communities in plots.

In general, the taxonomic composition and diversity metrics of the *S. patens* patches in this study agreed with past studies regarding salt marsh fungal communities (Yang et al. 2019; Lynum et al. 2020; Calabon et al. 2021; d'Entremont et al. 2021). The phylum Ascomycota predominated, with species from Sordiomycetes and Dothideomycetes making up over 60% of the relative abundance. Similar to Zhang et al. (2018), these two groups also tended to predominate among the interconnected clusters found in co-occurrence networks. Further, using least discriminant analysis we were able to determine that each of the four plot types (pure-interior, pure-edge, mixed-interior, mixed-edge) had unique fungi that contributed to the dissimilarity of that plot type. For example, mixed-edge plots had a high relative abundance of *Phaeospharia halima* ($>6\%$), whereas all other plot types had lower abundances ($<1\%$) or none. Commonly, *P. halima* has been associated with decomposing *Spartina alterniflora* biomass above-ground (Buchan et al. 2002, 2003; Calado et al. 2015, 2019) and below-ground (d'Entremont et al. 2021). Thus, it is somewhat surprising that *P. halima* was only found in mixed-edge plots and not mixed-interior plots or pure-edge plots, where *S. alterniflora* also occured. Further, there were entire fungal orders that only appeared in mixed patches (Saccharomycetales) or at habitat edges (Eurotiales; Fig. 3B).

Our experiment revealed the potential for habitat edge effects to impact the fungal communities in coastal salt marshes. However, our results were partly in contrast to our original predictions, as habitat edge effects only impacted

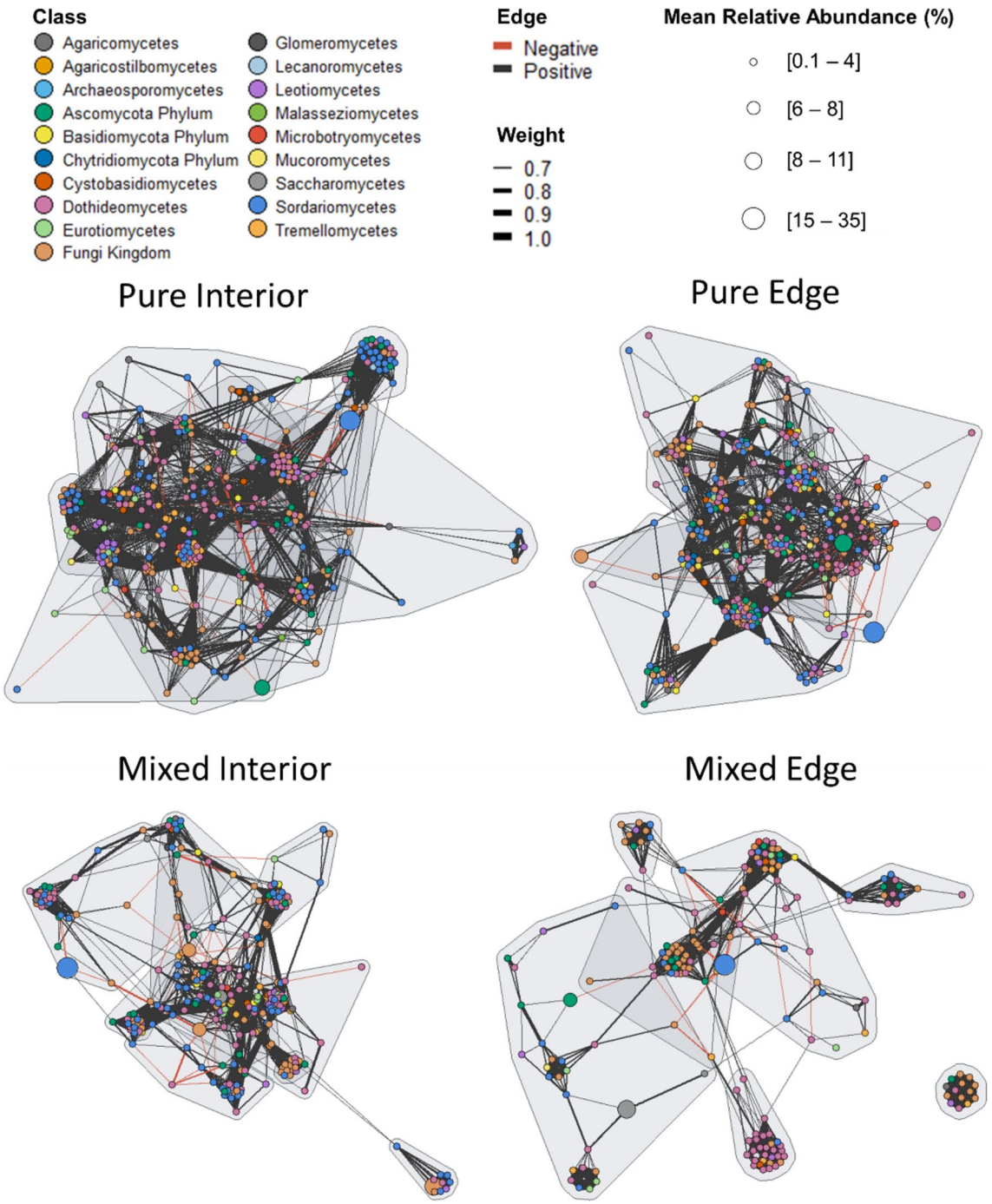

Fig. 6 Co-occurrence networks based on the relative abundance of ASVs that occurred in each plot type, constructed from Spearman correlations (rho > 0.7, $P < 0.01$). The sizes of nodes are based on relative abundance. Edges are colored based on negative (red) or positive (black) correlations and their weights (co-occurrence) are based on rho values

mixed patches and did not influence the fungal community composition of pure *S. patens* patches despite differences in physicochemical soil properties between interiors and edges. We suspected that since pure-interior plots do not come into contact with *S. alterniflora*, and likely have the highest elevations, these plots would be the most disparate from other plots. For pure-edge plots, one may expect that lower elevations, higher salinities, less above-ground biomass, and shared border with *S. alterniflora* would alter the fungal communities present (Kearns et al. 2019). Yet, no alpha diversity or community composition metrics differed between pure-interior and pure-edge plots, nor did soil

properties robustly explain community shifts. *S. alterniflora* biomass, soil C:N ratios, and distance between interior and edge plots were associated with the presence/absence of species in pure patches, but they did not lead to overall differences between interior and edge plots. Although no community composition changes were detected, microbial co-occurrence networks for pure-edge plots were unique relative to pure-interior plots. Pure-edge plot networks had a lower network density (association between ASVs), indicating a simplification of soil fungal interactions (Zhang et al. 2021). Despite similar network sizes, pure-edge plots had considerably higher network heterogeneity, which is further indicated by its low clustering coefficients. Pure-edge plots also had lower modularity which may indicate lower community stability and less resistance to disturbance (de Vries et al. 2018). Thus, pure-edge networks were different from pure-interior networks, but it is unclear what drove these alterations, as edges did not have unique fungal community compositions.

The infiltration of *S. alterniflora* into *S. patens* patches is a serious sign of habitat disturbance and deterioration. Although we did not measure the temporal progression of *S. alterniflora* in mixed patches over time, it is extremely unlikely that these are new *S. patens* patches forming in *S. alterniflora* areas (Rippel and Minsavage-Davis et al. 2023). Thus, pure and mixed patches represent a continuum of *S. alterniflora* infiltration and its effects on microbial community structure. *S. alterniflora* is a superior competitor to *S. patens* at lower elevations (higher tidal inundations) and in high nutrient conditions (Bertness 1991; Levine et al. 1998). Further, *S. patens* has a much steeper decline in both above- and below-ground biomass in response to tidal flooding relative to *S. alterniflora* (Visser and Sandy 2009; Snedden et al. 2015). As hypothesized, we revealed that when *S. alterniflora* infiltrates *S. patens* patches sediment fungal communities and their networks can be profoundly altered. This was especially apparent for mixed-edge plots. Mixed-edge plots were divergent in their fungal alpha diversity, community composition, and co-occurrence networks relative to all other plot types (Figs. 3, 4 and 6). Mixed-edge plots had fewer species present, unique species, unique relative abundances of species, and simplified co-occurrence networks relative to other plots.

Unlike pure patches, fungal communities in mixed patches were distinct at edges relative to interiors and were impacted by the configuration of patches. This is contrary to our predictions and the habitat edge literature, as one would expect larger edge effects where there is a greater contrast in edge properties (Laurance and Yensen 1991; Laurance et al. 2007). Yet, the contrast in physicochemical properties between our pure and mixed edge and interior plots was similar. Thus, the difference in fungal communities between interior and edge plots in mixed patches may be related to a reduced fungal species pool. Thus, changes in edge properties may have an increased impact when overall fungal biodiversity is lower. The differences in fungal communities between mixed edges and interiors were partly driven by high abundances of *Candida gosingica* and *Phaesphaeria halima* and low abundances of *Acidomelania panicola* and *Bulleribasidium variabile* in mixed-edge plots. These compositional shifts could have functional consequences, for example, *P. halima* and *B. variabile* are known lignocellulose decomposers (Raghukumar 2017; Calabon et al. 2021). The amount of *S. alterniflora*, the percent carbon of sediment, and sediment bulk density were associated with changes in relative abundances of species while plant (*S. alterniflora* biomass, *S. patens* biomass), patch (distance from edge) and sediment characteristics (sediment C:N ratio, salinity) were associated with changes in presence/absence of species. These findings confirm multiple studies regarding the environmental modulators of the abundance and presence/absence of fungal communities in coastal and marine ecosystems (Mohamed and Martiny 2011; Kearns et al. 2019; Calabon et al. 2021).

Co-occurrence networks in mixed patches had smaller network sizes compared to pure plots, and edge plots had smaller network sizes than interior plots. This confirms that mixed patches have a reduction in fungal diversity as you move from interiors to edges. Reduced network sizes also suggest a simplification of fungal interactions, which could have an overall negative effect on ecosystem functioning (Zhang et al. 2021). Paradoxically, mixed-edge networks were highly clustered and modular, which may offer stability to moderate disturbance (de Vries et al. 2018). Similar patterns of network simplification but increased modularity have been detected when comparing rhizosphere soils to bulk soils (Mendes et al. 2014; Fan et al. 2018) and irrigated to non-irrigated agricultural fields (Zhang et al. 2018). However, within mixed patches, clustering, density, and degree heterogeneity did not vary as much between edge and interior plots compared to pure habitats. These network metrics are known to depend on network size (292 mixed-interior vs. 179 mixed-edge) and thus we are unable to make reliable inferences as to how edge effects impact these particular aspects of co-occurrence network structure in mixed habitats. In sum, mixed-edge plots represented the most disturbed plots, with altered physicochemical properties and diminished fungal richness, community compositions, and co-occurrence networks.

Conclusions

Understanding spatial patterns of biodiversity and nutrient cycling is essential for monitoring the impact of habitat transformation and global change on ecosystems. Few

studies have examined the impact of habitat edge effects on ecosystem processes and the microbial communities that regulate them. Here, we determined that habitat edge effects and changing plant community dynamics concurrently impact the community composition and co-occurrence networks of sediment fungal communities in coastal salt marshes. Pure *S. patens* patches differed in physicochemical sediment properties, but not fungal communities, between edge and interior plots. However, the infiltration of *S. alterniflora* into *S. patens* patches (mixed patches) brought with it changes in the fungal community structure of plots in general, as well as the prevalence of habitat edge effects. Further, we found that differences in sediment properties were apparent in both mixed and pure patches, but these are not necessarily what altered the fungal communities at habitat edges. Future research should track the changes in belowground properties as *S. patens* patches are transformed and lost due to sea level rise.

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Author Contributions Study conception and design was conceived by Tyler M. Rippel and Gina M. Wimp. Material preparation and data collection were performed by Cathilyn L. Mcintosh, Shannon. M. Murphy, and Tyler M. Rippel. Data analysis was performed by Tyler M. Rippel. Data interpretation was performed by Alexandra L. DeCandia, Melissa A. Collier, and Tyler M. Rippel. The first draft of the manuscript was written by Tyler M. Rippel, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

References

Bass J, Granse D, Hache I, Jensen K, Karius V, Minden V, Stock M, Suchrow S, Kleyer M (2022) Plant traits affect vertical accretion of salt marshes. Estuar Coast Shelf Sci 276:108010

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1–48

Berry D, Widder S (2014) Deciphering microbial interactions and detecting keystone species with co-occurrence networks. Frontiers in Microbiology 5:1–14

Bertness MD (1991) Zonation of Spartina patens and Spartina alterniflora in New England salt marsh. Ecology 72:138–148

Bolyen E, Rideout JR, Dillon MR, Bokulich NA, Abnet CC, Al-Ghalith GA, Alexander H, Alm EJ, Arumugam M et al (2019) Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. National Biotechnology 37:852–857

Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. Marine Ecology Progress Series 427:191–217

Buchan A, Newell SY, Butler M, Biers EJ, Hollibaugh JT, Moran MA (2003) Dynamics of Bacterial and Fungal communities on Decaying Salt Marsh Grass. Applied and Environmental Microbiology 69:6676–6687

Buchan A, Newell SY, Moreta JL, Moran MA (2002) Analysis of internal transcribed spacer (ITS) regions of rRNA genes in fungal communities in a southeastern US salt marsh. Microbial Ecology 43:329–340

Burke DJ, Hamerlynck EP, Hahn D (2002) Effect of arbuscular mycorrhizae on soil microbial populations and associated plant performance of the salt marsh grass Spartina patens. Plant Soil 239:141–154

Burke DJ, Hamerlynck EP, Hahn D (2003) Interactions between the salt marsh grass Spartina patens, arbuscular mycorrhizal fungi and sediment bacteria during the growing season. Soil Biology and Biochemistry 35:501–511

Cahoon DR, McKee KL, Morris JT (2021) How plants influence resilience of Salt Marsh and Mangrove wetlands to Sea-Level rise. Estuaries Coasts 44:883–898

Calabon MS, Jones EBG, Promputtha I, Hyde KD (2021) Fungal biodiversity in Salt Marsh ecosystems. Journal of Fungi 7:648

Calado M, Carvalho L, Barata L, Pang M (2019) Potential roles of marine fungi in the decomposition process of standing stems and leaves of Spartina maritima. Mycologia 111:371–383

Calado M, Carvalho L, Pang L, Barata K-L (2015) Diversity and ecological characterization of sporulating higher Filamentous Marine Fungi Associated with Spartina maritima (Curtis) Fernald in two Portuguese salt marshes. Microbial Ecology 70:612–633

Campbell AD, Wang Y (2020) Salt marsh monitoring along the Mid-atlantic coast by Google Earth Engine enabled time series. PLoS ONE 15:e0229605

Cao Y, Dong Q, Wang D, Zhang P, Liu Y, Niu C (2022) microbiomeMarker: an R/Bioconductor package for microbiome marker identification and visualization. Bioinformatics 38:4027–4029

Caporaso JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK, Fierer N, Peña AG, Goodrich JK, Gordon JI (2010) QIIME allows analysis of high-throughput community sequencing data. Nature Methods 7:335–336

Carroll JM, Keller DA, Furman BT, Stubler AD (2019) Rough around the edges: lessons learned and future directions in Marine Edge effects studies. Current Landscape Ecology Reports 4:91–102

Chen Y, Li Y, Thompson C, Wang X, Cai T, Chang Y (2018) Differential sediment trapping abilities of mangrove and saltmarsh vegetation in a subtropical estuary. Geomorphology 318:270–282

Chung NC, Miasojedow B, Startek M, Gambin A (2019) Jaccard/Tanimoto similarity test and estimation methods for biological presence-absence data. BMC Bioinformatics 20:644

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18:117–143

d'Entremont TW, López-Gutiérrez JC, Walker AK (2018) Examining arbuscular mycorrhizal fungi in saltmarsh hay (Spartina patens) and smooth cordgrass (Spartina alterniflora) in the Minas Basin, Nova Scotia. Northeastern Naturalist 25:72–86

d'Entremont TW, Migicovsky Z, López-Gutiérrez JC, Walker AK (2021) Saltmarsh rhizosphere fungal communities vary by sediment type and dominant plant species cover in Nova Scotia, Canada. Environmental Microbiology Reports 13:458–463

Denno RF (1977) Comparison of the assemblages of sap-feeding insects (Homoptera-Hemiptera) inhabiting two structurally different salt marsh grasses in the genus Spartina. Environmental Entomology 6:359–372

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515

Faith DP, Minchin PR, Belbin L (1987) Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69:57–68

Fan K, Weisenhorn P, Gilbert JA, Chu H (2018) Wheat rhizosphere harbors a less complex and more stable microbial co-occurrence pattern than bulk soil. Soil Biology and Biochemistry 125:251–260

Faust K, Sathirapongsasuti JF, Izard J, Segata N, Gevers D, Raes J, Huttenhower C (2012) Microbial Co-occurrence relationships in the human microbiome. PLoS Computational Biology 8:e1002606

Fletcher RJ Jr, Didham RK, Banks-Leite C, Barlow J, Ewers RM, Rosindell J, Holt RD, Gonzalez A, Pardini R, Damschen EI (2018) Is habitat fragmentation good for biodiversity? Biological Conservation 226:9–15

Grilli G, Longo S, Huais P, Pereyra M, Verga E, Urcelay C, Galetto L (2017) Fungal diversity at fragmented landscapes: synthesis and future perspectives. Current Opinion in Microbiology 37:161–165

Grilli G, Urcelay C, Galetto L (2012) Forest fragment size and nutrient availability: complex responses of mycorrhizal fungi in native–exotic hosts. Plant Ecology 213:155–165

Grilli G, Urcelay C, Galetto L, Davison J, Vasar M, Saks Ü, Jairus T, Öpik M (2015) The composition of arbuscular mycorrhizal fungal communities in the roots of a ruderal forb is not related to the forest fragmentation process. Environmental Microbiology 17:2709–2720

Jaccard P (1912) The distribution of the flora in the alpine zone. New Phytologist 11:37–50

Jiang X-T, Peng X, Deng G-H, Sheng H-F, Wang Y, Zhou H-W, Tam NF-Y (2013) Illumina sequencing of 16S rRNA tag revealed spatial variations of bacterial communities in a Mangrove Wetland. Microbial Ecology 66:96–104

Kearns PJ, Bulseco-McKim AN, Hoyt H, Angell JH, Bowen JL (2019) Nutrient Enrichment alters Salt Marsh Fungal communities and promotes putative fungal denitrifiers. Microbial Ecology 77:358–369

Kiesewetter KN, Afkhami ME (2021) Microbiome-mediated effects of habitat fragmentation on native plant performance. New Phytologist 232:1823–1838

Kõljalg U, Nilsson RH, Abarenkov K, Tedersoo L, Taylor AFS, Bahram M, Bates ST, Bruns TD, Bengtsson-Palme J, Callaghan TM, Douglas B, Drenkhan T, Eberhardt U, Dueñas M, Grebenc T, Griffith GW, Hartmann M, Kirk PM, Kohout P, Larsson E, Lindahl BD, Lücking R, Martín MP, Matheny PB, Nguyen NH, Niskanen T, Oja J, Peay KG, Peintner U, Peterson M, Põldmaa K, Saag L, Saar I, Schüßler A, Scott JA, Senés C, Smith ME, Suija A, Taylor DL, Telleria MT, Weiss M, Larsson K-H (2013) Towards a unified paradigm for sequence-based identification of fungi. Molecular Ecology 22:5271–5277

Kuczynski J, Stombaugh J, Walters WA, González A, Caporaso JG, Knight R (2012) Using QIIME to analyze 16S rRNA gene sequences from microbial communities. Current Protocols in Microbiology 27:1E – 5

Laurance WF, Nascimento HEM, Laurance SG et al (2007) Habitat Fragmentation, Variable Edge effects, and the Landscape-Divergence hypothesis. PLoS ONE 2:e1017. https://doi.org/10.1371/journal.pone.0001017

Laurance WF, Yensen E (1991) Predicting the impacts of edge effects in fragmented habitats. Biological Conservationa 55:77–92

Levine JM, Brewer JS, Bertness MD (1998) Nutrients, competition and plant zonation in a New England salt marsh. Journal of Ecology 86:285–292

Lippok D, Beck SG, Renison D, Hensen I, Apaza AE, Schleuning M (2014) Topography and edge effects are more important than elevation as drivers of vegetation patterns in a neotropical montane forest. Journal of Vegetation Science 25:724–733

Lynum CA, Bulseco AN, Dunphy CM, Osborne SM, Vineis JH, Bowen JL (2020) Microbial Community response to a Passive Salt Marsh Restoration. Estuaries and Coasts 43:1439–1455

Mendes LW, Kuramae EE, Navarrete AA, van Veen JA, Tsai SM (2014) Taxonomical and functional microbial community selection in soybean rhizosphere. ISME Journal 8:1577–1587

Mohamed DJ, Martiny JB (2011) Patterns of fungal diversity and composition along a salinity gradient. ISME Journal 5:379–388

Newell SY, Porter D, Lingle WL (1996) Lignocellulolysis by ascomycetes (fungi) of a saltmarsh grass (smooth cordgrass). Microscopy Research and Technique 33:32–46

NJDEP (New Jersey Department of Environmental Protection) (2022) NJDEP Bureau of GIS. NJDEP open data. Available at: New Jersey Department of Environmental Protection. https://gisdata-njdep.opendata.arcgis.com/.

Nilsson RH, Larsson K-H, Taylor AFS, Bengtsson-Palme J, Jeppesen TS, Schigel D, Kennedy P, Picard K, Glöckner FO, Tedersoo L, Saar I, Kõljalg U, Abarenkov K (2019) The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. Nucleic Acids Research 47:D259–D264

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) Package 'vegan'. Community ecology package, version 2:1–295

Onufrak A, Rúa MA, Hossler K (2020) The missing metric: an evaluation of fungal importance in wetland assessments. Wetlands 40:825–838

Pennings SC, Selig ER, Houser LT, Bertness MD (2003) Geographic Variation in positive and negative interactions among Salt Marsh plants. Ecology 84:1527–1538

Perreault R, Laforest-Lapointe I (2022) Plant-microbe interactions in the phyllosphere: facing challenges of the anthropocene. The ISME Journal 16:339–345

Püttker T, Crouzeilles R, Almeida-Gomes M, Schmoeller M, Maurenza D, Alves-Pinto H, Pardini R, Vieira MV, Banks-Leite C, Fonseca CR (2020) Indirect effects of habitat loss via habitat fragmentation: a cross-taxa analysis of forest-dependent species. Biological Conservation 241:108368

Raghukumar S (2017) The Salt Marsh Ecosystem. Pages 87–101 Fungi in Coastal and Oceanic Marine Ecosystems. Springer, Cham

Ramírez-Viga TK, Aguilar R, Castillo-Argüero S, Chiappa-Carrara X, Guadarrama P, Ramos-Zapata J (2018) Wetland plant species improve performance when inoculated with arbuscular mycorrhizal fungi: a meta-analysis of experimental pot studies. Mycorrhiza 28:477–493

Ries L, Murphy SM, Wimp GM, Fletcher RJ (2017) Closing persistent gaps in knowledge about edge ecology. Current Landscape Ecology Reports 2:30–41

Rillig MC, Ryo M, Lehmann A, Aguilar-Trigueros CA, Buchert S, Wulf A, Iwasaki A, Roy J, Yang G (2019) The role of multiple global change factors in driving soil functions and microbial biodiversity. Science 366:886–890

Rippel TM, Minsavage-Davis CD, Shirey V, Wimp GM (2023) Simple machine learning with aerial imagery reveals severe loss of a salt Marsh Foundation species. Estuaries and Coasts. https://doi.org/10.1007/s12237-023-01192-z. (**Last accessed 24/04/2023**)

Rippel TM, Mooring EQ, Tomasula J, Wimp GM (2020) Habitat edge effects decrease litter accumulation and increase litter decomposition in coastal salt marshes. Landscape Ecology 35:2179–2190

Ruwanza S (2018) The edge effect on plant diversity and soil properties in abandoned fields targeted for ecological restoration. Sustainability 11:140

Smith S (2019) Phylosmith: An R-package for reproducible and efficient microbiome analysis with phyloseq-objects. Journal of Open Source Software 4(48):1442. https://doi.org/10.21105/joss.01442

Snedden GA, Cretini K, Patton B (2015) Inundation and salinity impacts to above- and belowground productivity in Spartina patens and Spartina alterniflora in the Mississippi River deltaic plain: implications for using river diversions as restoration tools. Ecological Engineering 81:133–139

Su N, Jarvie S, Yan Y, Gong X, Li F, Han P, Zhang Q (2022) Landscape context determines soil fungal diversity in a fragmented habitat. CATENA 213:106163

Su G, Morris JH, Demchak B, Bader GD (2014) Biological Network Exploration with Cytoscape 3. Current Protocols in Bioinformatics 47:8.13.1–8.13.24

Team RC (2021) R: A language and environment for statistical computing (Version 4.0. 5)[Computer software]. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Vinent OD, Herbert ER, Coleman DJ, Himmelstein JD, Kirwan ML (2021) Onset of runaway fragmentation of salt marshes. One Earth 4:506–516

Visser J, Sandy E (2009) The effects of flooding on four common Louisiana Marsh plants. Gulf of Mexico Science 27(1). https://aquila.usm.edu/goms/vol27/iss1/3

de Vries FT, Griffiths RI, Bailey M, Craig H, Girlanda M, Gweon HS, Hallin S, Kaisermann A, Keith AM, Kretzschmar M, Lemanceau P, Lumini E, Mason KE, Oliver A, Ostle N, Prosser JI, Thion C, Thomson B, Bardgett RD (2018) Soil bacterial networks are less stable under drought than fungal networks. Nature Communications 9:3033

Wang H, Wu C, Zhang H, Xiao M, Ge T, Zhou Z, Liu Y, Peng S, Peng P, Chen J (2022) Characterization of the belowground microbial community and co-occurrence networks of Tobacco plants infected with bacterial wilt Disease. World Journal of Microbiology and Biotechnology 38:155

Watson EB, Szura K, Wigand C, Raposa KB, Blount K, Cencer M (2016) Sea level rise, drought and the decline of Spartina patens in New England marshes. Biological Conservation 196:173–181

Welsh AK, Burke DJ, Hamerlynck EP, Hahn D (2010) Seasonal analyses of arbuscular mycorrhizae, nitrogen-fixing bacteria and growth performance of the salt marsh grass Spartina patens. Plant Soil 330:251–266

Wimp GM, Murphy SM (2021) Habitat edges alter arthropod community composition. Landscape Ecology 36:2849–2861

Wu L, Feng S, Nie Y, Zhou J, Yang Z, Zhang J (2015) Soil cellulase activity and fungal community responses to wetland degradation in the Zoige Plateau, China. Journal of Mountain Science 12:471–482

Yang W, Zhang D, Cai X, Xia L, Luo Y, Cheng X, An S (2019) Significant alterations in soil fungal communities along a chronosequence of Spartina alterniflora invasion in a Chinese Yellow Sea coastal wetland. Science of the Total Environment 693:133548

Yeager LA, Estrada J, Holt K, Keyser SR, Oke TA (2020) Are habitat fragmentation effects stronger in marine systems? A review and meta-analysis. Current Landscape Ecology Reports 5:58–67

Zhang G, Bai J, Tebbe CC, Huang L, Jia J, Wang W, Wang X, Yu L, Zhao Q (2021) Spartina alterniflora invasions reduce soil fungal diversity and simplify co-occurrence networks in a salt marsh ecosystem. Science of the Total Environment 758:143667

Zhang B, Zhang J, Liu Y, Shi P, Wei G (2018) Co-occurrence patterns of soybean rhizosphere microbiome at a continental scale. Soil Biology and Biochemistry 118:178–186