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ARTICLE

Coastal and Marine Ecology

Can biodiversity of preexisting and created salt marshes match across scales? An assessment from microbes to predators

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Abstract

Coastal wetlands are rapidly disappearing worldwide due to a variety of processes, including climate change and flood control. The rate of loss in the Mississippi River Delta is among the highest in the world and billions of dollars have been allocated to build and restore coastal wetlands. A key question guiding assessment is whether created coastal salt marshes have similar biodiversity to preexisting, reference marshes. However, the numerous biodiversity metrics used to make these determinations are typically scale dependent and often conflicting. Here, we applied ecological theory to compare the diversity of different assemblages (surface and below-surface soil microbes, plants, macroinfauna, spiders, and on-marsh and off-marsh nekton) between two created marshes (4–6 years old) and four reference marshes. We also quantified the scale-dependent effects of species abundance distribution, aggregation, and density on richness differences and explored differences in species composition. Total, between-sample, and within-sample diversity (γ, β, and α, respectively) were not consistently lower at created marshes. Richness decomposition varied greatly among assemblages and marshes (e.g., soil microbes showed high equitability and α diversity, but plant diversity was restricted to a few dominant species with high aggregation). However, species abundance distribution, aggregation, and density patterns were not directly associated with differences between created and reference marshes. One exception was considerably lower density for macroinfauna at one of the created marshes, which was drier because of being at a higher elevation and having coarser

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substrate compared with the other marshes. The community compositions of created marshes were more dissimilar than reference marshes for microbe and macroinfauna assemblages. However, differences were small, particularly for microbes. Together, our results suggest generally similar taxonomic diversity and composition between created and reference marshes. This provides support for the creation of marsh habitat as tools for the maintenance and restoration of coastal biodiversity. However, caution is needed when creating marshes because specific building and restoration plans may lead to different colonization patterns.

KEYWORDS
diversity, estuary, restoration, salt marshes, spatial scale

INTRODUCTION

Habitat loss, degradation, and fragmentation are considered some of the main causes of species extinctions and population declines worldwide (Maxwell et al., 2016; Turvey & Crees, 2019; WWF, 2016). Aquatic organisms, especially from inland waters (e.g., streams and wetlands), are among the most imperiled (WWF, 2016), with the proportion of threatened and endangered species often exceeding those of their terrestrial counterparts (Johnson et al., 2017; Pimm et al., 1995; Strayer & Dudgeon, 2010). In this sense, there is an urgent need for enabling natural recovery or direct intervention to stop the declines in biodiversity and either maintain or restore ecosystems services that biodiversity provides (Geist & Hawkins, 2016). However, despite the increasing number of restoration projects in recent decades, comprehensive evaluations of their successes (and failures) are scarce (NASEM, 2022; Perring et al., 2015; Suding, 2011). This is particularly concerning for threatened but relevant ecosystems, such as coastal wetlands.

Coastal regions harbor around 40% of the global human population, and highly productive coastal wetland ecosystems (including tidally influenced salt marshes) provide important ecosystem services, including food provision and mitigation of impacts caused by natural disasters (e.g., storms, cyclones, and tsunamis) (Barbier, 2019; Marois & Mitsch, 2014; Sun & Carson, 2020), as well as refuge, nursery, and foraging habitats for resident and migratory species (Chabreck, 1988; McDevitt-Irwin et al., 2016). Globally, around 46%–50% of coastal wetlands have been lost, at rates 4.2 times faster in the 20th and early 21st centuries compared with the pre-industrial period (Davidson, 2014; Ramsar Convention on Wetlands, 2018; Williams et al., 2022). But rates of decline are not uniform (Davidson, 2014) and are controlled by natural and human-influenced processes, including sea level rise (Fagherazzi et al., 2020), coastal development and shoreline armoring (Gittman et al., 2015), geologic subsidence (Cahoon et al., 1995), reduction in sediment supply (Ezcurra et al., 2019), sediment dredging (Day et al., 2000; Turner, 1997), increases in the frequency and magnitude of extreme climate events (e.g., cyclones, typhoons; Babcock et al., 2019), and saltwater intrusion (Tully et al., 2019). The current rate of coastal wetland loss is alarming, especially considering our knowledge on how to restore these ecosystems is substantially lower than for terrestrial and freshwater ecosystems (Abelson et al., 2020; Craig, 2002; Suding, 2011).

The coastal wetland loss rates in the Mississippi River Delta of Louisiana (USA) are some of the highest in the world (Day et al., 2007). More than 4800 km^2 have been lost since the 1930s, with rates as high as 100 km^2/year (Couvillion et al., 2017; Day et al., 2007). An additional 4500 km^2 could be lost in the next 50 years if successful restoration measures are not implemented (CPRA, 2017). Thus far, restoration efforts in the region have included diversions to reconnect the Mississippi River to adjacent estuaries, the restitution of barrier islands, and the construction of new tidal marshes (Day et al., 2007). In 2017, a $50 billion Louisiana Coastal master plan was designed to build and maintain ~2000 km^2 of land on the Louisiana coast (CPRA, 2017). Despite the massive scale of restoration efforts to create marshes, little is known about whether these efforts will be sufficient to maintain marsh physical and ecological integrity and restore coastal habitat and lost biodiversity. A key unanswered question is whether newly created marshes harbor similar biodiversity to the preexisting, reference marshes.

Assessing and comparing diversity between created (or restored) and preexisting marshes are challenging tasks because biodiversity is both multidimensional and scale dependent (Magurran & McGill, 2011). Diversity often increases nonlinearly with spatial scale, which may lead to contrasting conclusions regarding diversity

differences among sites depending on the sampling resolution of the study (Arrhenius, 1921; Preston, 1960; Rosenzweig, 1995). In addition, diversity metrics are determined by four fundamental elements: the size of the regional species pool, the number of individuals (i.e., density) that can occur in each site, the relative abundance of different species (i.e., evenness), and the degree of intraspecific aggregation (Chase & Knight, 2013; He & Legendre, 1996; May, 1975; Preston, 1962). Consequently, biodiversity cannot be summarized into a single metric and different measures of biodiversity (e.g., richness, Shannon, and Simpson indices) are often weakly correlated (Chase et al., 2018; Hurlbert, 1971; Purvis & Hector, 2000). In this sense, assessing the contribution of the species pool, density, evenness, and level of aggregation to diversity differences may help identify the underlying mechanisms that structure communities (McGlinn et al., 2021). Unfortunately, most studies comparing diversity among sites and treatments (e.g., regions with and without management) disregard the intricate nature of biodiversity and focus on a single indicator and spatial scale (e.g., Chase et al., 2018; Perring et al., 2015).

Conclusions about biodiversity similarities between preexisting marshes and those created through restoration efforts may also vary according to the taxa studied (e.g., birds, fish, plants) because they interact with the environment at different scales and have different physiological requirements and life history strategies (Brown, 2004). For example, dispersal is a limiting factor in the colonization of created (or restored) areas (Brederveld et al., 2011). Thus, animals with high mobility (e.g., birds, flying insects, ballooning spiders, and large-bodied terrestrial species) and sessile organisms with high dispersal and growth rates (i.e., r-strategist plants) are likely to respond faster to restoration projects (Brederveld et al., 2011). Additionally, generalist species are expected to occupy created areas initially, followed by specialists and species that rely on the presence of others (e.g., top predators, parasites, and obligate mutualists; Massol et al., 2017). Belowground soil microbial communities, which would be inherited from dredged material used for marsh creation, may respond to new environmental conditions on different timescales (e.g., due to ecological carry-over effects; O'Connor et al., 2014) that could slow or accelerate plant and infauna growth (e.g., Farrer et al., 2022). As such, comparisons across assemblages may clarify whether the entire system has been restored or whether only specific ecosystem compartments have returned (Noreika et al., 2020; Pärtel et al., 2013). Examining the community through this comprehensive lens can provide a snapshot of where the created ecosystem is in the succession process and can serve as a reference for other restoration projects.

Here, we applied ecological theory to compare multiple dimensions of biodiversity across a wide range of assemblages from two created and four preexisting, reference marshes. Marshes were located within the coastal landscape of the Mississippi River Delta of southeastern Louisiana (Figure 1a). The studied assemblages included belowground soil microbes, plants, macroinfauna, spiders, nekton associated with marsh ponds (herein referred to as on-marsh nekton), and nekton associated with surrounding open waters (herein referred to as off-marsh nekton). We also quantified the scale-dependent effects of species abundance distribution (SAD; i.e., evenness), aggregation, and density on richness differences. Marsh assemblages with an equivalent number of species may still differ in their composition, which ultimately affects ecosystem function and stability (Carrick & Forsythe, 2020; van der Plas, 2019). Therefore, we conducted additional assemblage structure analysis to complement our biodiversity comparisons. The created marshes studied were constructed starting in August 2012 and completed in May 2014, four to six years prior to sampling, and are interspersed within a larger landscape of marshes at varying stages of overall health and stability. As such, we expected small differences in diversity between marsh types, but with created marshes exhibiting greater homogeneity (i.e., lower between-sample [β] diversity) and lower total (γ) and within-sample (α) diversity than reference marshes. We anticipated that assemblages with lower dispersal capability and higher sensitivity to local conditions (e.g., microbes, plants, and macroinfauna) would show greater biodiversity differences between created and reference marshes. In addition, differences between created and reference marshes are expected to be more evident at the γ scale as changes at the α scale are often more linked with biotic interactions (e.g., competition; McGill, 2010) and local specificities (e.g., elevation and proximity to marsh edge; Bertness & Ellison, 1987; Netto & Lana, 1997).

MATERIALS AND METHODS

Study area

The study area was in Plaquemines Parish on the western side of the Mississippi River and just northwest of Port Sulphur, Louisiana (Figure 1a). The area encompasses a salt marsh landscape composed of marsh platforms and their associated microhabitats (e.g., ponds, tidal creeks, and subtidal edge), as well as surrounding open waters. The climate is subtropical with hot and humid summers (mean lows: 19°C, mean highs: 32°C) and mild and short winters (mean lows: 7°C, mean highs: 19°C; Hiatt et al., 2019). The tidal area has a mean depth of 2.3 m, diurnal tides with a range of approximately 0.3 m, and turbid waters with salinities ranging from 0 to 28 PSU,
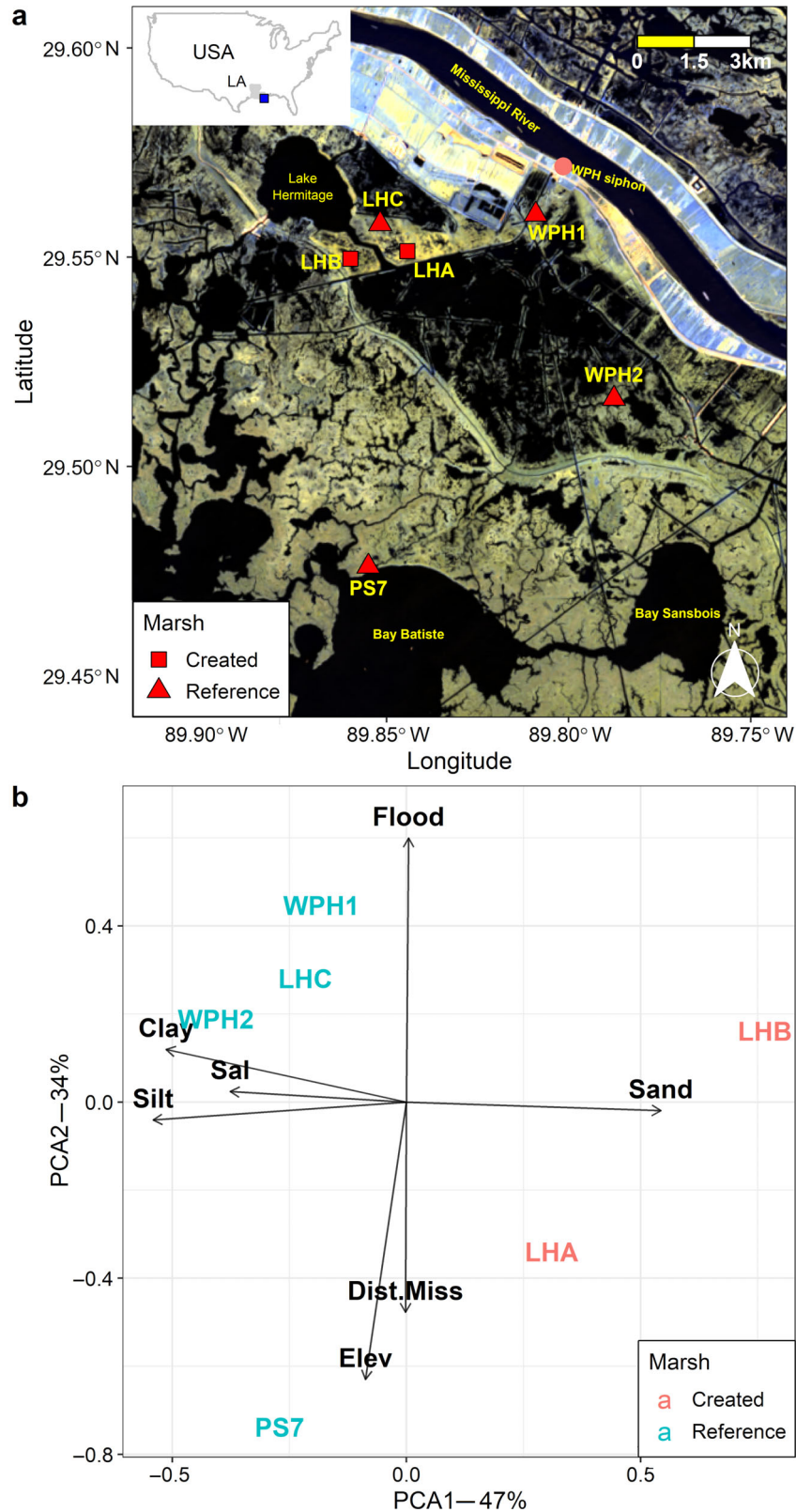
FIGURE 1 (a) Study area map indicating the general location (inset, blue square) and the specific sampled marshes (red squares and triangles). (b) Principal components analysis (PCA) showing the similarity of the sites according to five environmental variables (Elev, elevation; Dist. Miss, distance to the Mississippi River; Sal, salinity; Flood, average of the number of hours flooded; and sediment composition [clay, silt, and sand]). The PCA was run in the R package vegan (Oksanen et al., 2020) and the first two axes explained 81% of data variation. Details about the environmental variables used in the PCA can be found in Appendix S1: Table S1. LHA, Lake Hermitage A; LHB, Lake Hermitage B; LHC, Lake Hermitage Control; PS7, Port Sulphur 7; WPH, West Pointe à la Hache.

depending on freshwater input, season, and location within the region (Able et al., 2015; Conner & Day, 1987; Marton et al., 2015).

The study included two created marshes, "Lake Hermitage A" and "Lake Hermitage B" (herein referred to as sites LHA and LHB, respectively), and one reference marsh, "Lake Hermitage Control" (referred to as site LHC), that were located along the southeastern channel leading into Lake Hermitage. Three other reference marshes were nearby, within 12 km (linear distance) from each other, from the West Pointe à la Hache (WPH) siphon, "West Pointe à la Hache 1" and "West Pointe à la Hache 2" (referred to as sites WPH1 and WPH2), and from Bay Batiste, "Port Sulphur 7" (referred to as site PS7) (Figure 1a). Reference marshes were considered those that had no history of restoration, existed prior to and during the marsh creation project, and represented a continuum of potential ecological conditions and species inocula within the landscape. Moreover, because all marshes are being impacted by regional-scale processes like sea level rise and shoreline degradation (e.g., Couvillion et al., 2017; Day et al., 2007; Gittman et al., 2015), as well as invasive species colonization (Birnbaum et al., 2021), we considered the term "natural" may be misleading.

An exploratory principal components analysis (PCA; Figure 1b) using abiotic data available (see Appendix S1: Table S1) indicated that PS7 and LHA had higher elevation and therefore experience less flooding than the other marshes. The created marshes had sediments composed of coarser grain sizes (i.e., more sand) than reference marshes. A weak salinity gradient from marshes closer to Lake Hermitage (LHA, LHB, and LHC) to marshes closer to Bay Batiste (PS7) and Bay Sansbois (WPH2) was also present during the sampling time. PS7 is considerably farther from the Mississippi River when compared with the other marshes and is more exposed to persistent winds and waves from the southeast and strong cold fronts from the north and northeast.

The created marshes were established as part of the Coastal Protection and Restoration Authority's (CPRA) Lake Hermitage Marsh Creation Project (Base Project: BA-42; CPRA, 2022). The deterioration of the Lake Hermitage rim exposed surrounding marshes to stronger wave energy and prolonged tidal exchange, which led to the erosion and loss of a substantial proportion of marsh habitat in the east and south portions of the lake. From 1985 to 2006, the project area had an annual loss rate of −1.64% (CWPPRA, 2019). In 1992, the WPH siphon was constructed under the Coastal Wetlands Planning, Protection and Restoration Act (CWPPRA) program to replace the ecological functions (e.g., supply of sediment) supported by periodic over-bank flooding that occurred

prior to the placement of the Mississippi River flood control levee. This was a pivotal step for the Lake Hermitage Marsh Creation Project because sediment and freshwater provided by diversion projects facilitate the establishment and function of created salt marshes (Peyronnin et al., 2013). Noteworthy, the WPH siphon was off from 2017 to 2021, a period that encompasses our sampling surveys. Overall, ~409 ha of marsh platforms were created in the region from 2012 to 2015 by filling open water areas and fragmented marsh with dredged material from the Mississippi River. The marshes at site LHA were constructed from August 2012 to October 2013, whereas marshes at site LHB were constructed from December 2013 to May 2014. Upon project completion, gaps were made in the containment levees to allow aquatic organisms access at multiple locations and to reopen tidal channels. The areas were allowed to colonize naturally, without any planting effort (Kevin Roy, USFWS, personal communication).

Biological data collection

All biological sampling was done in May 2018. The sampling design, effort, and method varied according to the assemblage studied (see below; Table 1).

Belowground soil microbes

Microbes were sampled via 0.01-m^2 sediment cores taken along an on-marsh transect at distances 1, 10, 50, and 100 m from the marsh edge. Core samples were obtained at each distance from two soil depths, 0–2 cm and 8–10 cm. Detailed analyses were done for these two depths because microbes from shallower soil (referred to herein as "surface") would be affected by surface processes (e.g., sedimentation, burrowing, rooting) and likely have different compositions compared with deeper (referred to herein as "below surface") microbial communities that might experience more stable conditions (LaMontagne et al., 2003). Soil microbial diversity was determined after DNA extraction using a modified sucrose lysis method (Mitchell & Takacs-Vesbach, 2008; Zhou et al., 1996), following protocols described in Engel et al. (2017), and based on comparisons of retrieved V4 regions of bacterial and archaeal 16S rRNA genes to classified taxonomy according to the Silva 132 database using the mother pipeline (Kozich et al., 2013; Schloss et al., 2009). Classification to the order level was used for this study and relative abundances for each taxonomic group were determined from the total number of sequence reads per sample.

TABLE 1 Taxonomic resolution, sampling method, data type, and the total number of replicates for each assemblage analyzed in this study.

Assemblage	Taxonomic resolution	Sampling method	Data type	Spatial replicates/marsh	Total no. samplings/marsh
Surface microbes	Order	Core (0–2 cm depth)	Gene sequence count	4	4
Below-surface microbes	Order	Core (8–10 cm depth)	Gene sequence count	4	4
Plants	Species	Quadrats	Biomass	15	15
Infauna	Species/genus	Core	Individuals count	10	10
Spiders	Morphotype	Sweeps	Individuals count	1	4
On-marsh nekton	Species	Minnow trap	Individuals count	3	27
Off-marsh nekton	Species	Trawling	Individuals count	8	8

Note: For on-marsh nekton and spiders, more than one sampling was conducted in each location. For more details, see *Biological data collection*.

Plants

Vegetation was sampled along three transects covering ~100 m of marsh edge at each marsh. Along each transect, on-marsh sampling stations were present at 1, 10, 25, 50, and 100 m, beginning at the marsh edge. Aboveground plant biomass was quantified in a 25 × 25 cm quadrat at each sampling station. Stems were destructively harvested by cutting them at the sediment surface and later processed in the laboratory. Stems were separated by species, rinsed free of sediment and epiphytes, and then dried to constant mass at 70°C to determine aerial aboveground biomass (in grams) by species for each plot (Hill & Roberts, 2017).

Macroinfauna

Infauna (i.e., animals living in the marsh sediment) was sampled at distances 10 and 50 m from the marsh edge. At each distance, five replicates of benthic cores (45.6 cm^2) were taken from within an area of ~5 m^2. In the lab, samples were sieved to retain only infauna larger than 0.5 mm. Animals were then identified to the lowest taxonomic level possible (generally species/genus level) and counted.

Spiders

Spiders were collected in each marsh with sweep nets along a single 40 × 2 m linear transect perpendicular to the marsh edge. A sample was taken with a 37.5-cm diameter standard sweep net by swinging the net from side to side in a 180° arc. Live spiders were preserved in 95% ethanol immediately. Each marsh was sampled once per day (morning between 6:30 am and 10:30 am) for four consecutive days. Spiders were separated into morphotypes, which overall corresponded to genus or species level, and counted.

On-marsh nekton

On-marsh nekton, including fishes and aquatic macro-invertebrates (i.e., crabs and shrimp), were sampled from marsh ponds following methods described in detail by Able et al. (2015). Ponds are low, unvegetated areas nested within the marsh platform, which received limited water input from sources exclusive of tide and precipitation. Three ponds were sampled in each marsh. Samples were conducted on three consecutive days using three wire mesh cone traps (41 × 22 cm, 3-mm mesh, and 3-cm-diameter opening). Traps were baited with dry dog food and deployed underwater for an average of 1.3 h (SD = 0.24). Sampled individuals were identified to species level and counted.

Off-marsh nekton

Off-marsh nekton, including fishes and macroinvertebrates, were sampled from channels adjacent to the marsh platform. Samples were collected using a 4.9-m otter trawl with 38-mm mesh body and a 13-mm cod end mesh size. Eight 3-min tows, at a speed of 2–3 knots, were conducted parallel to each marsh edge. Sampled individuals were identified to species level and counted.

Data analysis

We compared the diversity among our six sampled marshes within each assemblage using the measurement of biodiversity (MoB) analytical framework outlined by Chase et al. (2018) and McGlinn et al. (2019). The MoB

approach partitions the scale-dependent changes in species diversity into SAD, the total number of individuals (density), and intraspecific spatial aggregation (spatial aggregation) using three types of rarefactions: (1) individual-based rarefaction (IBR), (2) nonspatial, sample-based rarefaction (nsSBR), and (3) spatially constrained, sample-based rarefaction (sSBR) (Chase et al., 2018; McGlinn et al., 2019, 2021). The method allowed us to calculate several diversity statistics for each marsh (see below) at α (i.e., single samples) and γ (i.e., all samples combined) scales, which are derived from IBR curves (Chase et al., 2018; McGlinn et al., 2019, 2021). Noteworthy, we converted plant biomass (in grams) values into integers to allow the calculation of individual-rarefaction curves. Although biomass is not necessarily a proxy for numerical abundance (Chiarucci et al., 1999), we considered these variables correlated and representative of similar processes.

Four main metrics were used to compare the diversity among marshes: (1) richness (S), which is the number of taxa sampled in a given area; (2) rarefied richness (S_n), which is the expected richness for a fixed number (here, the minimum number across sampling units) of randomly sampled individuals; (3) abundance, which is individuals counts (but converted to relative values to construct SAD plots and describe species dominance); and (4) effective number of species (ENS) of the probability of interspecific encounter (PIE) (herein, S_{pie}), which is the total number of equally abundant species needed to yield PIE,

$$PIE = \left[\frac{N}{N-1}\right] \times \left[1 - \sum_{i=1}^{S} p_i^2\right], \quad (1)$$

where S is the total number of species, N is the total number of individuals, and p_i is the proportion of species i (Hurlbert, 1971). S_{pie} is equivalent to the inverse Simpson index and is more sensitive to common species compared with S (Jost, 2007). S, S_n, abundance, and S_{pie} were calculated at α (${}^{\alpha}S$, ${}^{\alpha}S_n$, ${}^{\alpha}$abundance, and ${}^{\alpha}S_{pie}$, respectively) and γ (${}^{\gamma}S$, ${}^{\gamma}S_n$, ${}^{\gamma}$abundance, and ${}^{\gamma}S_{pie}$, respectively) scales. In addition to α and γ diversity estimates, we also calculated Whittaker's multiplicative β diversity (Whittaker, 1960) for three diversity metrics (${}^{\beta}S$, ${}^{\beta}S_n$, and ${}^{\beta}S_{pie}$, respectively) to assess the degree of variation among sampling units within each marsh.

We compared S, S_n, abundance, and S_{pie} diversity metrics using permutation tests ($n = 1000$). More specifically, we compared observed test statistics with null expectations generated by randomly rearranging the samplings among the marshes (Legendre & Legendre, 2012; McGlinn et al., 2019). At the α scale, ANOVA F-statistic was used as our test statistic (Legendre & Legendre, 2012). But, because there was a single diversity value per

marsh at the γ scale, we used the average of the absolute differences ($\overline{D}$) as the test statistic (McGlinn et al., 2019). $\overline{D}$ was calculated between all unique pairwise marsh comparisons, for example, for the species richness difference between LHA and PS7,

$$\overline{D}_{obs} = |S_{LHA} - S_{PS7}|. \quad (2)$$

The p value for the $\overline{D}$ test is determined using the following equation:

$$p = \text{rank}(\overline{D}_{obs})/(m+1), \quad (3)$$

where $\text{rank}(\overline{D}_{obs})$ is the number of times the m permuted $\overline{D}_{null}$ was larger than or equal to $\overline{D}_{obs}$.

Differences were considered significant if the observed test statistic fell outside the 95% confidence intervals of the null expectations (i.e., $p < 0.05$). $\overline{D}$ was also used as a measure of effect size for both α and γ scales (McGlinn et al., 2019).

Curves for IBR, nsSBR, and sSBR were used to isolate the distinct effects of spatial aggregation, density, and SAD on richness. sSBR is the most comprehensive rarefaction that reflects the effect of spatial aggregation, density, and SAD. It was generated by accumulating samples from the closest sites first. The resulting curve was an average of all possible focal sites. For on-marsh nekton, samples taken from the same location were accumulated in random order. Conversely, nsSBR is a product of both SAD and density. In this case, spatial aggregation is removed by shuffling individuals across sampling units, while keeping the same density of each sampling unit. Sampling units were then accumulated randomly. IBR accumulates individuals randomly without reference to sampling unit density and location, which isolates the effect of SAD. To isolate the density effect, we took the difference between nsSBR and IBR. Conversely, to isolate the effect of spatial aggregation, we subtracted the sSBR curve from the nsSBR curve (Chase et al., 2018; McGlinn et al., 2019). Although the size of the regional species pool, which is mostly unknown, could affect local species diversity (Chase & Knight, 2013; He & Legendre, 1996; May, 1975; Preston, 1962), the effect of SAD and the size of the regional pool of species could not be disentangled (Chase et al., 2018; McGlinn et al., 2019). However, because all our sampled marshes are in the same biogeographical region, we assumed that diversity differences among marshes would not be a product of regional pool size.

The contribution of spatial aggregation, density, and SAD to marsh richness differences was calculated by subtracting the rarefaction curves from each other following McGlinn et al. (2019). Because the importance of

density, aggregation, and SAD may vary according to the type of marsh being evaluated, we conducted pairwise comparisons of the studied marshes. Here, we focused on the absolute differences between (1) individual reference marshes (e.g., LHC vs. WPH1), (2) created and reference marshes (e.g., LHA vs. PS7), and (3) created marshes (i.e., LHA vs. LHB). We conducted these comparisons for all assemblages except spiders, for which we could not estimate the importance of spatial aggregation, density, and SAD to richness differences due to the lack of spatial replicates, which are required for sSBR.

In addition to the diversity comparisons, we measured the similarity among assemblage composition using Bray–Curtis distance. To visualize similarity among marshes, we calculated the centroids for each group and then constructed a dendrogram using ward.D's algorithm (Murtagh & Legendre, 2014). A formal test regarding assemblage similarity among marshes was conducted using a pairwise permutational multivariate analysis of variance (PERMANOVA; Arbizu, 2017). p values associated with each PERMANOVA comparison were adjusted using Bonferroni correction to control for error type I (Dunn, 1961).

All analyses and data processing were conducted in R (R Core Team, 2022). Procedures associated with the MoB analytical framework (rarefactions and comparison among S, S_n, and S_{pie}) were carried out with the package mobr (McGlinn et al., 2019). PCA and PERMANOVA procedures used vegan (Oksanen et al., 2020) and pairwise Adonis (Arbizu, 2017) R packages, respectively.

RESULTS

Surface microbes

A total of 526 taxa were detected from the 0–2 cm deep soil samples. Overall, evenness was high without a clear dominance of any taxa (Appendix S1: Figure S1). The only exception was the order Bacillales at WPH2, which had a relatively high relative abundance (24.1%). The richness of the samples was 345 ± 48 taxa (mean $\pm$ SD). S, S_n, abundance, and S_{pie} did not vary significantly (all $p > 0.05$; see Appendix S1: Table S2) among marshes, at both α and γ scales (Figures 2 and 3; Appendix S1: Figures S2 and S3). β diversity was also not significantly different among marshes ($p > 0.05$). nsSBR and IBR curves showed strong overlap among marshes, whereas sSBR indicated lower diversity at PS7 and WPH1 (both were reference marshes), especially at small sample sizes (Figure 4).

Species richness variations were mainly associated with SAD (Appendix S1: Figure S4). SAD had a positive

effect on richness, whereas the spatial aggregation effect varied from neutral to negative, and density depended on the marsh (negative for PS7 and WPH1; positive for others). Overall, there was considerable variation in the importance of aggregation, density, and SAD to richness differences (Appendix S1: Figure S5) among marshes. We found lower importance of density to explain the richness difference between LHA and LHB when compared with other pairwise comparisons, reflecting the similar abundances between these two created marshes (LHA = 480,323; LHB = 482,541).

Our hierarchical cluster analysis showed that the created marshes (LHA and LHB) were more similar to each other than to the reference marshes (Figure 5). However, the pairwise PERMANOVA suggested that the composition differences among marshes were overall nonsignificant ($p > 0.05$; Appendix S1: Table S3).

Below-surface microbes

A total of 552 taxa were detected from the 8–10 cm deep soil samples, and the richness was 350 ± 51 taxa/sample. Similar to the surface soil samples, the below-surface assemblages had high equitability levels without the dominance of any specific taxonomic order (Appendix S1: Figure S1). Although no differences were found at the γ scale, α diversity tended to vary significantly among marshes (Figure 2; Appendix S1: Table S2, Figures S2 and S3). $^{\alpha}S$ and $^{\alpha}S_n$ were lower at WPH1 and PS7 (two reference marshes) than the other marshes. Rarefaction curves confirmed this (especially sSBR), which indicated consistently lower richness at WPH1 and PS7 (Figure 4). Abundance differences among marshes were not statistically significant at both α and γ scales (Figure 3; $p > 0.05$). We also did not find significant differences in β diversity.

SAD was the most important component driving richness variation, followed by spatial aggregation (Appendix S1: Figure S4). SAD effect was positively associated with richness, whereas spatial aggregation was neutral to negative, and density depended on the marsh (negative for LHA, PS7, and WPH2, and positive for the others). We found higher importance of density to explain the richness differences between created marshes, which reflected the relatively high abundance differences (LHA = 453,648 and LHB = 543,410) between these two sites (Appendix S1: Figure S5).

Assemblages in the created marshes (LHA and LHB) were more similar to each other than to the other marshes (Figure 5). However, these differences were considered nonsignificant according to our PERMANOVA tests (Appendix S1: Table S3).
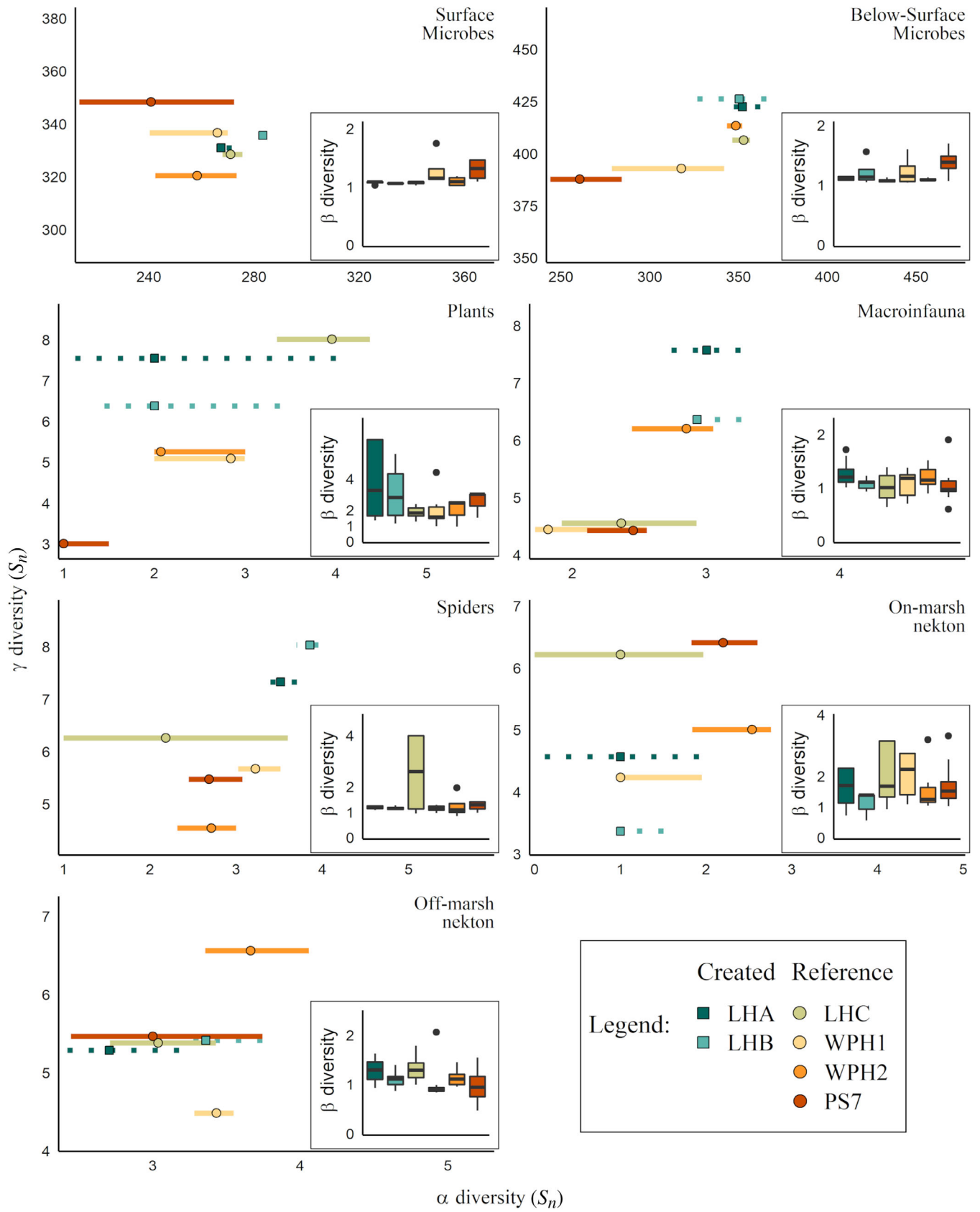
FIGURE 2 Legend on next page.

Plants

A total of 14 plant species were sampled. The species density was 2.64 ± 1.44 species/quadrat. *Spartina alterniflora* was the dominant species (relative abundance = 57.7%, frequency of occurrence = 77%), followed by *Distichlis spicata* (20%, 65.5%), *Juncus roemerianus* (9.1%, 16.1%), and *Spartina patens* (6.6%, 31%) (Appendix S1: Figure S1). All α diversity metrics varied significantly among marshes, with higher diversity at LHC and lower diversity at PS7 (Figure 2; Appendix S1: Table S2, Figures S2 and S3). Diversity metrics at the γ scale showed the same pattern observed at the α level, but, for S, the difference was marginally significant ($p = 0.08$). These results were supported by the rarefaction curves that showed consistently higher and lower diversity for LHC and PS7, respectively (Figure 4). We also found significant differences in β diversity, as created marsh (LHA and LHB) samples tended to be more dissimilar. We did not find significant differences in abundance among marshes at either α or γ scales (Figure 3).

Spatial aggregation and SAD were the most important components driving changes in plant richness (Appendix S1: Figure S4). Spatial aggregation had a negative effect on plant richness, SAD had a positive effect, and density was positive for LHC, WPH1, and WPH2, and negative for the other marshes. Pairwise comparison among marshes indicated considerable variation in the contribution of density, SAD, and spatial aggregation to species richness differences (Appendix S1: Figure S5). However, these differences did not depend on the type of marsh being compared (e.g., created vs. reference).

Plant assemblage composition varied among marshes (Appendix S1: Table S3). Dendrograms indicated two main clusters: (1) LHB, PS7, WPH1, and WPH2; and (2) LHA and LHC (Figure 5). Members of groups 1 and 2 were significantly different from each other according to PERMANOVA ($p < 0.05$). LHA and LHC also had significantly different assemblage compositions ($p = 0.04$).

Macroinfauna

A total of 37 taxa were identified. The taxa density was 5.65 ± 2.04 taxa/sample, where the dominant taxon was Oligochaeta (relative abundance = 55.6%, frequency of

occurrence = 88.3%), followed by Nematoda (16.8%, 80%), and Chironomidae larvae (6.0%, 55%) (Appendix S1: Figure S1). S varied significantly at the α scale, with WPH2 harboring the highest values and WPH1 harboring the lowest (Appendix S1: Table S2 and Figure S2). For S_n, we found significant differences among marshes at both α and γ scales (Figure 2), with higher values associated with WPH2 and the created marshes LHA and LHB. LHA, LHB, and WPH2 also had significantly higher $^γS_{pie}$ values (Appendix S1: Figure S3). $^βS_{pie}$ was significantly higher at LHA and WPH2. Abundance was lower at LHA for both α and γ scales. Rarefaction curves showed different patterns. For sSBR, WPH2 had consistently higher richness, whereas WPH1 had consistently lower (Figure 4). For IBR, LHA was consistently richer than the other marshes. Patterns for nsSBR were less clear with considerable overlap among curves.

Richness variation was mainly associated with the effect of SAD and density (Appendix S1: Figure S4). The effect of spatial aggregation on macroinfauna richness was for the most part negative; the effect of SAD was positive, and the effect of density was negative for LHA and WPH1 and positive for the other marshes. Our pairwise comparisons of marshes indicated that the importance of density depended on the type of marsh being analyzed (Appendix S1: Figure S5). Comparison between the created marshes and between created and reference marshes showed higher importance of density than comparisons among reference marshes.

The hierarchical cluster analysis separated macroinfauna assemblages into two main groups: (1) LHA and LHB (created marshes); and (2) LHC, WPH2, PS7, and WPH1 (all reference marshes) (Figure 5). Members of group 1 were considerably more dissimilar than members of group 2. Results of the PERMANOVA indicate that significant differences ($p < 0.05$) were mainly associated with differences between groups 1 and 2, corroborating the dendrogram (Appendix S1: Table S3).

Spiders

A total of 38 morphotypes were identified. *Marpissa* spp. (jumping spiders, Salticidae) were the most common, with a relative abundance of 24.6% and a frequency of

FIGURE 2 Relationship between α and γ diversity for each marsh and assemblage studied. Central points and squares represent average values, and lines indicate the first and third quartile. Created marshes (Lake Hermitage A [LHA] and Lake Hermitage B [LHB]) are highlighted with dotted lines and greenish colors. β diversity variation is also presented in the bottom left corner of each panel. In this case, central horizontal lines within the boxes are the median values; upper and lower hinges are the third and first quartiles, respectively; and whiskers indicate the largest and lowest values no further than 1.5 × interquartile range from the hinge. Data beyond the end of the whiskers (shown as individual points in the panels) are considered outliers. Diversity metrics were derived from S_n (rarefied richness). For more details about the variation of S and S_{pie}, see Appendix S1: Figures S2 and S3. LHC, Lake Hermitage Control; PS7, Port Sulphur 7; WPH, West Pointe à la Hache.
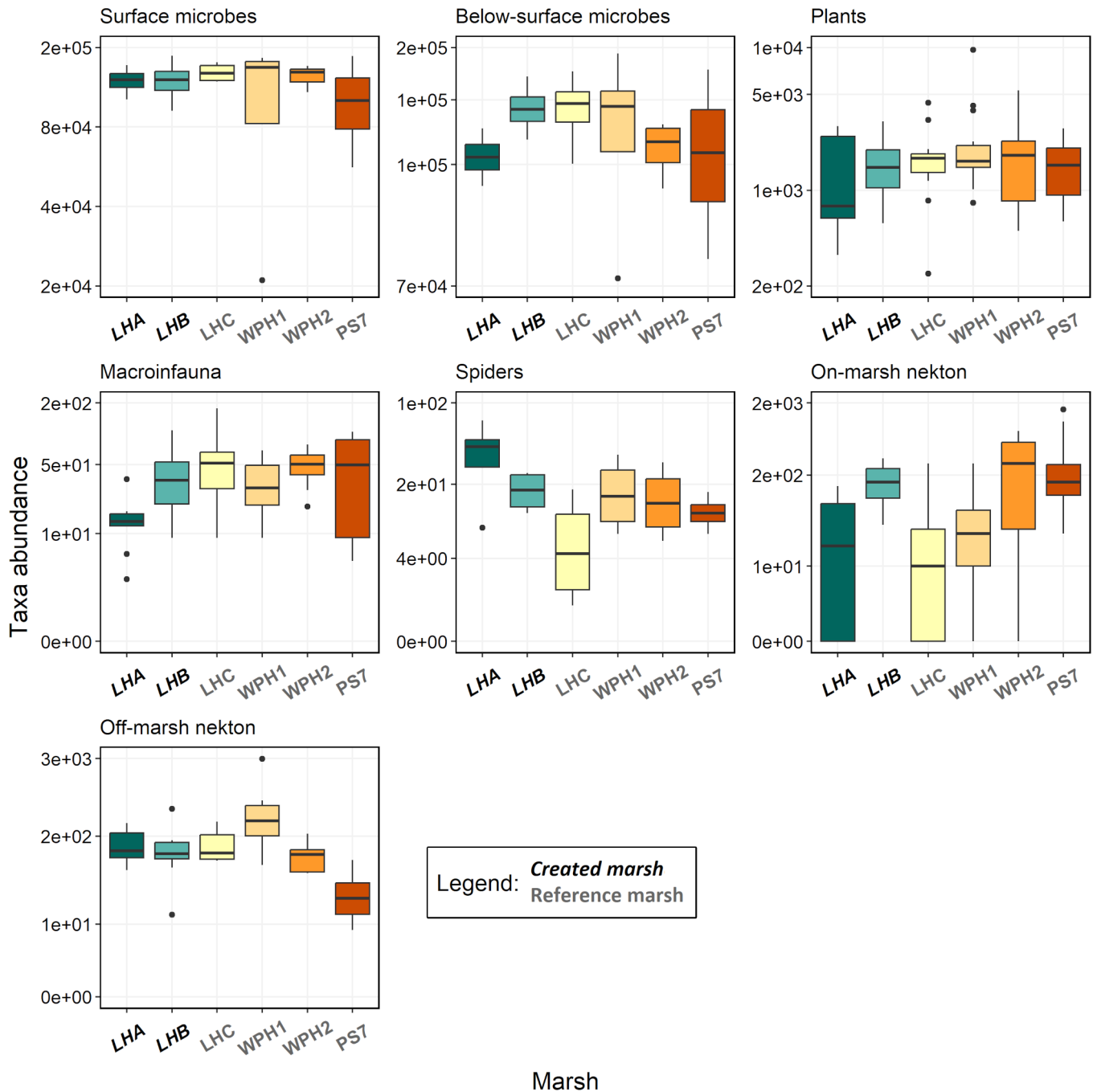
FIGURE 3 Taxa abundance among marshes and assemblages. Lake Hermitage A (LHA) and Lake Hermitage B (LHB) are created marshes (axis labels in italic and black) and Lake Hermitage Control (LHC), West Pointe à la Hache 1 (WPH1), West Pointe à la Hache 2 (WPH2), and Port Sulphur 7 (PS7) (axis labels in gray) are reference marshes. Central horizontal lines within the boxes are the median values; upper and lower hinges are the third and first quartiles, respectively; and whiskers indicate the largest and lowest values no further than 1.5 × interquartile range from the hinge. Data beyond the end of the whiskers (shown as individual points in the panels) are considered outliers. Box colors are associated with marsh identity.

occurrence of 70.8% (Appendix S1: Figure S1). Richness was 5.63 (±2.04) spider morphotypes/sweep sample. The created marshes (LHA and LHB) had significantly higher $^{\alpha}S$ than the reference marshes (Appendix S1: Table S2 and Figure S2). $^{\gamma}S_n$ was slightly higher at LHA and LHB and lower at WPH2 ($p < 0.05$; Figure 2). All other diversity metrics did not vary significantly among marshes. Abundance was significantly higher at the α scale for LHA (Figure 3; Appendix S1: Table S2). nsSBR and IBR curves indicated that LHA and LHB were richer than the other marshes, especially at larger samples sizes (Figure 4).
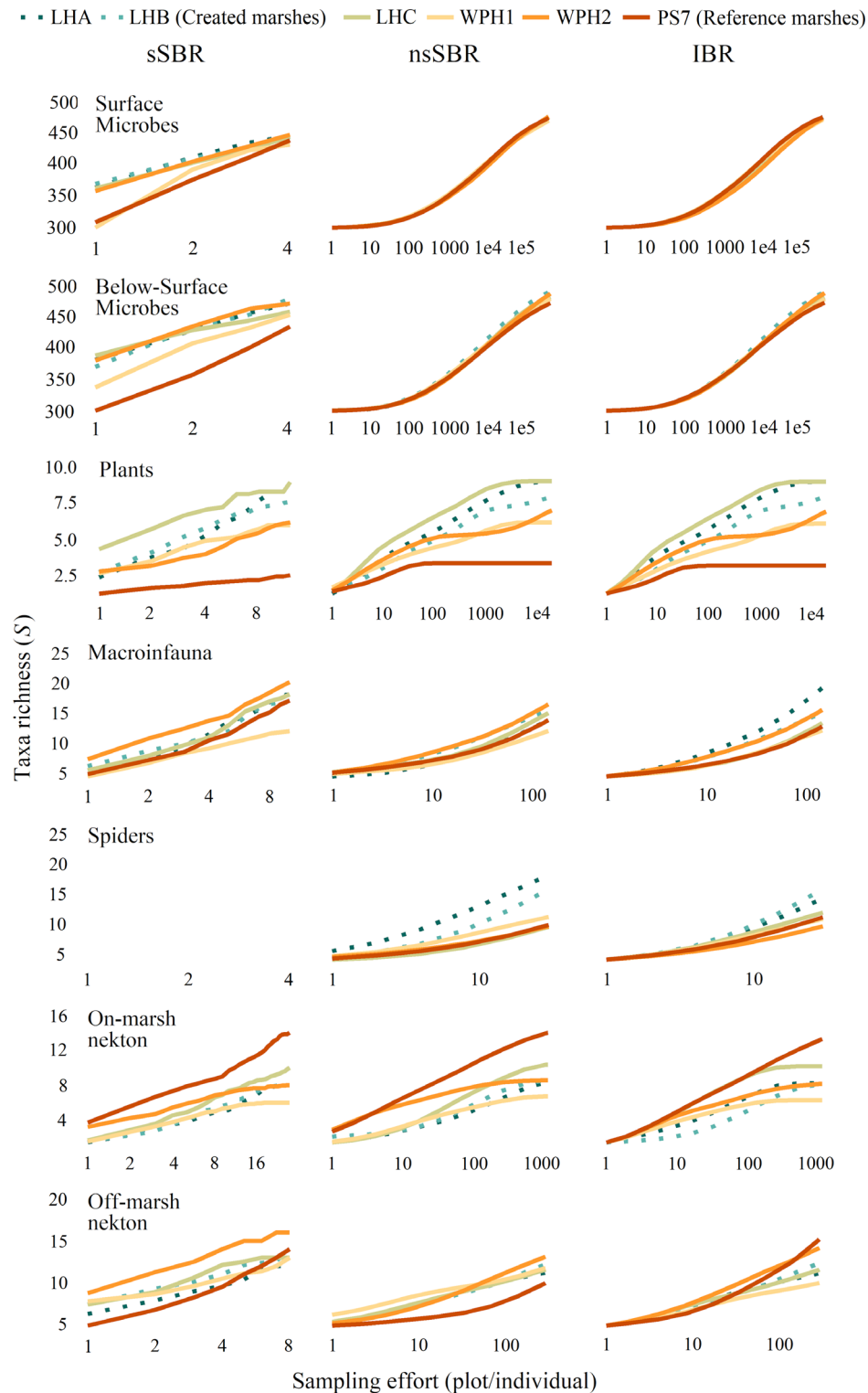
FIGURE 4 Accumulation of richness with sampling effort for created (dashed lines) and reference (solid lines) marshes and different assemblages (panels) based on spatial sample-based rarefactions (sSBR, left column), nonspatial sample-based rarefactions (nsSBR, middle column), and individual-based rarefactions (IBRs, right column). For aggregation, sampling effort is the number of plots, whereas for density and species abundance distribution sampling effort is the number of individuals. LHA, Lake Hermitage A; LHB, Lake Hermitage B; LHC, Lake Hermitage Control; PS7, Port Sulphur 7; WPH, West Pointe à la Hache.

Our PERMANOVA analyses indicated that spider assemblage compositions were not significantly different among marshes ($p > 0.05$; Appendix S1: Table S3).

Dendrograms also did not show consistent clusters, although WPH1 and WPH2 had the most similar spider assemblages (Figure 5).
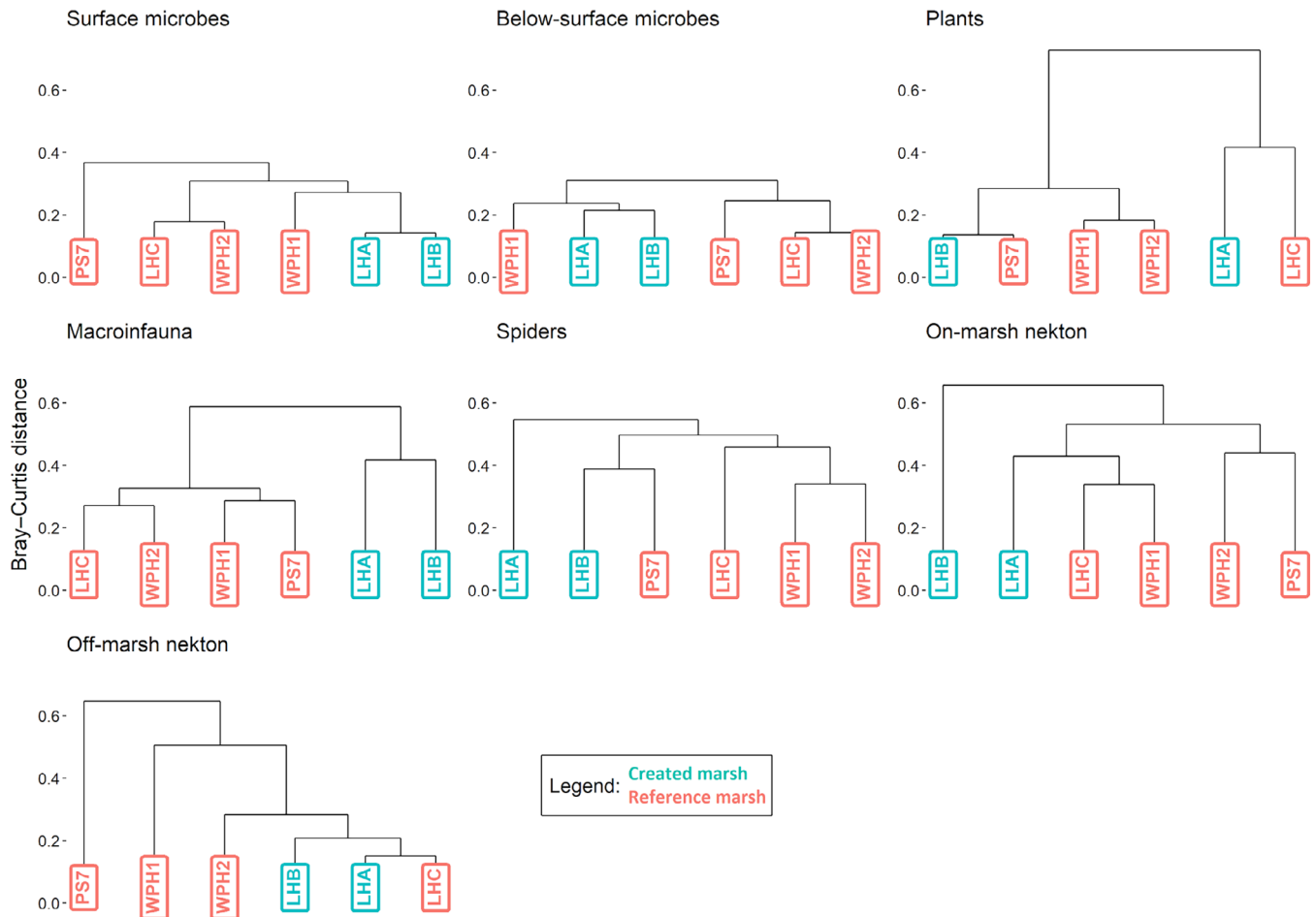
FIGURE 5 Dendrograms show the similarity among marshes for each assemblage. The dendrograms were created using the centroid of each marsh, the ward.D's algorithm, and Bray–Curtis dissimilarity. LHA, Lake Hermitage A; LHB, Lake Hermitage B; LHC, Lake Hermitage Control; PS7, Port Sulphur 7; WPH, West Pointe à la Hache.

On-marsh nekton

Seventeen species were collected in marsh ponds with minnow traps. The most abundant species were *Fundulus grandis* (gulf killifish; relative abundance = 31.7%, frequency of occurrence = 60.5%) and *Fundulus xenicus* (diamond killifish; 22.3%, 28.4%). Richness was 2.21 ± 1.72 species/sample. Overall, PS7 and WPH2 had significantly higher diversity at the α scale than the other marshes (Figure 2; Appendix S1: Table S2, Figures S2 and S3). $^{\gamma}S_n$ and $^{\gamma}S_{pie}$ were significantly lower at the created marshes (LHA and LHB). Abundance was significantly higher for PS7, WPH2, and LHB at both α and γ scales. β diversity was significantly lower for WPH2 when analyzing S and lower for LHB when analyzing S_n and S_{pie}. Cumulative curves for LHA and LHB tended to be positioned lower in our rarefaction analyses, but this lower diversity pattern was inconsistent, as the LHA and LHB lines overlapped with the lines of the other marshes

along the sampling effort gradient (mainly WPH1 and WPH2) (Figure 4).

SAD was the most important component driving changes in species richness (Appendix S1: Figure S4), followed by spatial aggregation. SAD had a positive effect on on-marsh distribution, whereas the effect of spatial aggregation was negative; the effect of density was negative for LHB, WPH2, and PS7, and positive for the other marshes. Variation in the importance of SAD, density, and spatial aggregation did not depend on the type of marsh being compared (e.g., created vs. reference pairwise comparison; Appendix S1: Figure S5).

According to PERMANOVA, all marshes were considered distinct from each other in terms of on-marsh nekton assemblage composition (Appendix S1: Table S3). The dendrogram suggested that LHB was the most unique marsh (Figure 5). LHC and WPH1 (both reference marshes) and LHA (created marsh) were more similar to each other than to PS7 and WPH2 (both references marshes).

Off-marsh nekton

We collected 28 species with trawl nets. Richness was 7.06 ± 1.81 species/trawl. The dominant species were *Brevoortia patronus* (gulf menhaden; relative abundance = 36.6%, frequency of occurrence = 37.5%), *Farfantepenaeus aztecus* (brown shrimp; 30.2%, 100%), *Anchoa mitchilli* (bay anchovy; 11.9%, 77.1%), *Micropogonias undulatus* (Atlantic croaker; 8.2%, 92%), and *Leiostomus xanthurus* (spot; 7.3%, 87.5%) (Appendix S1: Figure S1). PS7 had the lowest $^{\alpha}S$ ($p < 0.05$), which was compensated by an increase in $^{\beta}S$ (Appendix S1: Figure S2). No significant differences were found for S_n and S_{pie}, except for $^{\beta}S_{pie}$ that tended to be higher at the Lake Hermitage area, which included the created marshes (LHA and LHB) and the reference LHC (Figure 2; Appendix S1: Figure S3). Abundance was significantly higher at WPH1 and lower at PS7 at both α and γ scales (Figure 3). Overall, rarefactions curves showed strong overlap, except for a consistent higher richness for LHA at sSBR and consistently lower richness for PS7 at nsSBR (Figure 4).

SAD was the most important component associated with species richness variation, followed by density (Appendix S1: Figure S4). SAD had a positive effect on off-marsh nekton richness; the effect of spatial aggregation varied from neutral to negative, and the effect of density was positive for WPH1 and negative for the other marshes. Contributions of SAD, spatial, aggregation, and density for off-marsh nekton varied considerably depending on the marshes being compared (Appendix S1: Figure S5). Density tended to be less important to explain richness differences between the created marshes due to their high abundance similarity (LHA = 1262, LHB = 1232).

Our composition analyses suggested a close similarity among all Lake Hermitage sites ($p > 0.05$; Figure 5; Appendix S1: Table S3). WPH2 was also not significantly different than the created marshes or LHC. WPH1 and PS7 were the most dissimilar off-marsh nekton assemblages, with significant differences in most of the other marshes.

DISCUSSION

Coastal wetland restoration projects along the Louisiana coast have successfully rebuilt land that can be used to support and sustain diverse species, including those vital to recreational and commercial fisheries (CPRA, 2017). However, restoration efforts have not typically assessed whether created marsh biodiversity matches that of preexisting marshes (e.g., Perring et al., 2015). For this study, we evaluated multiple dimensions of biodiversity and assemblage structure from soil microbes to on- and

off-marsh nekton (i.e., predators) for two created marshes and four reference marshes to determine whether there were biodiversity differences, and which taxonomic assemblages may explain those differences. We expected there to be limited diversity differences between created and reference marshes because the recently created marshes were interspersed within the existing coastal landscape. We hypothesized that assemblages with lower dispersal capability and higher sensitivity to local conditions (e.g., microbes, plants, and macroinfauna) would show greater biodiversity differences and anticipated that created marshes would exhibit greater species and assemblage homogeneity and lower total α and γ diversity than the reference marshes.

We observed relatively high diversity in the created marshes compared with reference marshes across some taxonomic groups and measured limited differences in the diversity of assemblages between the created and reference marshes. As such, the created marshes may be considered an important habitat for the local biota. High colonization success and rapid community establishment for created marshes could be due to the marshes having high connectivity within the landscape (Sundermann et al., 2011; Wolters et al., 2008), as well as generalist, opportunistic, and *r*-strategist organisms having high dispersal and growth rates to respond faster and occupy created habitats (Brederveld et al., 2011; Keppeler et al., 2021; Lurgi et al., 2012; Massol et al., 2017), and increased tolerance among some taxa to suboptimal environmental conditions (Garbutt et al., 2006; Mazik et al., 2010; Wolters et al., 2005). For example, we found a higher abundance of crowngrass (*Paspalum* spp.), a pioneer plant genus that occupies disturbed and sandy sites, at LHA and LHB. Similarly, on-marsh nekton assemblage diversity at the created marshes was mainly associated with the dominance of Gulf killifish, a generalist fish with broad environmental tolerances (Crego & Peterson, 1997; Rozas & LaSalle, 1990).

Diverse estuarine assemblages (e.g., microbes, plants, macroinvertebrates, and fishes) tend to be tolerant of severe environmental stress (Elliott & Whitfield, 2011; Stevens, 1989), such as oil spills (Able et al., 2015; Engel et al., 2017; Fleeger et al., 2020; Fodrie et al., 2014; Fodrie & Heck, 2011; McCann et al., 2017; Zengel et al., 2022) and hurricanes (Chen et al., 2020), although there can also be high and fast turnover of species and diversity in estuaries due to salinity gradients (Elliott & Whitfield, 2011; Watson & Byrne, 2009; Whitfield et al., 2012). Both LHA and LHB were located near Lake Hermitage and the Mississippi River, a region with lower salinity levels that experiences weaker storms coming from Barataria Bay and the Gulf of Mexico compared with other marshes. The most distant marsh to the Mississippi River in our study, PS7,

had lower diversity in most assemblages, including soil microbes, macroinfauna, plants, and off-marsh nekton. In this sense, one may argue that the location of the created marshes to the Mississippi River contributed to the relatively fast colonization and establishment of local species. On the other hand, LHC, which was located in Lake Hermitage and close to LHA and LHB, did not have consistently higher diversity values than the created marshes, suggesting some level of equivalence between created and reference marshes.

Diversity comparisons depended on the spatial scale, as evidenced from rarefaction curves that crossed in all assemblages studied, and the contribution of spatial aggregation, density, and SAD to diversity differences that varied greatly for some assemblages but tended to be similar between created and reference marshes. Sampling scale can change conclusions about the direction and magnitude of biodiversity differences because different factors operate at different spatial scales (Chase et al., 2018), so nonlinear changes in species accumulation should be expected. Biotic interactions tend to be more relevant at small scales, whereas environmental filtering processes operate at larger scales (Levin, 1992; McGill, 2010; Wiens, 1989). This is especially evident for groups such as spiders and some marsh fish (e.g., mosquito fish, topminnows) that have territorial behavior (Marshall & Rypstra, 1999; Sutton et al., 2012) or plants that form monodominant patches (Emery et al., 2001). In these cases, the effect of marsh type (created vs. reference) is expected to be more evident at γ scales because α scale richness would be lower due to competition. Spatial aggregation was important for plants, as our quadrat-based assessments revealed dominance by a single or few plant species. Plant distribution is tightly controlled by salt marsh zonation due to physical conditions and stress (e.g., inundation, temperature, salinity, nutrient availability) and interspecific competition (Emery et al., 2001; Hill & Roberts, 2017; Zengel et al., 2022). Conversely, macroinfauna and on-marsh nekton had important components associated with density. Density effects are often linked with the so-called "more-individuals hypothesis" (Srivastava & Lawton, 1998; Storch et al., 2018; Wright, 1983), as increased productivity leads to higher resource availability (i.e., higher carrying capacity, K) and, consequently, to an increased number of individuals and species. However, the effect of density varied from positive to negative depending on the marsh, which may suggest that other ecological processes may be involved (e.g., productive areas with low habitat/resource diversity supporting few abundant species). Significant SAD contribution was present in most assemblages due to changes in species proportion among marshes. Changes in SAD may be related to different nonexclusive hypotheses, including changes in

competitive dominance, environmental filtering, and even dispersion (McGlinn et al., 2021). These processes are, unfortunately, hard to disentangle without further field experiments.

We found evidence that microbes and infauna assemblages at the two created marshes, LHA and LHB, were more similar to each other than to reference marshes. Density explained some richness differences, especially for macroinfauna that had consistently lower abundance at LHA. The assemblage structure differences could reflect a relatively weak species sorting process related to the soil substrate. The created marsh soils were mainly composed of sand, which holds less water, contains fewer nutrients and lower organic matter content, is less stable for burrowing fauna, and is often related to earlier successional stages (Castillo et al., 2021; Luzier, 2017). Moreover, LHA also had a higher elevation compared with the other marshes, which would contribute to a drier and potentially less productive marsh environment. Microbial assemblage differences between created and reference marshes may alter basic ecosystem functions because microbes serve as food sources for higher trophic levels within the marsh food web, as well as play essential roles in biogeochemical processing and ecosystem development, including (but not limited to) organic carbon decomposition and recycling, nitrogen fixation, gas transport, sediment cohesion, establishing and maintaining redox conditions, and forming symbiotic associations with plants and other fauna (e.g., Abbott et al., 2022; Bodelier & Dedysh, 2013; Farrer et al., 2022). Similarly, macroinfauna are also an important element of marsh food webs because they regulate nutrient recycling, sedimentary processes via bioturbation, and serve as a source of energy to larger animals, among other processes (Adam, 1990; Fleeger et al., 2020). In this sense, differences in microbial and macrofauna assemblage structure and lower macroinfauna abundance may affect marsh functioning and propagate to other food web levels. Previous studies have raised questions about the relevance of created marshes to biodiversity since they often lack the topographic diversity needed to support different microhabitats (e.g., creek, ponds, hummocks; Lawrence et al., 2018) and may contain different community compositions and functions (Mossman et al., 2012). Although the differences were subtle in our study, our results highlight the fact that the basic build structure (e.g., elevation, substrate composition) of created marsh platforms may lead to different colonization patterns at the microbial level and for soil macroinfauna due to carryover diversity and their responses to newly established conditions (e.g., O'Connor et al., 2014). This could have important implications for biological conservation within coastal systems.

In conclusion, the statistical framework used in this study (MoB; McGlinn et al., 2019) provided a robust approach to compare the diversity among marshes that could be used in future studies to assess the efficiency of restoration projects. We demonstrated that the general taxonomic biodiversity of created salt marshes, which began with dredged material, was comparable to reference salt marshes in southern Louisiana within the Mississippi River Delta after four to six years. Recent billion-dollar efforts and similar types of projects to contain land loss (CPRA, 2017; Day et al., 2007) are likely to benefit coastal biodiversity maintenance and restoration. However, it still remains to be seen whether created marshes maintain diversity at metacommunity scales. For example, do created sites function as a source or sink for population growth in salt marsh landscapes? Answering this question will be essential for understanding the extent to which created marshes contribute to improving the overall ecological integrity and ecosystem services at larger scales. Future studies that focus on functional and phylogenetic approaches are needed to better understand the link between diversity and ecosystem processes in salt marshes (Flynn et al., 2011). Moreover, additional investigations should consider potential sources of bias in our study. First, the study area was in the Mississippi River Delta, a region that has been historically influenced by fisheries (Grimes, 2001) and anthropogenic impacts, including high nutrient loads (Rabalais et al., 2002), regulation and channelization of the Mississippi River discharge (Day et al., 2007), and oil spills (Fleeger et al., 2020). In this sense, although the studied reference marshes formed naturally via vertical accretion controlled by inorganic sedimentation and biomass production and decomposition (FitzGerald & Hughes, 2019), they may not be considered completely pristine references. Arguably, the concept of "pristine" ecological baselines is untenable given the extent of global changes (Kopf et al., 2015), and many restoration projects are carried out in areas of human-induced stress precisely because of the large anthropogenic effects. In this context, our study and others like it are increasingly relevant for assessing the efficiency of created marshes and restoration efforts more generally. Second, although differences found among marshes are legitimate because our sampling design was standardized within assemblages, sampling design and effort, as well as taxonomic resolution, were not standardized among assemblages. Thus, the responses for different assemblages to marsh type cannot be attributed only to a specific assemblage's peculiarities, but also to sampling effects and taxonomic resolution. Finally, our study took place in a single year and after relatively short timescales in the marsh creation timeline. Currently, marsh creation projects in Louisiana are generally scoped for a moderate future scenario of relative sea level rise to result in no net land loss after approximately 20 years and achieve land gains after 30 years (Khalil & Raynie, 2015). This means that restoration may be slower than the rate of land loss over time, and that created marshes are temporary phenomena within the landscape where species can be maintained but not buffered from climate change and its impacts on sea level rise, increases in the frequency of extreme climate events, rising temperatures, and the spread of invasive species (e.g., Birnbaum et al., 2021; Scanes et al., 2020; Törnqvist et al., 2020). As such, there is concern that the integrity of the marsh landscape and maintenance of the regional pool of native species are still at risk. Additional long-term studies are needed to assess the biodiversity changes of all marshes, not only created ones, to improve our understanding of what changes to the salt marsh landscape will occur in the future.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

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

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