

Article

Shifts in Macrobenthic Assemblage on Red Mangrove (*Rhizophora mangle* L.) Prop Roots Along a Latitudinal Gradient

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Abstract

Mangrove prop root epifaunal communities support coastal biodiversity by providing habitat and refuge for associated sessile species and contributing to larval supply. Yet, regional surveys across latitudinal gradients in southeast Florida remain scarce. Understanding how these communities vary spatially and temporally is essential for forecasting biodiversity responses to environmental change. This study tested how macrobenthic assemblage composition and beta diversity on red mangrove prop roots vary from Key West to Melbourne, Florida. Presence-absence data from 32 sites in four zones were analyzed using beta diversity partitioning, indicator species analysis, and temporal turnover metrics. A strong biogeographic boundary near Palm Beach County delineated a species-rich southern pool, formed by the Florida Keys and Miami-Dade and characterized by tropical sponges. Of the 41 indicator species, 34 were associated with these two southern zones, while neither northern zone had exclusive indicators. Northern beta diversity was dominated by nested subsets of a larger species pool rather than species replacement. Over the three years, only Broward-Palm Beach gained species, while the other three zones lost species, though this was not statistically significant. These findings highlight the ecological significance of the potential biogeographic ecotones and provide a baseline study from which to gain insight into how climate-driven mangrove range expansion may impact coastal biodiversity and ecosystem resilience.

Keywords: mangrove; *Rhizophora mangle*; epifauna; β -diversity; LCBD; SCBD; latitudinal gradient; Sørensen partitioning; community ecology; Florida



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1. Introduction

Mangrove forests in Southeast Florida, although extensive, exhibit varying levels of intactness, with some areas showing sparse or absent trees [1]. The overall trend of habitat fragmentation is seen throughout the globe, and its impact is especially noticeable in marine environments, which are highly sensitive to phenological and ecological alterations [2–4]. Throughout the tropics and subtropics, mangrove trees act as the primary foundation species that dominate the intertidal zone [5]. Here, systemic shifts have cascading effects on the food web, productivity, and event timing. In particular, red mangroves (*Rhizophora mangle*) play a crucial role by acting as substrate for sessile species within their ecosystems [6–8]. As mangrove trees migrate further north, they bring with them new habitat structure as well as their associated epifaunal species [9–11]. On the east coast of Florida, the historic northern range of mangroves has doubled as a consequence of climate change [12].

Changes in community structure are not limited to new mangrove habitat; climate change will also affect what species are found on prop roots within a region. One example is the novel use of mangrove prop roots by corals as refuge and protection from bleaching events [2,13]. In addition, mangrove prop roots may act as a refuge for species that are outcompeted in reef systems or as climate change requires species to seek new suitable habitat [14]. Climate change is causing shifts in the geographic distribution of species and forcing ecosystem changes, such as alterations in temperature, dissolved pCO₂, precipitation, sediment supply, sea level rise, and tidal inundation [15–19]. The presence of the Gulf Stream has caused the eastern coastline of the United States to warm two to three times faster than the global mean [20]. Warmer waters are associated with changes in larval dispersal patterns [21]. These macroclimate drivers coupled with ‘tropicalization’ may not allow for the return to historic ecosystem states. The consequences for prop-root macrobenthic assemblages along latitudinal gradients are not well understood.

Despite their tremendous ecological importance, mangrove ecosystems are estimated to have decreased by 35% worldwide [15,22]. This degree of habitat loss is even greater than that in rainforest ecosystems [22]. While we are still learning the extent of the importance of mangrove ecosystems, habitat loss is ongoing. Mangroves are proving to be especially important in counteracting several effects of climate change, such as the reduction in wave action during storms [23,24], sediment accretion [25], refuge for corals [2,13], acting as carbon sinks [26,27], and many more ecosystem services and functions. Another key ecosystem service provided by mangroves is habitat for sessile species [28,29].

Animals residing on mangrove prop roots are extremely varied, and some are classified as vulnerable or threatened [30]. In estuaries, mangroves are one of the few natural hard surfaces to which larval supplies can attach. Without mangroves, critical hard surfaces would not exist in estuarine mudflats and biodiversity would suffer. Mangroves not only provide habitat but may also provide an enhanced food source, thereby allowing a more complex food web [15,31,32]. Animals found on mangrove prop roots include sponges, oysters, barnacles, ascidians, polychaetes, sipunculids, and bryozoans [28,33–36]. Mangroves host many other taxa, including fish, elasmobranchs, reptiles, amphibians, insects, rodents, birds, Key deer, and more [1,28,37–41].

However, despite these ecological shifts, broad-scale latitudinal characterizations of macrobenthic assemblages on red mangrove prop roots, particularly concerning their community structure and diversity partitioning, remain limited. Providing information on how community composition on red mangrove prop roots changes along the latitudinal gradient and how it changes between the years of the study furnishes a historical baseline for comparison against future shifts [42]. The core objectives of this study were to establish how the macrobenthic assemblages differ in composition among the four latitudinal zones of southeast Florida (Florida Keys, Miami-Dade, Broward-Palm Beach, and Martin-Indian River) and parcel out how much species replacement or nestedness drives those changes. Additionally, the study was designed to examine which sites and species contribute disproportionately to the among-zone β -diversity.

2. Materials and Methods

2.1. Study Sites

The 2013 survey covered 32 sites along 515 km of southeast Florida coastline from Key West (24.56° N) to Melbourne Shores (27.96° N), with sites grouped into four latitudinal zones: Florida Keys ($n = 4$), Miami-Dade ($n = 5$), Broward-Palm Beach ($n = 7$), and Martin-Indian River (southern Indian River Lagoon; $n = 16$) (Figure 1). Eighty candidate sites were visited, and 32 met the requirements and were used in the presence and absence study. Each study site had to meet several factors for inclusion in the survey, namely 500 m of

uninterrupted fringe mangrove shoreline, water salinity of 30 to 38 psu, and water clear enough for the species on the mangrove prop roots to be identified and photographed. Mangroves dominate much of the intertidal zone throughout the study area, though with some patchiness, and sites that did not meet these requirements or that were not accessible for permitting or other reasons strongly influenced site selection. Sites were not controlled for differences in tidal fluctuations or other oceanographic characteristics. The four latitudinal zones are a structural part of this study's design, derived in a companion paper [36] and used here to delineate compositional shifts in biodiversity. The same protocol was applied to the 2014 ($n = 5$) and 2015 ($n = 7$) surveys.

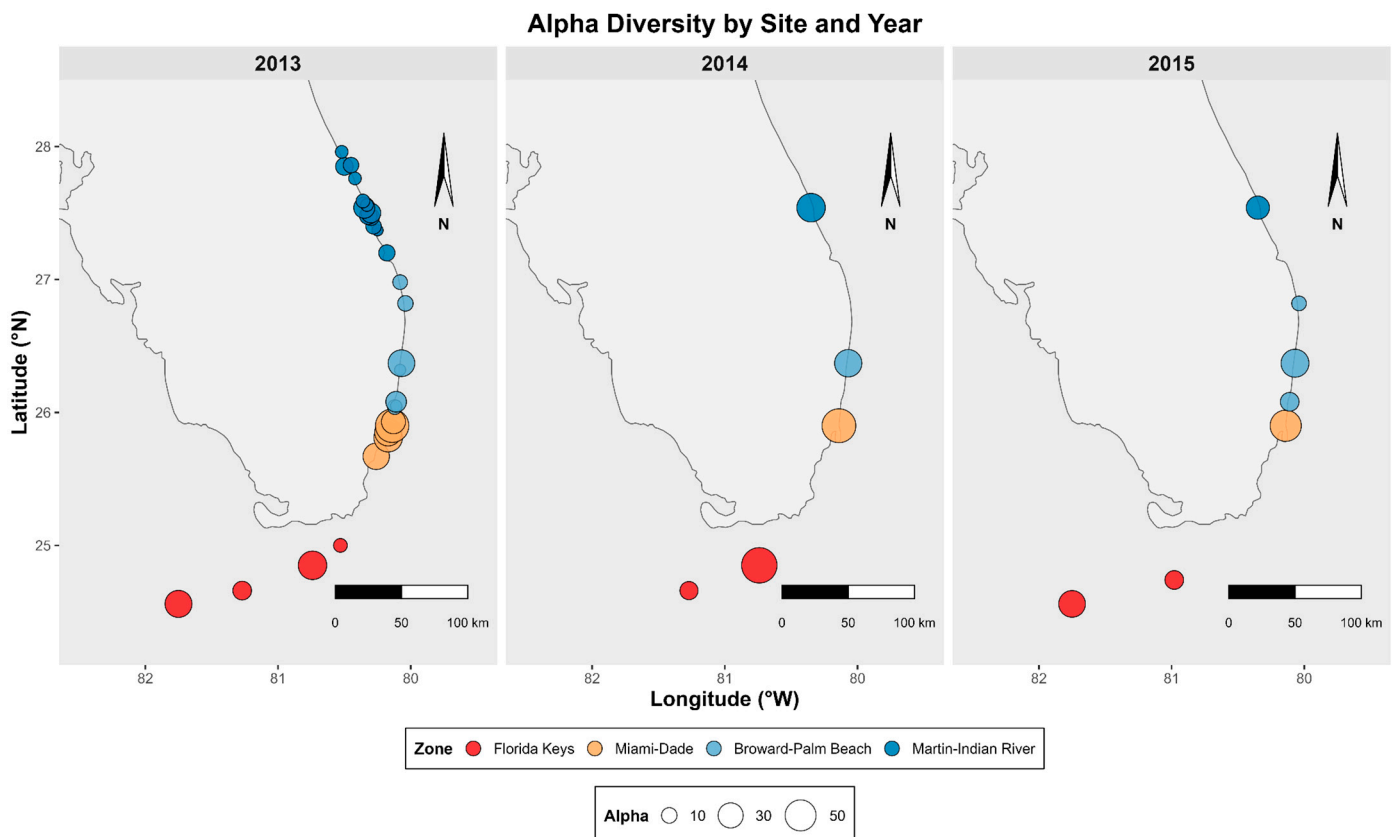


Figure 1. Study sites and alpha diversity by site and year. Sites are plotted at their coordinates, with exact locations found in Table S8. The three panels show 2013 ($n = 32$ sites), 2014 ($n = 5$), and 2015 ($n = 7$). Bubbles are sized by species richness (alpha) and colored by latitudinal zone. The Florida Keys are red, Miami-Dade orange, Broward-Palm Beach light blue, and Martin-Indian River dark blue.

In eastern Florida, the continental shelf gets narrower with increasing latitude [43]. Latitude, species composition, and the possibility of the same larval supply origin were used to indicate that sites belonged to a particular zone. Established latitudinal boundaries for estuarine macroinvertebrate communities have placed Palm Beach County as a tropical to temperate biogeographic change point [44]. Previous benthic surveys have found a distinct compositional change between 25° and 27° latitude [44,45].

2.2. Sampling Methods

The 32 sites were visited at low tide from May to October 2013, during the warmer months when the benthic sessile community is actively growing and most developed [46]. At each site, two transects examined 50 prop roots at 2 m intervals along a 100 m transect of fringe mangrove forest [47]. Transects were not constrained to straight lines but instead

followed the natural contours of the mangrove forest. Although the sites were visited at low tide, tidal inundation was not controlled, so at some trees the prop roots remained submerged even at low tide. This was a between-site and within-site variable that was not controlled for. Organisms on each prop root were identified in situ and organized into taxonomic groups. The survey was non-destructive, and samples of the organisms were not collected, which limited the ability to identify some organisms to the species level. Specimens that could not be identified in the field were photographed for later identification. A single observer was present at all but one site visit. Extensive photographs were taken at that site. The majority of site visits included more than one person surveying.

2.3. Taxonomic Resolution

Due to the limitations of the non-destructive survey methods, taxonomic resolution varied even within a taxonomic group. Bivalves were all identified to species level, except for a scallop specimen that was identified to the Superfamily Pectinoidea. Sponges, ascidians, and anemones were typically identified to the family or species level. Bryozoans were identified to species level, though microscopy is often needed for some bryozoan identifications. All specimens in class Polychaeta were identified to species level. Only one Oculinidae specimen was observed, and identification beyond family was not achieved. Across the sponges, ascidians, and bryozoans, some individuals could not be identified further, eight sponges too small to identify, two unknown ascidians, and seven bryozoans lacking microscopy, but each was clearly separable as its own species and was retained in the richness counts. The validity of the classifications was checked against the World Register of Marine Species and the World Porifera Database. A total of 103 taxa were identified over the three years.

2.4. Statistical Methods

2.4.1. Diversity and Sampling Adequacy

Species richness/alpha diversity was calculated for each site. The null hypothesis (H_0) was that species composition on red mangrove prop roots does not differ among the four latitudinal zones. This was tested with PERMANOVA on the pairwise Sørensen dissimilarity matrix. Rejecting the H_0 led to the further analyses reported below, which were exploratory rather than specified in advance.

To assess sampling, species accumulation curves were computed for the pooled 2013 surveyed sites and for each of the zones using 100 permutations. The richness was estimated using Chao and Jackknife (first and second order) estimators to account for rare species and undetected biodiversity. The 2014 and 2015 study years lacked sufficient sampling for meaningful analysis.

2.4.2. Shared Species Across Zones

Indicator species analysis, utilizing 999 permutations, was conducted on the zone classification found from the 2013 survey [48]. Species deemed significant at $\alpha = 0.05$ constitute the inferential results, while those with marginal associations ($0.05 < p \leq 0.10$) are also listed in Table S4 as suggestive associations. The IndVal.g (group-equalized) statistic was used to correct for unequal sites per zone (Florida Keys = 4, Miami-Dade = 5, Broward-Palm Beach = 7, Martin-Indian River = 16 in 2013). Despite this correction, the statistical power for detecting indicators of the smaller zones is reduced, and individual zone-exclusive indicators with B-values from a few sites should be interpreted as consistent with broader compositional patterns rather than as independent species-level claims. Additionally, indicator species need to be frequent within a zone and found almost exclusively in it.

2.4.3. Spatial β -Diversity Partitioning

Total beta diversity was found using a pairwise Sørensen dissimilarity matrix, which has a linear relationship and depends on the proportion of species shared between sites [49–51]. The Sørensen index was used because it weights the species occurring in both samples more strongly [51]. β -diversity was explored using presence and absence data because the use of abundance data makes it difficult to separate nestedness from turnover, as abundance-based dissimilarity combines species turnover with balanced changes in abundance [52]. The Simpson dissimilarity index was used to describe spatial turnover because it does so without the inclusion of species richness gradients [53,54]. Species turnover looks at species loss where replacement is by a different species. The nestedness-resultant dissimilarity was measured in order to look for site differences that may occur simply because one or more species are missing [55]. The nestedness-resultant examines species presence in terms of species present at a site that are nested within the species present at another site, the lost species are not replaced, and the remaining species can be found at the other sites. Additionally, gamma diversity was calculated for each zone and the entire survey area.

To standardize sampling efforts for year 2013 across zones (Florida Keys $n = 4$, Miami-Dade $n = 5$, Broward-Palm Beach $n = 7$, Martin-Indian River $n = 16$), bootstrap β -diversity was computed by subsampling sites without replacement to the zone with the smallest number of sites sampled minus one ($n = 3$), with 1000 iterations. Three sites were used rather than four because the Florida Keys contained only four sites. A subsample of four would have drawn the same four sites in every iteration and returned no sampling variance for that zone. Sampling with replacement was not used because this would allow picking the same site twice, making a zone appear more similar than it really is, and in turn affecting the beta diversity calculations.

2.4.4. Permutational Tests and Geographic Structure

Permutational multivariate analysis of variance (PERMANOVA) was used to test whether community composition changed across the latitudinal gradient. PERMANOVA was applied to the Sørensen distance matrix with zone identity as a predictor. Since PERMANOVA can be sensitive to heterogeneity in the data within a group, PERMDISP was also run to ensure that the results were not due to within-zone variation. Principal coordinates analysis (PCoA) was performed using the Sørensen dissimilarity matrix to visualize the compositional differences among zones. The ellipses represent one standard deviation around the centroid for each zone. All tests used 999 permutations, with significance assessed at $\alpha = 0.05$. To determine if these differences were simply a result of distance between the sites, Mantel tests compared geographic distance against the Sørensen distance matrix using 999 permutations and Spearman rank correlation. The compositional distance was broken down into turnover and nestedness components, with each tested separately.

2.4.5. Local and Species Contributions to β -Diversity

To identify the sites and species contributing most to overall β -diversity, the Local Contribution to Beta Diversity (LCBD) and Species Contribution to Beta Diversity (SCBD) were computed [56]. LCBD was computed within each survey year separately using a Hellinger transformation and 999 permutations to identify sites that were unique within a given year. The permutation test introduces stochastic variation in p -values for sites with marginal LCBD, and the reported p -values come from a single run with 999 permutations. To test for stability 100 runs were completed. The per-site D component from the temporal TBI analysis was additionally used as a temporal LCBD to identify zones in which the

between-year compositional change was exceptional. The Holm-Bonferroni correction method was used to correct for repeated testing [57]. To identify the key drivers of these community shifts, SCBD was calculated from the same 2013 decomposition.

2.4.6. Temporal β -Diversity

Temporal turnover in species was found for yearly diversity at the zone level. Temporal turnover analysis was accomplished by calculating the dissimilarity for each region or site between years considering the turnover, nestedness components, and overall change. The temporal beta diversity dissimilarity index examines multivariate observations over two different time steps. The Sørensen index was the dissimilarity coefficient used with 999 permutations for the B (species loss) and C (species gain) components [58]. A permutational paired t-test with a p -value of less than 0.05 was used to test for significance.

2.5. R Packages

All analyses were done in R version 4.6.0 [59] using the betapart package version 1.6.1 [55] for β -diversity partitioning and bootstrap β -diversity, adespatial version 0.3-29 [60] for local contributions to β -diversity (LCBD) and temporal β -diversity (TBI), vegan version 2.7-3 [61] for Chao2 estimates and the species accumulation curves, indicspecies version 1.8.0 [48] for indicator species analysis, VennDiagram version 1.8.2 [62] for set comparisons, geosphere version 1.6-8 [63] for calculating the distance between sites, and tidyverse version 2.0.0 [64] for data manipulation and visualization. The Florida coastline in Figure 1 was drawn using maps version 3.4.3 [65].

3. Results

3.1. Alpha and Gamma Diversity

Across the three survey years, site-level alpha richness varied widely and showed a clear latitudinal pattern (Figures 1 and 2, Table S1). In 2013, alpha richness ranged from 5 species at northern Martin-Indian River sites to 60 species at Arch Creek East (Miami-Dade), with zone-mean alpha values of 25 ± 16 (Florida Keys), 39.6 ± 12.5 (Miami-Dade), 13.4 ± 10.5 (Broward-Palm Beach), and 9.9 ± 4.3 (Martin-Indian River). Gamma diversity at the zone level followed a similar pattern as alpha, with the Florida Keys ($\gamma = 60$) and Miami-Dade ($\gamma = 74$) holding the largest species pools and Broward-Palm Beach ($\gamma = 41$) and Martin-Indian River ($\gamma = 27$) the smallest. The total survey richness in 2013 was 89 species across 32 sites. The 2014 survey of 5 sites and the 2015 survey of 7 sites recovered 90 and 77 species, respectively, with the higher 2014 total reflecting a single Miami-Dade site (Arch Creek East, alpha = 62) and a Martin-Indian River site (HBOI, alpha = 41).

Site-level alpha richness was negatively correlated with latitude in 2013 (Spearman $\rho = -0.462$, $n = 32$, $p = 0.004$) and in the pooled 2013–2015 dataset ($\rho = -0.474$, $n = 44$, $p = 0.0006$, with sites in the lower-latitude Florida Keys and Miami-Dade zones consistently supporting higher richness than sites in the higher-latitude Broward-Palm Beach and Martin-Indian River zones). The relationship was not significant in 2014 ($\rho = 0.100$, $n = 5$, $p = 0.564$) or 2015 ($\rho = -0.252$, $n = 7$, $p = 0.293$), where small site counts limited the statistical power and motivated the pooled analysis. The transition zone, Miami-Dade, had the highest alpha diversity along the latitudinal gradient (Figure 2, dashed loess).

3.2. Sampling Adequacy

Species accumulation curves for the 2013 survey approached, but did not in all cases reach, asymptote (Figure S1). The whole-survey curve flattened above ~25 sites, with the median of randomized accumulations approaching ~85 species at 30 sites, consistent with the 89 species observed and an estimated whole-survey richness of 95 (Chao) to

102 (jackknife-1) species (Table S2). The Florida Keys had 60 observed species against a Chao estimate of 89 (95% CI $\approx$ 62–84% completeness). The Miami-Dade curve (bottom-right, $n = 5$) reached 74 species against a Chao estimate of 81 (~91% completeness, the highest of any zone). The Broward-Palm Beach survey cataloged 41 species while the Chao estimated about 71 with a completeness range of 57–83%, the lowest. The Martin-Indian River species accumulation curve ($n = 16$, Figure S1) showed continued accumulation but with diminishing returns, ending at 27 species against Chao = 28 (~95% completeness, the highest of any zone). The Broward-Palm Beach and the Florida Keys results indicate that the zones may have been undersampled relative to their expected richness, while the Miami-Dade and Martin-Indian River were adequately sampled.

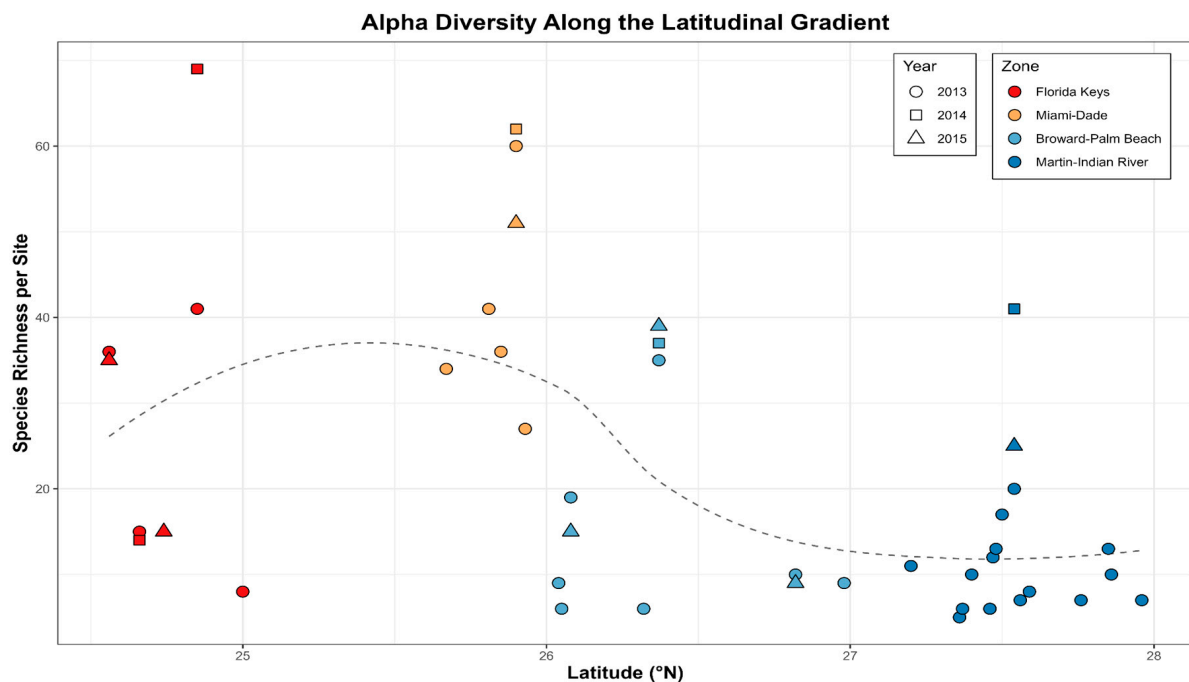


Figure 2. Alpha diversity along the latitudinal gradient. Each point represents a site-year combination. The shapes represent the survey years (circle = 2013, square = 2014, triangle = 2015). The Florida Keys are red, Miami-Dade orange, Broward-Palm Beach light blue, and Martin-Indian River dark blue. The dashed line is a loess smoother across all site-years.

3.3. Shared Species Across Zones

In 2013, 15 species were common to all four zones, forming the core epifaunal community (Figure 3). However, the Miami-Dade zone boasted the highest number of zone-unique species (16), highlighting its status as the regional alpha-richness peak and its inclusion of two highly diverse Biscayne Bay sites. Miami-Dade also had the greatest number of shared species, significantly contributing to its designation as the transition zone/ecotone, as it hosts a mix of species from other zones along with many unique species not found elsewhere. The Florida Keys contained 8 zone-unique species, mainly tropical sponges and ascidians, which were absent further north. In contrast, Broward-Palm Beach had no zone-unique species, with every taxon recorded there also present in at least one other zone. This contrasts with Miami-Dade, the tropical-temperate ecotone, where the co-occurrence of southern and northern taxa creates a distinctive zone-level signature. Martin-Indian River had 2 zone-unique species. The zone-unique species for each zone are listed in Table S3. The Florida Keys and Miami-Dade shared the most species between any two zones.

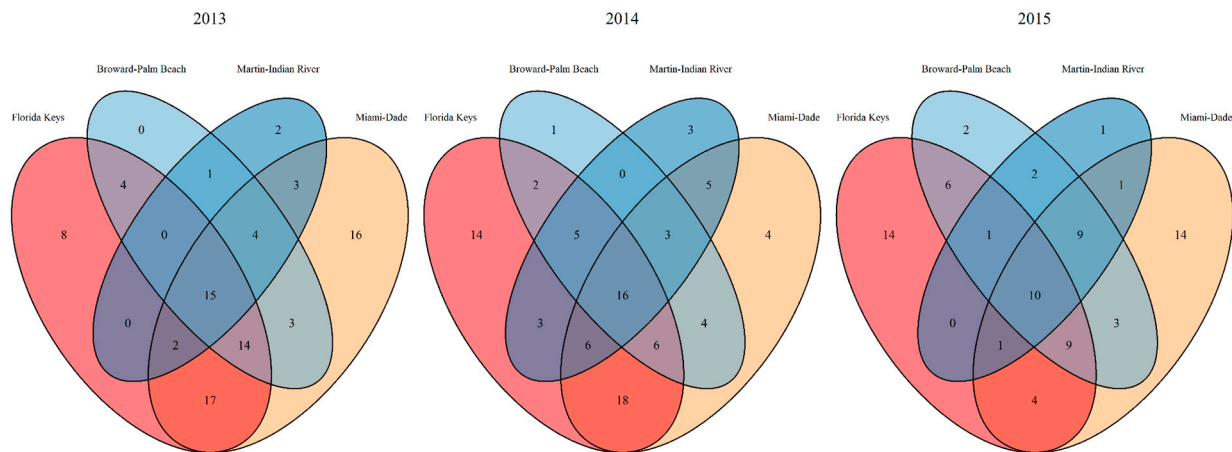


Figure 3. Venn diagrams of shared species for years (left) 2013, (middle) 2014, (right) 2015. The zones are listed above their respective ellipses. The numbers in each region represent the number of species occupying the intersection of the zones.

The 2014 survey, conducted at five sites (1–2 per zone), identified 16 species common to all four zones, a number comparable to 2013 despite the smaller sample size per zone. Additionally, 14 species were found to be unique to the Florida Keys, an increase from 2013 (Figure 3). In 2015, the survey at seven sites revealed 10 species shared across all zones and 14 species unique to both the Florida Keys and Miami-Dade (Figure 3). A comparison across the years indicated that the shared core of the four zones decreased from 15 species in 2013 to 10 in 2015, while the zone-unique species pools changed in identity but not significantly in size, suggesting sequential turnover rather than systematic species loss. The difference in the number of shared species must be examined in light of a difference in the number of sites that were visited from year to year. As there were fewer sites in 2014, the number of unique species could be a sampling artifact.

The indicator species analysis identified 41 species significantly associated ($\alpha = 0.05$) with either a specific zone or a combination of zones (Table S4). The Florida Keys and Miami-Dade zones hosted 34 of these species, with 5 unique to the Florida Keys, 10 exclusive to Miami-Dade, and 19 common to both zones. In contrast, neither the Broward-Palm Beach nor the Martin-Indian River zones had any indicator species exclusive to them. The 19 species characterizing the combined Florida Keys and Miami-Dade group were primarily tropical sponges, such as *Tedania ignis*, *Biemna caribaea*, *Dysidea etheria*, *Clathrina canariensis*, *Ircinia campana*, along with various *Haliclona* and *Mycale* species. This group was complemented by the anemone *Aiptasia* sp., the bryozoan *Bugula stolonifera*, and the fan worm *Sabella* sp. Three species exhibited high fidelity to the southern combined zone: *Tedania ignis* (IndVal = 0.966), *Biemna caribaea* (0.943), and *Dysidea etheria* (0.865), which appeared at nearly every site in the Florida Keys and Miami-Dade. Of these, *Biemna caribaea* was the only species entirely absent north of Palm Beach ($A = 1.000$). The other two occurred in northern zones at low frequency. Additionally, seven species associated with either Miami-Dade or the Florida Keys and Miami-Dade showed marginal associations ($0.05 < p \leq 0.10$), further supporting the distinctiveness of the southern faunal pool. The only significant indicator for a combination of northern zones alone (Broward-Palm Beach and Martin-Indian River) was the temperate *Brachidontes exustus* (scorched mussel; IndVal = 0.885, $p = 0.002$). The lack of zone-exclusive indicators for Martin-Indian River, the largest zone with 16 sites and thus the greatest statistical power to detect such indicators, is a notably strong negative result. This suggests that the zone lacks species that do not appear in adjacent zones. Foundation species indicators split into two distinct three-zone patterns. Ostreidae (IndVal = 1.000, $p = 0.001$) and *Amphibalanus amphitrite* (purple acorn barnacle; IndVal = 0.964, $p = 0.001$)

indicated the Broward-Palm Beach, Martin-Indian River, and Miami-Dade combination, absent from the Florida Keys. *Bugula neritina* (IndVal = 0.882, $p = 0.001$) and Isognomonidae (IndVal = 0.885, $p = 0.018$) indicated a different combination of Broward-Palm Beach, the Florida Keys, and Miami-Dade, absent from Martin-Indian River.

3.4. Spatial β -Diversity Partitioning

Pairwise Sørensen dissimilarity for the 2013 survey ($n = 32$ sites) was high ($\beta\text{SOR} = 0.917$), with the great majority carried by turnover ($\beta\text{SIM} = 0.772$) and a much smaller component attributable to nestedness ($\beta\text{SNE} = 0.145$). At the zone level, βSOR was highest in Martin-Indian River (0.756) and Broward-Palm Beach (0.744), both of which had more sites than the Florida Keys (0.699) and Miami-Dade (0.557). The component partition shows that within-zone β -diversity is turnover-dominated in all four zones ($\beta\text{SIM} > \beta\text{SNE}$), but the magnitude of the nestedness component varies. Broward-Palm Beach ($\beta\text{SIM} = 0.430$, $\beta\text{SNE} = 0.314$) has the highest within-zone nestedness component and the narrowest gap between turnover and nestedness. The Martin-Indian River ($\beta\text{SIM} = 0.476$, $\beta\text{SNE} = 0.280$) and the Florida Keys ($\beta\text{SIM} = 0.452$, $\beta\text{SNE} = 0.247$) zones fall in the middle. Miami-Dade ($\beta\text{SIM} = 0.401$, $\beta\text{SNE} = 0.156$) has by far the lowest nestedness component.

After bootstrap standardization to $n = 3$ sites per zone (Figure 4), the Florida Keys still had the highest βSOR (0.670 ± 0.054), followed by Broward-Palm Beach (0.597 ± 0.065), Miami-Dade (0.463 ± 0.026), and Martin-Indian River (0.412 ± 0.078). The bootstrap turnover component (βSIM) was highest in the Florida Keys (0.410 ± 0.023) and lowest in Martin-Indian River (0.165 ± 0.093), with Miami-Dade (0.309 ± 0.080) and Broward-Palm Beach (0.291 ± 0.129) intermediate. The bootstrap nestedness component (βSNE) was largest in Broward-Palm Beach (0.306 ± 0.169), followed by the Florida Keys (0.259 ± 0.056), Martin-Indian River (0.247 ± 0.118), and Miami-Dade (0.154 ± 0.070). The high βSNE in Broward-Palm Beach reflects the subset relationships between its species-poor and species-rich sites. Turnover increases with the number of sites compared, so zones sampled at different intensities cannot be compared directly. Martin-Indian River was sampled at 16 sites and the Florida Keys at 4. Both the observed and the standardized values provide information on the differences among the zones, and both are reported here. These standardized values reveal that the Florida Keys' high β -diversity is not a sample size artifact. Martin-Indian River's high raw β -diversity collapses once the site count is standardized, while Broward-Palm Beach drops but remains the second-highest in the bootstrap ranking.

In all four zones, the full pairwise comparison shows that βSIM is greater than βSNE , indicating turnover dominance. After bootstrapping, this trend reversed in the two Martin-Indian River, where βSNE (0.247) exceeded βSIM (0.165 ± 0.093). Broward-Palm Beach showed the same direction, with βSNE (0.306) slightly above βSIM (0.291 ± 0.129), but the difference between the two components was small relative to their variation and is not treated as a clear reversal. Consequently, in the northern regions, the differences between sites are not primarily due to species replacement but rather to the presence of different subsets from a relatively limited number of species in each zone. While nestedness remained relatively stable across all zones (with changes of ≤ 0.04), turnover significantly decreased in the northern zones. This was true even with different subsampling. Bootstrapping was done at two, three, and four sites per zone and was limited to four because one of the zones had only four sites. What it found was that the turnover ranking was the same, with the Florida Keys the highest and Martin-Indian River the lowest. The two southern zones had more turnover than the two northern zones. For Martin-Indian River, nestedness was higher than turnover for each of the subsample sizes. For Broward-Palm Beach, this was true at two and three sites but not at four.

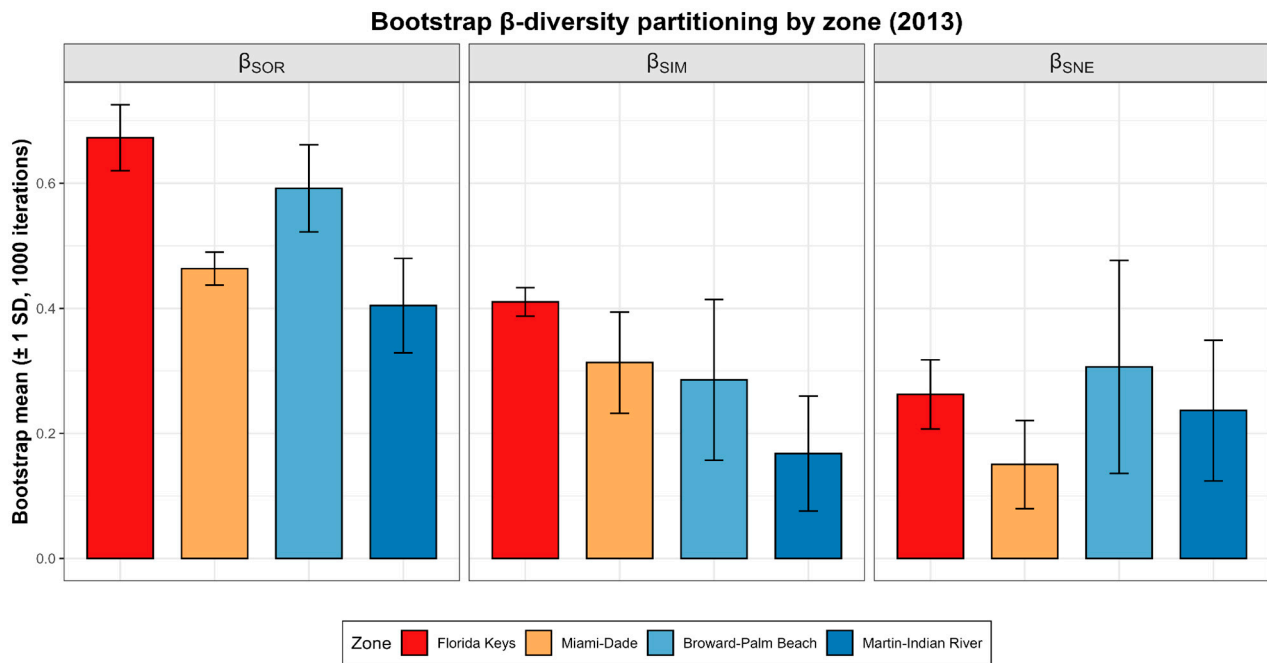


Figure 4. Bootstrap β -diversity partitioning by zone for the 2013 survey. Bars show bootstrap mean $\pm$ 1 SD over 1000 iterations of subsampling 3 sites without replacement from each zone. The three panels decompose the total Sørensen (β_{SOR}) into turnover (β_{SIM}) and nestedness-resultant (β_{SNE}) components.

Within-zone β -diversity could be computed for only three zone-years in the survey datasets because the other zone-years had only 1 site. In 2014, the Florida Keys (Bahia Honda + Islamorada) showed $\beta_{SOR} = 0.687$, almost entirely carried by nestedness ($\beta_{SNE} = 0.615$), with the Bahia Honda 2014 community largely a subset of Islamorada 2014. In 2015, the Florida Keys (Curry Hammock and Key West) showed $\beta_{SOR} = 0.800$ carried mostly by turnover ($\beta_{SIM} = 0.667$), and Broward-Palm Beach (3 sites) showed $\beta_{SOR} = 0.611$ carried mostly by nestedness ($\beta_{SNE} = 0.486$).

3.5. Permutational Tests and Geographic Structure

PERMANOVA confirmed that the latitudinal zone explained a substantial fraction of the among-site compositional variation in 2013. Zone identity emerged as a highly significant predictor of total Sørensen dissimilarity ($R^2 = 0.510$, $F_{3,28} = 9.70$, $p = 0.001$, 999 permutations), accounting for a greater proportion of the turnover component (β_{SIM} : $R^2 = 0.626$, $F_{3,28} = 15.59$, $p = 0.001$) compared to the nestedness component (β_{SNE} : $R^2 = 0.332$, $F_{3,28} = 4.64$, $p = 0.006$). PERMDISP analysis yielded a significant result for total Sørensen ($F_{3,28} = 6.16$, $p = 0.009$), suggesting that the zone groups also exhibited differences in within-group dispersion, indicating that the four zones were not equally compositionally heterogeneous. Thus, the PERMANOVA result aligns with both centroid separation and dispersion differences among zones. Distinct patterns of community dispersion were observed across zones (Figure 5). Samples from Miami-Dade and Martin-Indian River clustered relatively closely together, indicating a higher degree of similarity in their community composition, while samples from the Florida Keys and Broward-Palm Beach showed a greater spread. These differences in the within-group variability were visually supported by the sizes of the corresponding standard deviation ellipses. The zone centroids were separated along the first axis, which explained 43.27% of the variation, by distances greater than the within-zone spread in most pairwise comparisons, indicating that the zone differences reflect centroid separation as well as unequal dispersion. Bootstrap analysis

confirmed that the centroid component of this signal was genuine after controlling for the sample size (Figure 4).

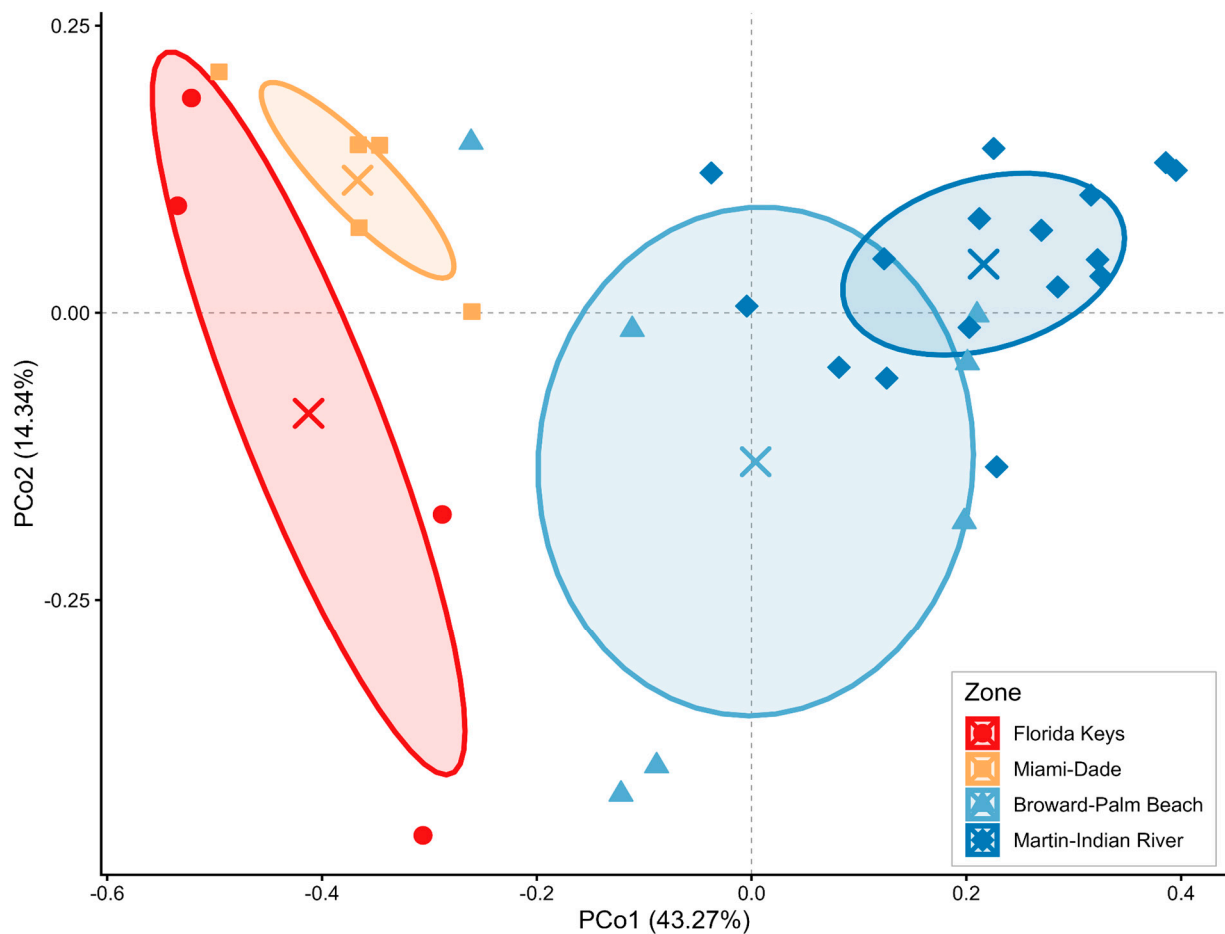


Figure 5. Ordination of the principal coordinates analysis (PCoA) of the benthic community composition on red mangrove prop roots based on the Sørensen distance matrix. Sørensen dissimilarity, a measure of beta diversity, quantifies the difference in species composition between samples based on presence and absence. Data represent the 32 sites surveyed in 2013 aggregated by latitudinal zone. Ovals represent the standard deviation for each zone. Colors and shapes coincide with zones, and the crosses mark the zone centroids. The first axis (PCo1) explained 43.27% of the total variation, while the second axis (PCo2) explained 14.34%.

Mantel tests conducted against geographic distance revealed the spatial signal (Figure 6). The total Sørensen dissimilarity increased steadily with geographic distance (Mantel $r = 0.676$, $p = 0.001$, 999 permutations), and a similar pattern was observed for the turnover component (Mantel $r = 0.598$, $p = 0.001$). In contrast, the nestedness-resultant component showed no correlation with geographic distance (Mantel $r = -0.001$, $p = 0.454$). Thus, the latitudinal compositional gradient discussed earlier is entirely driven by species replacement, indicating that sites farther apart geographically differ in species composition rather than in the nestedness of their communities.

3.6. Local Contributions to β -Diversity (LCBD)

Local Contributions to Beta Diversity (LCBD) identified individual sites with disproportionately distinct compositions (Figure 7, Table S5). After Holm-Bonferroni correction across all 32 sites in 2013, three sites had significantly elevated LCBD (Holm-corrected $p < 0.05$). All three of the sites were in the Florida Keys (Key West, Islamorada, Tavernier Key), consistent with the Sørensen-partitioning and bootstrap results that identified the

Florida Keys as the zone with the highest standardized β -diversity. The Tavernier Key site had the highest single-site contribution to among-site β . Four sites were significant raw, but did not survive the multiple-testing adjustment, the last of the Florida Keys sites (Bahia Honda), one site in Miami-Dade (Arch Creek East), and the two most southern sites in the Broward-Palm Beach zone (Anne Kold Center and Hollywood North Beach). Of note, none of the Miami-Dade reached Holm-corrected significance, despite Miami-Dade having the highest gamma diversity, because the Miami-Dade sites were relatively compositionally similar to one another.

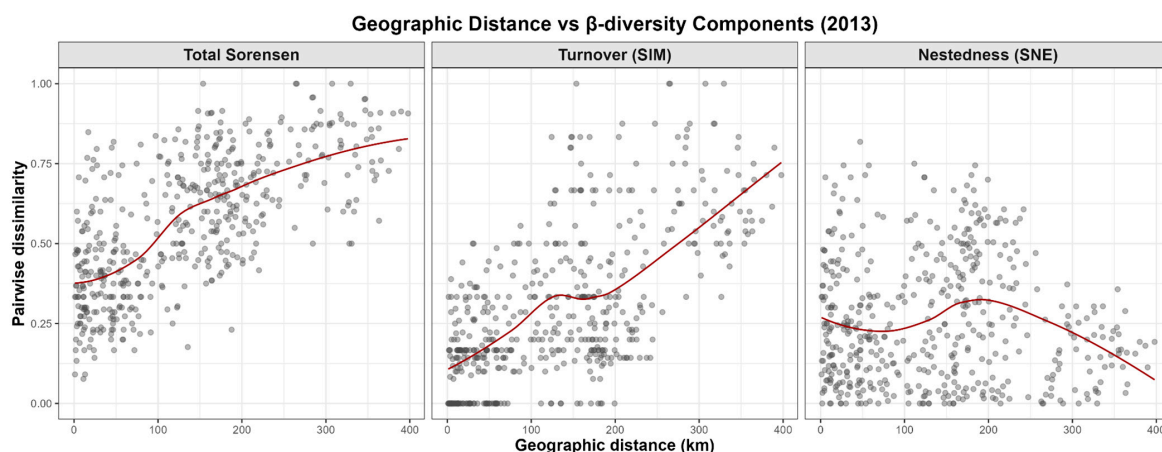


Figure 6. Geographic distance versus β -diversity components for the 2013 survey. Each point represents a pair of sites. The three panels show the total Sørensen dissimilarity (**left**), turnover component β SIM (**middle**), and nestedness-resultant component β SNE (**right**) plotted against pairwise geographic distance in km. The red lines represent loess smoothers.

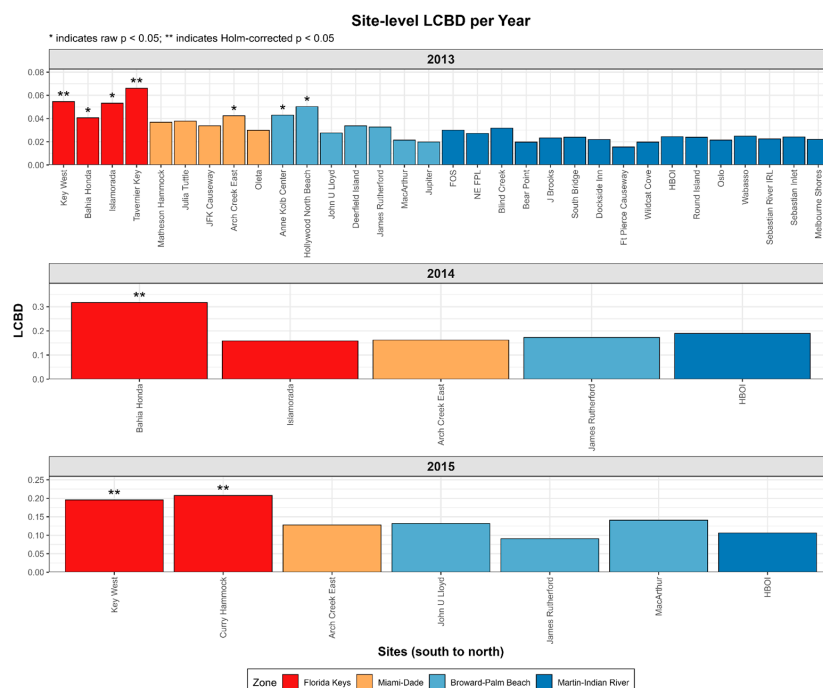


Figure 7. Site-level LCBD for each survey year. Bars show LCBD per site within each year (top: 2013, $n = 32$; middle: 2014, $n = 5$; bottom: 2015, $n = 7$), with sites ordered from south to north along the x-axis and colored by zone. Two asterisks above the bars indicate sites with Holm-corrected $p < 0.05$ within that year. One asterisk above the bars indicate sites with $p < 0.05$ within that year before Holm-corrected. Note the differing y-axis scales among the panels, reflecting different sample sizes. The values for the LCBD are presented in Table S5.

In the 2014 survey, Bahia Honda emerged as the sole Holm-significant site, consistent with its temporal turnover signal as shown in the TBI analysis (Section 3.8). In the 2015 survey, both Key West and Curry Hammock, located in the Florida Keys, were identified as Holm-significant. Tavernier Key (2013), Bahia Honda (2014), and Curry Hammock (2015) were the three Florida Keys sites that had resilient significance for spatial LCBD across repeated runs. On the other hand, Islamorada in 2013 and Key West in 2013 and 2015 had inconsistent significance across runs. Over the years, sites in the Florida Keys have consistently been recognized as compositionally unique, indicating that these areas are not just rich in species but also harbor distinct species pools at each site.

3.7. Species Contributions to β -Diversity (SCBD)

The Species Contributions to Beta Diversity (SCBD) analysis pinpointed the species that significantly influenced the variation in species composition across different sites (Figure 8, Table S6). Out of the 103 species in the collective pool from 2013 to 2015, 32 species exhibited SCBD values exceeding the equal-contribution threshold of $1/103$ (0.0097). This suggests that their distribution patterns contributed more to site variation than if all species had varied equally. The scorched mussel *Brachidontes exustus* was the leading contributor with an SCBD of 0.0559, followed by the ribbed mussel *Geukensia demissa* (0.0405), the calcareous tubeworm *Hydroides elegans* (0.0402), the purple acorn barnacle *Amphibalanus amphitrite* (0.0396), and the bryozoan *Bugula neritina* (0.0394). The 32 above-baseline species by taxon were: Porifera 11, Ascidiaceans 6, Bryozoans 5, Bivalves (not barnacles) 4, Polychaetes 3, Barnacles 2, and Anemones 1.

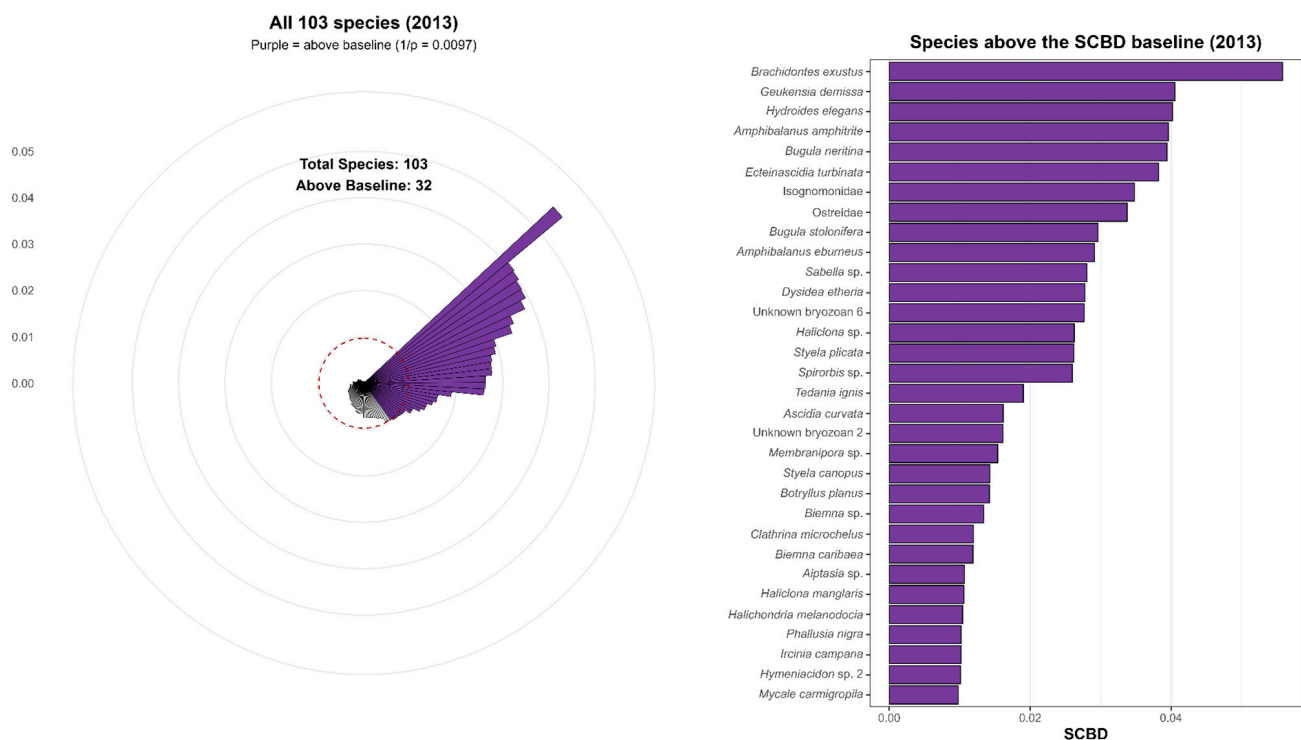


Figure 8. Species Contributions to β -Diversity (SCBD) for the 2013 dataset. Left panel: Rose plot of SCBD values for all 103 species, with each radial bar representing one species; the dashed red ring is the equal-contribution baseline of $1/103 = 0.0097$. The purple bars indicate species above the baseline ($n = 32$). Right panel: Linear bar chart of species above the baseline, ordered by SCBD value. Numerical SCBD values for the top species are reported in Table S6.

3.8. Temporal β -Diversity

Zone-level temporal β -diversity (Figure 9, Table S7) indicated that the compositional shifts between survey years were significant across all zones, though the directional trends varied by interval. From 2013 to 2014, the Florida Keys and Martin-Indian River experienced a net gain in species (points above the green 1:1 line), while Broward-Palm Beach and Miami-Dade saw a net loss. Over the entire period from 2013 to 2015, three of the four zones ended with a net loss (points below the 1:1 line), with only Broward-Palm Beach achieving a net gain. The permutational paired t-test for each interval did not reach significance at $\alpha = 0.05$, suggesting that the imbalance between gains and losses was not large enough to rule out chance given the small zone sample sizes.

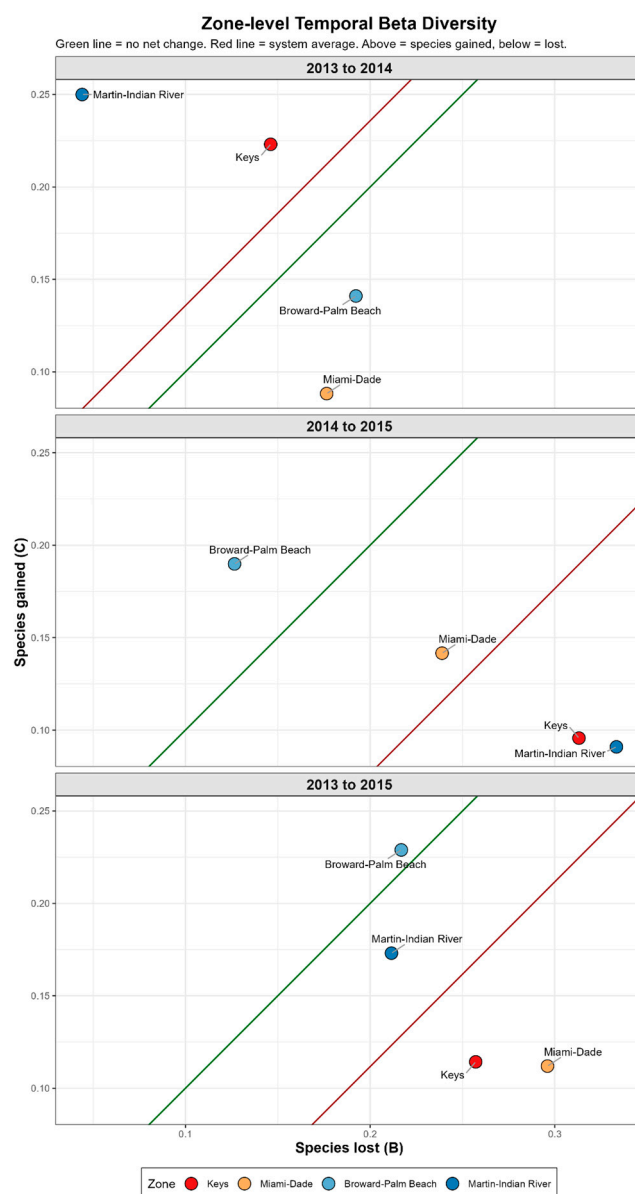


Figure 9. B-C plot for biodiversity for the four zones. The green line has a slope of 1, this is where the gains and losses are equal. The red line passes through the centroids of the points. Where the red line is below the green line it indicates overall biodiversity loss, above the green line it indicates overall biodiversity gain.

At the site level (Table S7), where identical sites were assessed over several years, Bahia Honda in the Florida Keys demonstrated the most notable single-site temporal D

between 2013 and 2014, with a value of 0.586. This was almost equally split between losses and gains, indicating a high turnover in composition within that year. Islamorada had the second-highest D for the same period, mainly due to gains. During the 2014–2015 interval, two of the three sites revisited (HBOI and Arch Creek East) experienced more losses than gains, while James Rutherford had a slight net gain. Over the entire 2013–2015 period, both James Rutherford and HBOI exhibited net gains, with Arch Creek East showing a net loss. The 2013–2015 comparison is calculated directly between endpoint years rather than summed across intervals. The frequent occurrence of high temporal D values at sites in the Florida Keys echoes the spatial-LCBD finding that the Florida Keys are the most compositionally dynamic area.

4. Discussion

More than the latitudinal gradient appears to influence the structure of the red mangrove (*Rhizophora mangle*) prop root epifaunal community across southeastern Florida. The number of species present on mangrove prop roots generally increased with decreasing latitude, with the exception of the transition zone, consistent with the broader latitudinal biodiversity gradient documented in marine benthic systems [66–69]. A total of 103 epifaunal species were found during this study while other studies have reported 32–96 species/taxa; 32 species in one mangrove forest in Brazil [70], 40 taxa in two bays in Colombia [71], 84 taxa in the Indian River Lagoon [72], and 96 taxa including algae at four cays in Belize [28]. Caution is required when comparing these numbers, as these surveys of the mangrove prop root epifaunal community used different experimental designs, occurred under different abiotic conditions, and differed in expertise in species classification and taxonomic resolution. As expected in the southern region of this survey, tropical species dominated on the prop roots, with dominance shared among several species of Porifera, several species of Ascidiacea, and *Isognomon alatus*. Miami-Dade, the transition zone, had the most biodiversity because it hosted many temperate species not found in the Florida Keys and some tropical species that did not occur north of Miami-Dade. The tropical assemblage of the Florida Keys and Miami-Dade appears to drop out almost entirely north of the Palm Beach biogeographic boundary, where previous benthic surveys have found a distinct compositional change between 25° and 27° latitude [44,45]. The macrobenthos present on red mangrove prop roots appear to be moderately influenced by location along the latitudinal gradient, although the exact mechanisms that influence the decrease in species richness towards the north remain unclear. Several sites also deviated from broad latitudinal expectations in ways consistent with hydrographic or anthropogenic features, notably Hollywood North Beach and Anne Kolb Center at the mouth of Port Everglades and Arch Creek East in northern Biscayne Bay. Various unmeasured environmental differences, including salinity range, wave action, tidal fluctuations, inlet exchange, and boat traffic may have contributed to the patterns observed.

The Florida Keys feature a unique macrobenthic community on red mangrove prop roots, distinguished by tropical species absent from other surveyed areas. Some of the South Florida larval supply comes from the Caribbean, contributing to a potentially more diverse benthic community [5,73–75]. The Florida Keys demonstrated both spatial and temporal instability, contributing to the area's compositional dynamics. The biodiversity increase in the Florida Keys may reflect changes in larval supply that could be influenced by climate-related shifts in ocean currents [20,21]. Many of the species in the Florida Keys are prominent in mangrove systems further south in the Caribbean and Central and South America [30,37,76]. Of the 13 species recorded here that are also listed among the most common sponges and ascidians on Caribbean mangrove prop roots [30,76], 10 were found in all four zones with one more species found in the three most southern zones. Species

that occur across the entire latitudinal gradient are more likely to be generalists. Notable indicator species unique to the Florida Keys in 2013 include various sponges, members of Pectinoidea, and the ascidian *Botrylloides nigrum*. Several sponge species appear in the above-baseline SCBD set, concentrated toward the lower end of the ranking. These sponges likely perform similar ecological roles on prop roots, so their collective functional impact may be more concentrated than the species count implies. Interestingly, the foundation species *Crassostrea virginica*, common on prop roots in other areas, was not found on the Florida Keys' mangrove prop roots, despite oysters being observed on dock pilings in the region (J. Aquino-Thomas, personal observation).

Miami-Dade had the highest species richness of any zone and shared the most species with the Florida Keys. In addition to hosting indicator species common to both the northern and southern regions, Miami-Dade also supported a substantial number of zone-exclusive indicators, offering quantitative evidence that it serves as a true transition zone rather than just a hotspot of richness. Freestone and Inouye [77] sampled within what would constitute the northern zone of this study, and described their Florida region as a transitional zone between their temperate and tropical sites. At the finer resolution of this study the transitional zone within Florida is Miami-Dade, approximately 167 km further south. The area's high species richness resulted in noticeable competition for space on the prop roots (J. Aquino-Thomas, personal observation), mirroring results from other research on intertidal competition [70,78–80]. The coexistence of multiple foundation species (Porifera, *Crassostrea virginica*, *Amphibalanus amphitrite*) within the Miami-Dade prop root habitat aligns with the Foundation Species Interaction-Biodiversity (FSIB) model, which predicts that interactions among multiple foundation species can influence heterogeneity in community biodiversity [36]. Additionally, Miami-Dade's increased gamma diversity is partly attributed to within-zone heterogeneity, marked by a diverse range of species richness and composition across its sites (Matheson Hammock, Julia Tuttle, JFK Causeway, Arch Creek East, Oleta). The transition zone classification is applicable not only at the zone level but also at the site level within the zone.

In contrast to the sponge- and tunicate-dominated southern community, the two northernmost zones, Broward-Palm Beach and Martin-Indian River, are characterized by oyster and barnacle dominance and lower species richness [36,72]. These zones did not have any zone-exclusive indicator species, with *Brachidontes exustus* appearing as the only significant indicator for the combined northern zones. The northern mangrove epifaunal communities are defined as much by the lack of certain species as by the presence of others. Within the northern zones, spatial heterogeneity is distinct, although the primary structuring factor appears to be nestedness rather than turnover. Partitioning β -diversity on the full dataset revealed that turnover was the dominant process in all four zones. The zones were sampled differently, with Martin-Indian River visited at four times as many sites as the Florida Keys, and turnover increases as the number of sites increases. Once sampling effort was standardized, turnover remained the dominant process in the Florida Keys and Miami-Dade, while nestedness was the dominant process in Martin-Indian River and the two processes contributed evenly in Broward-Palm Beach. Like Freestone and Inouye [77], this study found lower β -diversity in the zones at higher latitudes and higher spatial variation in the more southern zones after standardizing for sampling effort, even though this study covered a much smaller latitudinal scale. The LCBD scores for the northern sites characterize them as subsets of the larger species pool. Together these indicate that site-to-site differences in the north are driven by which subset of a limited species pool occurs at each site, rather than by species replacement.

The lack of zone-exclusive indicator species suggests that the northern sites are largely a subset of the southern species pool, consistent with ocean currents limiting larval supplies

from reaching the north [5,73–75]. Unlike the Florida Keys, when species were lost in the northern zones over the three study years, they were not replaced. Established latitudinal boundaries for estuarine macroinvertebrate communities identify Palm Beach County as a transition point from tropical to temperate biogeography [44]. Biogeographic barriers, such as the Bahamas Fracture Zone [45], could hinder the northward movement of southern propagules. This potential inability for propagules to move past may hold true even as the Gulf Stream, which flows within a few miles of the southeast Florida coast, warms 2 to 3 times faster than the global mean [20], with associated changes in larval dispersal patterns [21]. Even if adults can survive, the delivery of larvae might be the limiting factor.

Southeast Florida's mangrove prop root communities are shaped by a multi-scale mosaic of biogeographic, environmental, and temporal drivers. The latitudinal gradient is not only a gradient in overall biodiversity but also in the secondary foundation species that dominate, with cascading effects on the associated prop root community [29,36]. Within each zone, local hydrography can affect species richness, with proximity to inlets and ports increasing species richness at nearby sites [36]. In general, the latitudinal gradient along the south Florida coastline is well recognized although very few regional surveys have been done. Much research and the accompanying climate change predictions about transformations to mangrove and salt marsh ecosystems are being undertaken due to the noticeable shifts associated with climate change [9,12,81–83]. When viewed through the lens of global climate change and the documented poleward range expansion of mangrove forests [12,18,19,83], these multi-scale community dynamics take on a predictive urgency. Baseline surveys like this one are therefore essential for forecasting the prop root assemblages of today's and tomorrow's mangrove ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/hydrobiology5030024/s1>, Figure S1: Species accumulation curves for the 2013 survey; Table S1: Site-level alpha and zone-level gamma diversity by zone and survey year; Table S2: Non-parametric richness estimators by zone for the 2013 survey; Table S3: Zone-unique species recorded in the 2013 survey; Table S4: Indicator species analysis of 2013 mangrove prop root assemblages; Table S5: Local Contribution to Beta Diversity for all sites by year; Table S6: Species above the SCBD baseline; Table S7: Temporal β -diversity values at the zone and site level; Table S8: Site coordinates.

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