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Taxonomic and Functional Representations of Phytoplankton Beta Diversity Show Contrasting Sensitivity to Environmental Gradients in a Tropical Reservoir

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Abstract

Linking community variation to environmental gradients is central to reservoir ecology and monitoring, yet the strength of detected associations can depend on how community change is represented. Using phytoplankton surveys from a tropical reservoir (Corumbá River, Brazil) sampled across wet and dry seasons, we compared taxonomic beta diversity with two functional representations: Reynolds functional groups and a set of widely used morphological traits combined into functional beta-diversity indices. We partitioned beta diversity into turnover and richness-difference components and quantified environment–community associations with constrained ordination. Overall, the representation chosen altered both the magnitude and the seasonal consistency of environmental associations: trait-based indices (particularly dendrogram-based metrics weighted by biovolume) tended to show stronger associations with environmental gradients related to mixing, light availability and nutrients, whereas functional groups and species-level data emphasized complementary aspects of community change. Turnover and richness-difference components did not respond uniformly across representations, highlighting that component choice can shift ecological interpretation. Rather than providing a universal 'best' approach, our results suggest practical trade-offs among representations when the goal is to detect and interpret environmental structuring along reservoir gradients, especially during highly dynamic conditions typical of early post-impoundment phases.

Keywords: reservoir ecology; beta diversity partitioning; turnover; richness difference; functional traits; Reynolds functional groups; longitudinal gradient; seasonality; monitoring

1. Introduction

The environment shapes community composition across space and time [1], and understanding this variation is a core objective in freshwater ecology and reservoir management [2]. However, the question of which attribute of the communities is best to trace the effect of environmental change has no definitive answer [3–5].

Traditional measures such as the number of species (richness) may not always follow the spatial and temporal variation of the environment, whereas the variation in species composition and abundance (beta diversity) can be more informative [6]. However, even taxonomic turnover may not map directly onto changes in ecological roles. In this sense, environmental processes seemed to be more related to functional attributes than to taxonomic ones [7]. Functional approaches aim to represent community change in terms that are more directly linked to organismal strategies and environmental constraints, potentially improving interpretability and transferability across systems [8,9].

The advantage of functional attributes on the taxonomic ones relies on the causal relationships that can be established between environmental variation and the features of species [4,10]. For example, in the case of phytoplankton, the mixing of water columns relates to the kind of organisms that can domain in a particular habitat. In stratified water bodies (null mixing) heavy phytoplankters cannot survive since they have high sinking rates, while organisms with features enhancing buoyancy (e.g., gas vesicles) can domain [11].

For phytoplankton, phycologists have suggested grouping species into functional groups based on their shared morphological, physiological, and ecological features [9,12], which has been used to test ecological questions [e.g., 13], understand the effects of environmental changes [14], and propose it as a monitoring tool [15,16]. However, the functional group approach has been criticized for assuming that the species in a particular group are ecological equivalents, thereby failing to recognize the variability that species in a group may exhibit [17]. In contrast, the analysis of functional traits and measures based on them may be better in assessing environmental variation since they consider all possible values and combinations of species features present in communities [18].

Beta diversity provides a descriptive quantification of among-site or among-time compositional variation. Partitioning beta diversity into turnover and richness-difference components can be useful to characterize whether variation is driven mainly by species replacement or by gains/losses, but these components are not direct measures of dispersal limitation or environmental filtering without additional evidence [19–21]. Importantly, functional patterns remain derived from species composition; therefore, taxonomic and functional beta diversity should be viewed as alternative representations of the same underlying community variation rather than independent ‘responses’ [9,22].

Here we evaluate how taxonomic composition, functional groups and trait-based functional indices capture phytoplankton beta diversity and its association with environmental gradients in the Corumbá reservoir (Central Brazil). This system has been described as strongly structured along a directional longitudinal template in which hydrodynamics and limnological gradients covary [16], providing an opportunity to test how representation and beta components influence detected environment–community associations.

We addressed three questions: (i) does the strength and seasonal consistency of environment–community associations depend on whether beta diversity is represented taxonomically, by functional groups, or by trait-based indices? (ii) do turnover and richness-difference components show consistent environmental associations across representations? and (iii) does abundance weighting (biovolume) alter these associations relative to incidence-based metrics?

By framing the comparison as sensitivity and interpretability trade-offs among representations, we aim to inform the choice of metrics for reservoir monitoring and for ecological inference along strong environmental gradients.

2. Materials and Methods

2.1. Study Area

The Corumbá reservoir is located on the Corumbá River in the state of Goiás (Central Brazil, 15°79' S and 48°31' W). Its formation process was completed in November 1996, flooding an area of 65 km2, with an average depth of 23 m, and an approximate hydraulic residence time of 30 days. Its drainage area comprises approximately 27,800 km2, with its main tributaries being the Santo Antônio, Peixe, and Pirapetinga rivers. It experiences distinct hydrological periods, characterized by a rainy (November to May) and a dry (June to October) season.

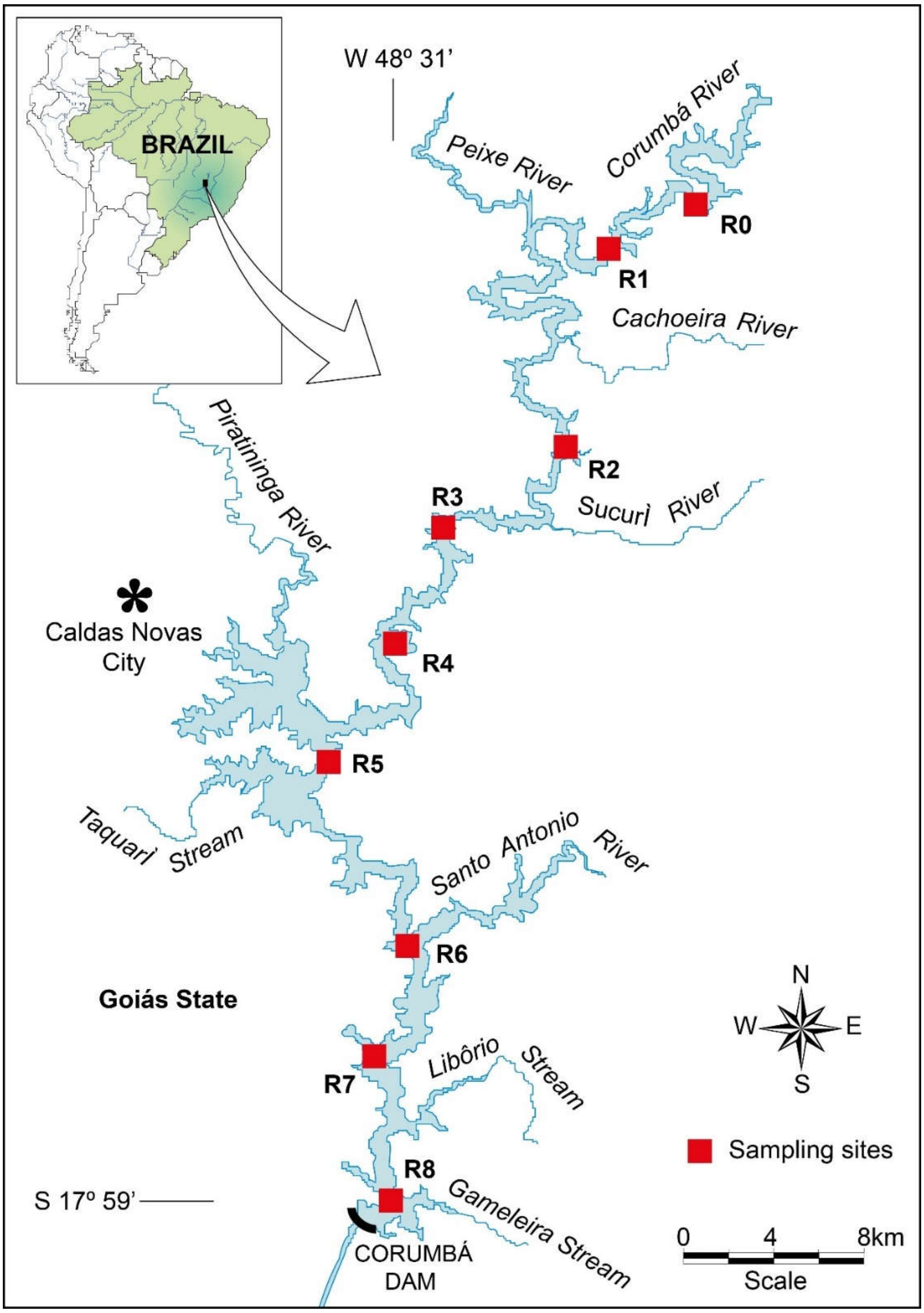

Figure 1. Location of sampling sites in the influence area of the Corumbá Dam on the Corumbá River.

2.2. Sample Collection and Analysis

Biological and environmental samples as well as in situ measurements were performed every six months between April 1997 and September 1999 (six sampling campaigns). Samples were collected in nine sites on the main channel of the Corumbá River (n = 48) embracing the lotic (R0 and R1), transition (R2 – R4), and lacustrine (R5 – R8) reservoir regions. However, in two sampling campaigns samples were lost (April 1997, two sites - R0 and R2; March 1999, four sites – R3, R5, R6, and R7).

Phytoplankton samples for quantitative analyses were collected from the sub-surface (at approximately~ 30 cm) depth directly using glass bottles (200 ml glass bottles) and fixed with acetic Lugol's solution 1%. Phytoplankters individuals (cells, colonies, and filaments) were counted in random fields using an inverted microscope the quantitative samples following the Utermöhl method

[23,24]. Random fields were selected until at least 400 individuals (cells, colonies, and filaments) were counted. Density was expressed as individuals per milliliter (ind mL^{-1}).

The cellular volume was calculated by approximating their shape to geometric forms [25]. The biovolume of each taxon was then multiplied by its density to calculate the biovolume in each sample, which was expressed as cubic millimeters per liter (mm^3 L^{-1}).

Important abiotic parameters for phytoplankton development were measured. Water temperature, pH, dissolved oxygen, electrical conductivity, turbidity and the maximum depth (Zmax) were measured in situ with digital portable potentiometers. The mixing zone (Zmix) was estimated according to the temperature profile of the water column, euphotic zone depth (Zeu) was measured using a radiometer. The ratio between the euphotic and mixing depths (Zeu:Zmix) was used as a measure of light availability (Jensen et al., 1994), while the ratio Zmix:Zmax was used as measure for mixing of water columns. Discharge, water residence time and precipitation data were provided by FURNAS Centrais Elétricas.

Water samples were collected to determine nutrients concentrations in laboratory. Total phosphorus (TP), dissolved phosphorus (DP), soluble reactive phosphorus (SRP), total Kjeldahl nitrogen (TKN), nitrate (N-NO3-) and ammonium (N-NH4+) were determined following the methods described in (APHA, 2005). The concentration of dissolved inorganic nitrogen (DIN) was calculated as the total of the amounts of nitrate, and ammonium.

2.3. Data Analysis

Environmental variation was summarized using principal component analysis (PCA) on standardized abiotic variables to visualize the dominant seasonal and longitudinal gradients. PCA scores were used for interpretation only; hypothesis testing of community–environment relationships was conducted with constrained ordination.

For taxonomic analyses we built community matrices using (i) species occurrence and (ii) species biovolume. Biovolume was used as an abundance proxy because it integrates cell size and density and is routinely applied to phytoplankton dominance and productivity-related questions. Functional-group matrices were constructed by aggregating species data into Reynolds functional groups for the same two data types (occurrence and biovolume).

Trait-based functional beta diversity was calculated from a compact set of morphological traits (including life form and cell size; Table 1) that has been widely used in freshwater phytoplankton functional ecology and is mechanistically linked to key reservoir constraints (mixing/turbulence, light climate and nutrient regime). The trait set was intentionally kept parsimonious to maintain comparability with previous studies and to avoid over-parameterization given the sampling design [9,26].

We computed total beta diversity and its turnover and richness-difference components using incidence- and abundance-based dissimilarities (Table 2). For incidence data we used Jaccard dissimilarity and its partitioning; for quantitative data we used the Ruzicka dissimilarity and its corresponding decomposition. Trait-based functional dissimilarities were calculated with dendrogram- and multidimensional approaches, using both incidence and biovolume weighting when applicable [19–21,27].

Table 1. Functional traits used for the functional beta diversity calculations. The presence of the trait is indicated by one, while the absence is indicated by zero. The GALD (greatest axial linear dimension) is continuous measurement. The life forms consider the cellular arrangement of each specimen: Unicellular: single-cell organisms. Filament: linear arrangement of cells intercommunicated by plasmodesmos or a linear chain of cells [28]. Colony: arrangement of multiple cells. Cenobium: when the number and arrangement of cells are determined from the origin of the organism and remains constant [29].

Trait	State	Related processes
Bristle	1 - 0	Grazing avoiding

Flagellum	1 - 0	Buoyancy
Spines	1 - 0	Grazing avoiding
Silica	1 - 0	Resistance to mechanical damage
Mucilage	1 - 0	Resources taking, desiccation avoidance
Aerotope	1 - 0	Buoyancy
Process	1 - 0	Buoyancy
GALD	µm	Grazing avoiding
Life form	Filament – Coenobium – Colony - Unicellular	Grazing avoiding, resources taking, buoyancy

Table 2. Dissimilarity measures and their components. Reference includes papers related to dissimilarity calculations or decomposing beta diversity.

Community attribute	Distance or method	Beta diversity components		Abbreviation	Reference
Species occurrence	Jaccard	Turnover	Rich. Diff.	sp.occu	[27]
Species biovolume	Ruzicka	Turnover	Rich. Diff.	sp.biovol	
FG occurrence	Jaccard	Turnover	Rich. Diff.	FG.occu	
FG biovolume	Ruzicka	Turnover	Rich. Diff.	FG.biovol	
Functional traits + occurrence	Convex hull	Turnover	Nestedness	mFD.index	[30]
Functional traits + occurrence	Dendrograms	Turnover	Rich. Diff.	bFD.index.occu	[31,32] and later expanded functional diversity by [21]
Functional traits + biovolume	Dendrograms	Turnover	Rich. Diff.	bFD.index.biovol	

To compare differences in the raw values of total beta diversity and its components among the different dissimilarity measures (e.g., sp.occu, FG.biovol, etc.), we used beta regression (GLM with beta error). Analyses were conducted separately for the dry and rainy seasons and for each component (Total, Turnover, Richness difference). The overall effect of the measure was summarized as Chi^2 tables to condense the information in a clear and comparable way, and pairwise comparisons among measures were performed with the emmeans package [33], which is based on estimated marginal means (least-squares means) and performs pairwise contrasts while adjusting for model structure [33]. In addition, we evaluated temporal differences for each dissimilarity measure by including season as a fixed factor and sampling as a random factor, since three independent samplings were available within both seasons.

To evaluate the strength of the relationship between the standardized environmental factors and the different dissimilarity measures at each sampling, we used distance-based redundancy analyses (dbRDA). For each case, we used the forward-selection procedure [34] to select the significant environmental factors ($P < 0.05$, 999 permutations). With the variance inflation factor (VIF) we examined the collinearity of the explanatory factors and removed those with VIF >10 [35]. As a strength measure of the environment–dissimilarity relationship, we considered the adjusted R2 calculated from the dbRDA, as these correct the influence of the number of explanatory variables allowing us to compare the results from the different samplings and dissimilarity measures [36].

We did not include an explicit spatial eigenfunction term (e.g., dbMEM/PCNM) because sampling units follow a strongly directional longitudinal gradient where spatial structure is largely expressed through hydrodynamic and limnological gradients already represented by measured predictors [16]. Therefore, inferences are limited to environment–community associations along this longitudinal template, and we do not attempt to partition pure spatial versus environmental effects.

We then compared adjusted R^2 values among dissimilarity measures to determine which were more sensitive to environmental variation. Because adjusted R^2 values ranged between 0 and 1, we applied beta regression (GLM with beta error), using a zero-inflated beta model when the response contained zeros (i.e., no detectable environment–community relationship). Analyses were performed separately for each beta-diversity component (Total, Turnover, Richness difference) and for each season. The overall effect of the measure was summarized as Chi² table.

We further evaluated temporal differences for each dissimilarity measure (within each beta-diversity component) by including season as a fixed factor and sampling as a random factor. For Richness Difference in the rainy season, the measures bFD.index.biovol and FG.occu were excluded because they consistently yielded zeros, indicating that the environment did not influence community variation under those metrics. Model diagnostics were checked with DHARMa [37], and regressions were fitted with glmmTMB [38]. Beta-diversity measures based on traits and convex hull were computed with the mFD package [39], while dendrogram-based indices were obtained with the BAT package [40]. Beta-diversity values and their components based on species and functional groups were calculated with adespatial [41]. Visualizations were produced with ggplot2 ([42]. All analyses were conducted in R [43].

3. Results

3.1. Environmental Seasonal Variation

Seasonality seemed to affect the environmental conditions in the study zone as revealed in the first axis of the PCA (Figure 2). Rainy periods were related to higher water flow (FR) and mixing of the water column, while dry showed higher conductivity, pH, and dissolved oxygen (Table 3). The second PCA axis revealed a spatial gradient in the abiotic conditions for both seasons, with lotic regions related to higher phosphorus concentration, and Zeu:Zmax and Zmix:Zmax ratios, while lentic conditions related to higher light availability (Zeu) and depth.

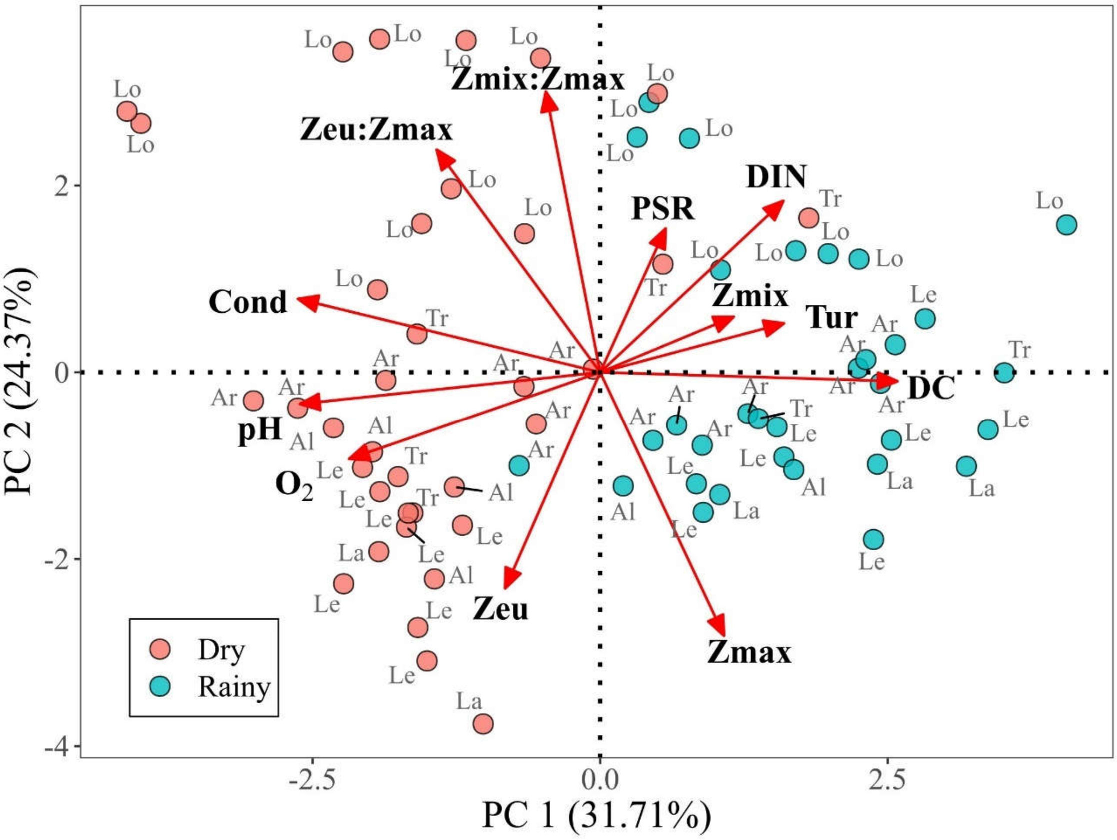

Figure 2. Seasonal and spatial variation in the environmental conditions in the influence area of the Corumbá Dam. Lo – lotic region; Le – lentic region, Tr – Tributary; Ar – right arm; Al – left arm. DIN – dissolved inorganic nitrogen; SRP – reactive soluble phosphorus; Tur – turbidity; Con – Conductivity; DC – discharge; Zeu – euphotic zone; Zeu:Zmax – Euphotic zone:depth max ratio; Zmix:ZmaxZmixZmax – mixed depth:depth max ratio.

Table 3. Mean values and coefficient of variation (CV—in %) of the environmental variables measured at the sampling sites during the rainy and dry periods. Temperature -WT (°C), dissolved oxygen - DO (mg L^{-1}), pH, electrical conductivity - Con (µScm^{-1}), turbidity -Tur (NTU), ammonium -NH4+ (µg L^{-1}), nitrate -NO3 - (µg L^{-1}), total Kjeldahl nitrogen—TKN (µg L^{-1}), dissolved phosphorus—DP (µg L^{-1}), soluble reactive phosphorus - SRP (µg L^{-1}), total phosphorus—TP (µg L^{-1}), water residence time—RT (days), Discharge—DC (m^3 S^{-1}), euphotic zone—Zeu (m), mixing zone—Zmix (m), maximum zone—Zmax (m), mixing zone/maximum zone ratio—Zmix:Zmax (m), euphotic zone/mixing zone ratio—Zeu:Zmix (m).

Variable	Rainy		Dry	
	mean	CV	mean	CV
Z_{mix}	5.621	128	5.000	120
Z_{max}	34.879	65	32.267	70
Z_{mix}:Z_{max}	0.371	125	0.369	118
Zeu	2.739	96	2.849	91
Z_{eu}:Z_{max}	0.186	148	0.217	138
WT	31.388	103	31.197	102
NO_3	147.603	91	170.333	104
NH_4	13.926	88	18.090	156
DIN	161.529	83	188.424	96
TKN	454.743	48	454.818	46
DP	9.157	34	9.873	40
SRP	5.422	32	5.455	31
TP	20.343	58	22.377	60
O_2	7.941	15	7.892	18
pH	7.717	12	7.845	12
Con	43.338	26	45.327	23
Tur	37.565	166	32.437	189
DC	418.241	79	318.583	97
RT	10.439	178	8.637	216

3.2. Beta Diversity Variation

Total diversity values (βT) varied among measures (Figure 3, Table 4). The measures based on species showed higher values, followed by FG.biovol, and bFD.index.biovol. Lower values were related to measures using species/FG occurrence in its calculus (bFD.index.occu, FG.occu, mFD.index). Turnover (βt) also had low correspondence among measures in both the rainy and dry seasons (supplementary material). Higher βt was observed for measures based on species while lower values were related to dendrogram-based measures (Figure 2). For richness difference/nestedness (βd), higher values were shown by bFD.index.biovol while the other measures did not show differences among them.

In general, we observed changes in the relative contribution of beta-diversity components from species-based to functional indices. At the species level, turnover (βt) dominated, but its contribution progressively decreased through RFG and functional indices, whereas richness difference (βd) gained importance along that gradient. In dendrogram-based measures, particularly when biovolume was considered, turnover was lower and richness difference became the main contributor (Figure 6).

In the case of the seasonal variation, just mFD.index, FG.biovol and sp.biovol showed differences for βT, with higher values in the rainy season. For βt, mFD.index, FG.biovol, sp.biovol, and sp.occu showed variation with higher values in the rainy season. Only sp.occu showed a difference for βd, with higher values in the dry (Table 5).

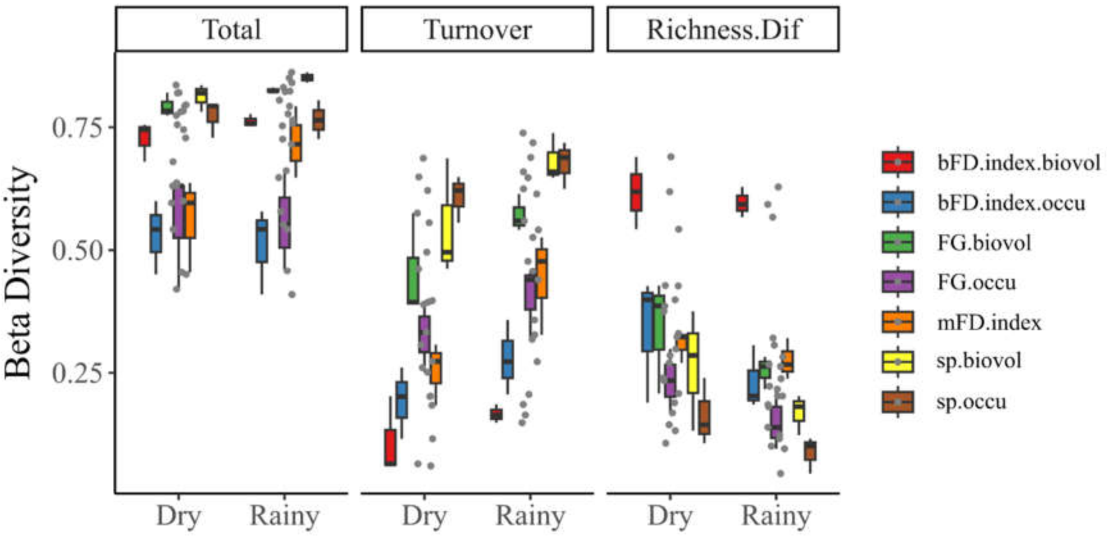

Figure 3. Variation of beta diversity and its components (Total, Turnover, and Richness Difference) across taxonomic and functional approaches in each season. Please refer to the supplementary material for detailed pairwise comparisons among measures within each season (Table A3 and A4).

3.2. Effect of Environment on Beta Diversity

In relation to the effect of the environment on beta diversity, in the dry seasons there were no differences among measures for any beta diversity component (Figure 4, Table 4). In the Rainy season, βT did not varied among metrics, while bFD.index.biovol showed the lowest explanation for βt, being lower than FG.biovol, mFD.index, sp.biovol, and sp.occu. In the case of βd, bFD.index.occu showed the highest explanation. Cases of null explanation of the environment on community variation were related mainly to the richness difference (Figure 5), related to the fact that no one explanatory factor was selected in the forward procedure (supplementary material, Table A2).

Considering the seasonal variation of the beta diversity component for each measure, no variation was observed in βT for any measure (Table 6). For βt, only mFD.index and FG.occu varied, with higher explanation in the rainy season. For βd, bFD.index.occu and sp.occu showed higher explanation in the rainy season, while sp.biovol had a higher explanation in the dry season (Table 4).

In general, we observed that explanation of environment on communities related to richness differences follow or expectation, increasing in a gradient from species to functional indices, especially related to biovolume (Figure 6).

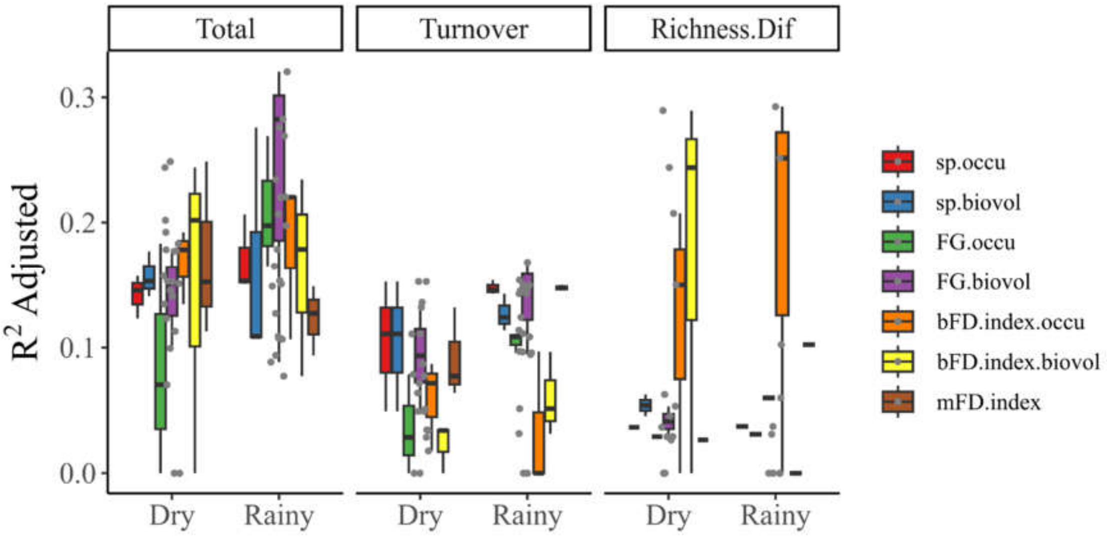

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Figure 4. Seasonal variation in the environmental explanation (adjusted R²) of beta-diversity components (Total, Turnover, and Richness Difference) across different taxonomic and functional approaches. Please refer to the supplementary material for detailed pairwise comparisons among measures within each season (Table A3 and A4).

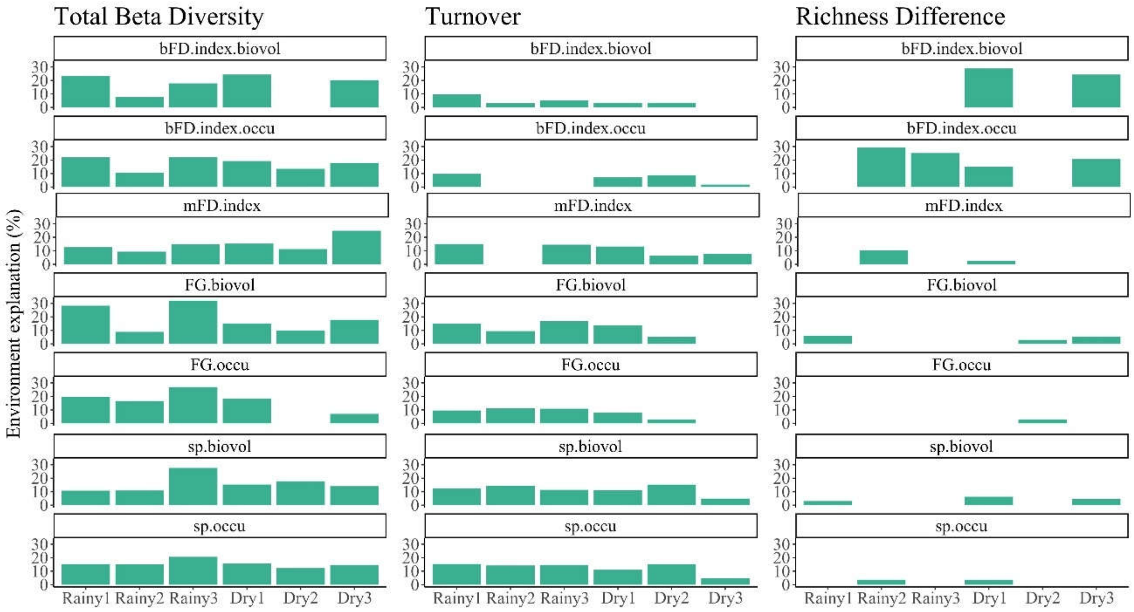

Figure 5. Environmental explanation (adjusted R², %) of community variation for each beta-diversity component (Total Beta Diversity, Turnover, Richness Difference) across the different dissimilarity measures. Results are shown separately for the three rainy (Rainy1–3) and dry (Dry1–3) samplings. Blank spaces indicate cases where the environment had no detectable effect on community variation.

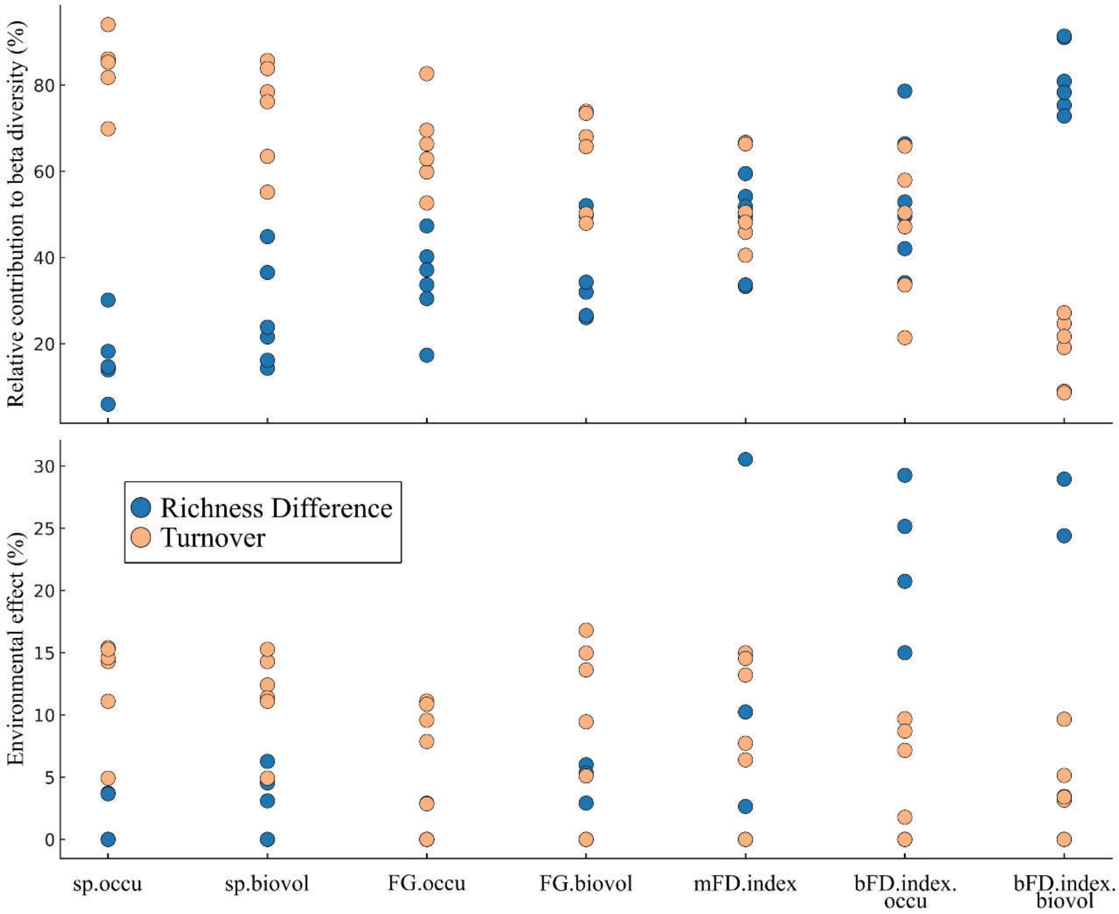

Figure 6. Variation in the relative contribution of beta-diversity components (Turnover and Richness Difference, top panel) and in the environmental explanation (adjusted R^2 × 100, bottom panel) across the different dissimilarity measures. The x-axis order is conceptual (from taxonomic to functional representations) and is used only to facilitate categorical comparison; it does not imply a quantitative gradient or a monotonic trend among measures. Each point represents an independent sampling; fewer points appear in the bottom panel because in some cases no environmental variables were selected, resulting in null explanatory power.

Table 4. Effect of measure type on observed beta diversity components and adjusted R^2 (environmental effect) across seasons. GLM results expressed as Chi^2 statistics. Significant effects ($p < 0.05$) are highlighted in bold. Contrasts are provided in Supplementary Material (Table A3 and A4).

Component	Season	beta diversity	Chisq	Df	Pr(>Chisq)
Diversity value	Rainy	**Total**	**208.21**	**6**	**2.20E-16**
		Turnover	**275.08**	**6**	**2.20E-16**
		Richness difference	**253.90**	**6**	**2.20E-16**
	Dry	**Total**	**128.76**	**6**	**2.20E-16**
		Turnover	**230.35**	**6**	**2.20E-16**
		Richness difference	**69.63**	**6**	**4.88E-13**
R^2 *Adjusted*	Rainy	Total	4.43	6	0.6185
		Turnover	**43.12**	**6**	**1.11E-07**
		Richness difference	**637.90**	**4**	**2.2E-16**
	Dry	Total	10.79	6	0.09516
		Turnover	8.46	6	0.2066
		Richness difference	10.30	6	0.1102

Table 5. Seasonal variation of beta-diversity components (Total, Turnover, Richness difference) calculated with different dissimilarity measures. Estimates represent the effect of the rainy season relative to the dry season (reference). For each model, the table reports the estimate, standard error, z value, and p value from beta regressions (GLM with beta error). Significant results ($p < 0.05$) are highlighted in bold.

Beta component	Measure	Estimate	Std. Error	z value	Pr(>|z|)
Total	**mFD.index**	**0.684**	**0.249**	**2.741**	**0.006**
	FG.biovol	**0.209**	**0.075**	**2.765**	**0.006**
	FG.occu	-0.011	0.298	-0.038	0.969
	sp.biovol	**0.270**	**0.097**	**2.783**	**0.005**
	sp.occu	-0.041	0.144	-0.283	0.777
	bFD.index.occu	-0.083	0.220	-0.376	0.707
	bFD.index.biovol	0.182	0.103	1.760	0.078
Turnover	**mFD.index**	**0.834**	**0.260**	**3.208**	**0.001**
	FG.biovol	**0.476**	**0.214**	**2.225**	**0.026**
	FG.occu	0.336	0.215	1.563	0.118
	sp.biovol	**0.549**	**0.262**	**2.095**	**0.036**
	sp.occu	**0.300**	**0.139**	**2.163**	**0.031**
	bFD.index.occu	0.491	0.282	1.740	0.082
	bFD.index.biovol	0.596	0.334	1.786	0.074
Richness difference	mFD.index	-0.160	0.122	-1.311	0.190
	FG.biovol	-0.372	0.274	-1.356	0.175
	FG.occu	-0.536	0.281	-1.910	0.056
	sp.biovol	-0.477	0.354	-1.346	0.178
	sp.occu	**-0.684**	**0.331**	**-2.067**	**0.039**
	bFD.index.occu	-0.475	0.335	-1.416	0.157
	bFD.index.biovol	-0.093	0.158	-0.589	0.556

Table 6. Seasonal variation of adjusted R^2 values for beta-diversity components (Total, Turnover, Richness difference) calculated with different dissimilarity measures. Estimates represent the effect of the rainy season relative to the dry season (reference). For each model, the table reports the estimate, standard error, z value, and p value from beta regressions (GLM with beta error). NA values appear when no model could be fitted due to lack of replication in one of the seasons. Significant results ($p < 0.05$) are highlighted in bold.

Beta component	measure	Estimate	Std. Error	z value	Pr(>|z|)
Total	mFD.index	-0.338	0.264	-1.276	0.202
	FG.biovol	0.437	0.412	1.059	0.290
	FG.occu	0.663	0.343	1.933	0.053
	sp.biovol	-0.040	0.314	-0.127	0.899
	sp.occu	0.208	0.125	1.665	0.096
	bFD.index.occu	0.056	0.245	0.227	0.820
	bFD.index.biovol	-0.453	0.340	-1.334	0.182
Turnover	**mFD.index**	**0.582**	**0.214**	**2.717**	**0.007**
	FG.biovol	0.490	0.348	1.411	0.158
	FG.occu	**0.820**	**0.273**	**3.003**	**0.003**
	sp.biovol	0.305	0.274	1.111	0.267
	sp.occu	0.477	0.262	1.825	0.068
	bFD.index.occu	0.667	0.516	1.293	0.196
	bFD.index.biovol	0.443	0.375	1.180	0.238
Richness difference	mFD.index	0.028	1.011	0.028	0.978
	FG.biovol	0.428	0.272	1.573	0.116
	FG.occu	0.000	NaN	NaN	NaN
	sp.biovol	**-0.561**	**0.203**	**-2.756**	**0.006**
	sp.occu	**0.017**	**0.000**	**6028.000**	**<2e-16**
	bFD.index.occu	**0.547**	**0.151**	**3.612**	**0.000**
	bFD.index.biovol	0.000	NaN	NaN	NaN

4. Discussion

Our results showed that the detected strength of environment–community association depend as much on the chosen representation (species, functional groups or traits) as on the beta-diversity component analyzed. This reinforces an important point: taxonomic and functional beta diversity are not independent responses, but different representations of the same underlying compositional variation that emphasize different ecological information and levels of aggregation.

Species-based measures reflected higher turnover (βt) than traits-based measures, suggesting that the change in species composition (or the species abundance) was not consistent with the functional turnover of the community. In other words, while communities can show higher rates of species substitutions it does not necessarily reflect higher rates of functional change. Such a situation indicates that the substitution of some species did not modify the functional characteristics of the communities.

It occurs since species in the communities can be functionally redundant and their contribution to the functional attributes of the community may be equivalent. For instance, species from the same genera may share features. Of course, the functional similarity of redundancy will also depend on the functional features considered in the calculus.

Although we did not evaluate the level of functional redundancy, we evidenced that in the case of the functional groups, some RFGs were represented by a high number of species while others were poorly represented (Table A1). For instance, considering the total diversity registered in the study, the RFG – F, composed of colonial Chlorophytes and associated with low nutrient concentration, was represented by 38 taxa, while the RFGs – X2 and SN, tolerant to stratification and to light – and nitrogen-deficient conditions, were represented by one taxon at each case. Moreover, five RFGs

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embraced almost 69% of the total observed richness, which means that those groups were highly represented over space, reducing the functional variation despite species shifts.

In the case of the richness difference (βd), we observed that the spatial variation was higher at the functional approach based on dendrograms and weighted by biovolume, and lower for species. This indicates that functional variation in our study area was more related to shifts in the relative weight of traits than to pure species replacement. In other words, dominant taxa at each site disproportionately determined the functional space, so that local differences emerged from the traits that were favored under local conditions (e.g., buoyancy-related features). Thus, functional richness differences revealed ecologically meaningful changes in the importance of traits across sites, even when species turnover alone did not capture them.

Environmental Associations Across Representations and Beta Components

There was no significant difference among measures when considering total beta diversity. This lack of difference may result from contrasting patterns in the individual components (e.g., stronger environmental relationships for functional groups in turnover, but for species in richness differences), which can cancel each other out when combined into a single total metric.

These findings highlight the importance of analyzing beta diversity components separately, as they are shaped by distinct ecological processes [19,27,44]. However, our approach considering species, functional groups, and traits allow us to suggest that taxonomic and functional turnover, as well as differences in local species and functional richness, may be influenced by different sets of drivers

Although all beta diversity components may respond to broad mechanisms such as dispersal limitation and environmental filtering [45], our results showed that the specific drivers and the strength of their relationships with the environment likely vary depending on the beta diversity component and the dissimilarity metric used and biodiversity facet. Furthermore, those relationships and the specific drivers may also shift in response to natural environmental change and could be influenced by anthropogenic disturbances [46].

Although we identified some differential associations between biodiversity facets and the environment, as well as between the methods used to evaluate dissimilarity, the results did not fully align with our expectations. For instance, and as shown above, the relationship between communities and the environment (considering total dissimilarity) did not differ significantly among species, functional groups, and traits. Moreover, clear differences were observed only during the rainy season.

One possible explanation for null differences during the dry season, is that local environmental conditions at each sampling point exerted more heterogeneous selective pressure on communities, promoting different traits. Indeed, spatial environmental heterogeneity is expected to increase in dry season [47]. Some of these traits may be directly captured by our functional trait or group-based metrics, while others may be embedded within species-level variation that is not explicitly represented in our chosen functional traits. This situation is not unique to our study area. Similar patterns have been reported in subtropical lowland rivers from urbanized areas, where species-level attributes, rather than functional traits, more effectively reveal the influence of the environment on phytoplankton communities [48].

In this sense, the relationship environment–community relationships may differ between species and functional groups, because the traits used to define groups do not necessarily reflect those traits being filtered by environmental conditions [13]. Indeed, our results showed that oxygen concentration and water residence time were significant predictors of beta diversity only at the species level. Therefore, for turnover during the rainy season, these environmental drivers appear to be the main factors shaping community composition. However, the selected traits and functional groups did not respond clearly to these variables, suggesting a mismatch between the traits used in the analysis and those mediating species–environment interactions.

Thus, in some locations, environmental effects may be stronger at the species level, in others at the group level, and in others at the level of individual traits, depending on the main drivers and the traits affected (which are not necessarily represented in groups or in the selected traits). As a result, we may observe overall weak or null differences in how each biodiversity facet responds to environmental variation. Interestingly, this explanation could apply both to community turnover and to differences in the number of species, functional groups, and traits.

On the other hand, our expectations were met when focusing on the richness difference component. In this case, trait-based richness differences showed the strongest relationship with environmental variation. However, in general, the effect of the environment on richness difference was weaker than for turnover.

The weaker relationship between species-based richness differences and environmental variables may be explained by the fact that biodiversity responses to environmental change often manifest primarily as shifts in community composition rather than in species richness itself [6]. Species richness is shaped by multiple underlying components, including individual aggregation, population density, and the species abundance distribution (SAD) ([49]. The contribution of these components to richness can vary substantially depending on environmental conditions and anthropogenic disturbance [50]. Despite this variability, the combined effect of opposing contributions may result in no net change in richness values. Consequently, species richness variation often exhibits weak or inconsistent associations with environmental gradients.

In contrast, richness differences based on functional traits are conceptually linked to the volume of the functional space occupied by each community [26]. This space reflects the range of traits present and, by extension, the range of ecological strategies available. Differences in this functional volume between sites may be related to niche availability and differentiation, as larger trait volumes imply a broader set of resource use strategies or ecological roles being fulfilled.

In this sense, the stronger relationship between functional trait-based richness and the environment may result from the fact that trait expression is directly linked to niche occupancy [51]. Communities that differ in functional richness may be responding to environmental filters that constrain which traits, and thus which strategies, are viable in each context. Therefore, variation in functional richness across sites may better reflect differences in ecological opportunities or constraints, enhancing the environment–community relationship for this component.

In our case, this pattern was particularly evident for dendrogram-based metrics weighted by biovolume, which showed the strongest environmental association. This suggests that, although functional traits were broadly distributed across sites (leading to low functional turnover), the relative importance of those traits varied considerably among locations. As a result, differences in the weight of dominant traits, rather than their mere presence, shaped the functional space and strengthened the link to environmental gradients.

From a practical perspective, these results argue against a single ‘best’ metric for reservoir studies. Instead, the choice should reflect the question: species data are essential when the aim is biodiversity accounting and detecting taxon-specific replacements; functional groups offer an interpretable ecological template; and trait-based indices can provide sensitive detection of shifts in dominant strategies, particularly when abundance information is available.

Finally, the dataset represents an early post-impoundment period, when reservoirs can exhibit pronounced ecological reorganization. While this limits direct extrapolation to mature reservoirs, it also provides a useful window to evaluate metric sensitivity under highly dynamic conditions, an important context for monitoring newly impounded systems and for interpreting ecological trajectories [16].

Overall, framing taxonomic and functional beta diversity as complementary representations helps reconcile apparent differences among metrics and reduces the risk of over-interpreting patterns as processes. Using multiple representations can therefore strengthen inference about how reservoir gradient’s structure phytoplankton communities. Future work could extend these comparisons by explicitly quantifying functional redundancy and by partitioning spatially structured environmental variation, but the present results already provide guidance for choosing beta-diversity representations in reservoir monitoring and comparative limnology.

5. Conclusions

Detecting environmentally structured phytoplankton variation along reservoir gradients depends on both how beta diversity is represented and how it is partitioned. Species, functional groups and trait-based indices capture complementary aspects of the same underlying community change, and their apparent performance differences largely reflect the level of aggregation and the weighting scheme used. In the Corumbá reservoir, abundance-weighted trait-based indices were particularly sensitive to environmental gradients, whereas species- and functional-group approaches provided complementary ecological information. We recommend selecting representations based on study objectives (monitoring sensitivity versus interpretability versus taxon-specific information) and, when possible, combining them to strengthen inference in reservoir ecology.

Supplementary Materials: The following supporting information can be downloaded at the website of this paper posted on Preprints.org.

Author Contributions: Conceptualization, A.P. and L.R.; methodology, A.P. and L.R.; formal analysis, A.P.; investigation, A.P. and L.R.; data curation, A.P. and L.R.; visualization, A.P. and L.R.; writing—original draft preparation, A.P.; writing—review and editing, A.P. and L.R. Both authors contributed equally to all stages of the study. Both authors have read and agreed to the published version of the manuscript.

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Appendix A

Table A1. Species richness for each one Reynolds functional group (RFG).

RFG	Species Richness	RFG	Species Richness
MP	12	S1	5
J	34	E	3
F	38	M	2
X1	14	D	3
K	3	X3	2
C	2	S_N	1
P	5	Z	1
X2	1	A	4
L0	6	W1	6
Y	8	H1	3
N	23	**Total**	176

Table A2. Selected variables for each sampling campaign and dbRDA results. "--", cases without selected variables.

Beta	Measure	Sampling	r2	r2adjust	Variables	F	P
Total	mFD.index	Rainy1	25.19	12.73	PSR	2.02	0.041

Total	mFD.index	Rainy2	16.35	9.38	DIN	2.35	0.012
Total	mFD.index	Rainy3	24.36	14.90	ZeuZmax	2.58	0.005
Total	mFD.index	Dry1	30.66	15.25	Zmax + TR	2.07	0.009
Total	mFD.index	Dry2	18.12	11.30	O2	2.66	0.019
Total	mFD.index	Dry3	41.58	24.88	DIN, pH	2.49	0.007
Total	FG.biovol	Rainy1	42.61	28.26	ZmixZmax + ZeuZmax	2.97	0.001
Total	FG.biovol	Rainy2	15.87	8.85	ZmixZmax	2.26	0.011
Total	FG.biovol	Rainy3	42.5	32.05	TR + ZmixZmax	4.07	0.001
Total	FG.biovol	Dry1	30.56	15.12	cond + ZmixZmax	1.98	0.001
Total	FG.biovol	Dry2	16.87	9.95	ZeuZmax	2.44	0.012
Total	FG.biovol	Dry3	24.07	17.74	DIN	3.80	0.002
Total	FG.occu	Rainy1	27.79	19.76	ZmixZmax	3.46	0.005
Total	FG.occu	Rainy2	22.93	16.51	ZmixZmax	3.57	0.001
Total	FG.occu	Rainy3	32.54	26.92	TR	5.79	0.001
Total	FG.occu	Dry1	33.17	18.31	Zmax + DIN	2.23	0.001
Total	FG.occu	Dry2	0	0	--	0.00	0
Total	FG.occu	Dry3	14.19	7.04	DIN	1.98	0.039
Total	sp.biovol	Rainy1	19.69	10.76	ZmixZmax	2.21	0.002
Total	sp.biovol	Rainy2	24.61	10.90	ZmixZmax + ZeuZmax	1.80	0.001
Total	sp.biovol	Rainy3	38.74	27.60	TR + ZmixZmax	3.48	0.001
Total	sp.biovol	Dry1	30.7	15.30	pH + temp	1.99	0.002
Total	sp.biovol	Dry2	30.37	17.70	ZeuZmax + DIN	2.40	0.001
Total	sp.biovol	Dry3	20.72	14.11	DIN	3.14	0.001
Total	sp.occu	Rainy1	32.27	15.33	Zmax + ZmixZmax	1.91	0.002
Total	sp.occu	Rainy2	21.61	15.08	ZmixZmax	3.31	0.001
Total	sp.occu	Rainy3	32.87	20.67	TR + temp	2.69	0.001
Total	sp.occu	Dry1	31.05	15.72	TR + DIN	2.03	0.001
Total	sp.occu	Dry2	19.07	12.32	ZmixZmax	2.83	0.002
Total	sp.occu	Dry3	21.15	14.57	DIN	3.22	0.001
Total	bFD.index.occu	Rainy1	29.83	22.03	ZmixZmax	3.83	0.005
Total	bFD.index.occu	Rainy2	17.54	10.67	pH	2.55	0.001
Total	bFD.index.occu	Rainy3	28.05	22.05	Zmax	4.68	0.004
Total	bFD.index.occu	Dry1	33.92	19.23	ZmixZmax + DIN	2.31	0.001
Total	bFD.index.occu	Dry2	20.12	13.46	DC	3.02	0.003
Total	bFD.index.occu	Dry3	24.15	17.83	DIN	3.82	0.011
Total	bFD.index.biovol	Rainy1	38.76	23.45	ZmixZmax + zeuzmax	2.53	0.001
Total	bFD.index.biovol	Rainy2	14.82	7.73	ZmixZmax	2.09	0.022
Total	bFD.index.biovol	Rainy3	24.17	17.86	ZmixZmax	3.83	0.001
Total	bFD.index.biovol	Dry1	38.16	24.41	pH + ZmixZmax	2.78	0.001
Total	bFD.index.biovol	Dry2	0	0.00	--	0.00	0
Total	bFD.index.biovol	Dry3	26.33	20.19	DIN	4.29	0.004
Turnover	mFD.index	Rainy1	27.14	14.99	o2	2.23	0.009
Turnover	mFD.index	Rainy2	0	0	--	0.00	0
Turnover	mFD.index	Rainy3	24.03	14.54	TR	2.53	0.008
Turnover	mFD.index	Dry1	29	13.21	Zmax+ PSR	1.84	0.003
Turnover	mFD.index	Dry2	13.59	6.39	pH	1.89	0.003
Turnover	mFD.index	Dry3	17.98	7.73	pH	1.75	0.016
Turnover	FG.biovol	Rainy1	23.48	14.98	ZmixZmax	2.76	0.014
Turnover	FG.biovol	Rainy2	23.38	9.45	ZeuZmax + DIN	1.68	0.001
Turnover	FG.biovol	Rainy3	29.61	16.81	Zmax + temp	2.31	0.001
Turnover	FG.biovol	Dry1	21.47	13.62	Zmax	2.73	0.001
Turnover	FG.biovol	Dry2	12.38	5.1	ZeuZmax	1.70	0.006
Turnover	FG.biovol	Dry3	0	0		0.00	0

Turnover	FG.occu	Rainy1	18.63	9.58	ZmixZmax	2.06	0.026
Turnover	FG.occu	Rainy2	17.97	11.12	ZmixZmax	2.63	0.001
Turnover	FG.occu	Rainy3	17.71	10.86	ZmixZmax	2.58	0.004
Turnover	FG.occu	Dry1	16.24	7.87	Zmax	1.94	0.006
Turnover	FG.occu	Dry2	10.34	2.86	Zmax	1.38	0.061
Turnover	FG.occu	Dry3	0	0	ZmixZmax	0.00	0
Turnover	sp.biovol	Rainy1	29.93	12.41	Zmax + ZmixZmax	1.71	0.005
Turnover	sp.biovol	Rainy2	20.89	14.29	ZmixZmax	3.17	0.001
Turnover	sp.biovol	Rainy3	25.02	11.39	Zmax + temp	1.84	0.001
Turnover	sp.biovol	Dry1	19.19	11.1	TR	2.37	0.001
Turnover	sp.biovol	Dry2	21.78	15.27	ZmixZmax	3.34	0.001
Turnover	sp.biovol	Dry3	12.24	4.92	O2	1.67	0.006
Turnover	sp.occu	Rainy1	32.32	15.4	DC + pH	1.91	0.001
Turnover	sp.occu	Rainy2	20.89	14.29	ZmixZmax	3.17	0.001
Turnover	sp.occu	Rainy3	34.3	14.59	TR + temp + Zmax	1.74	0.001
Turnover	sp.occu	Dry1	19.19	11.1	TR	2.37	0.001
Turnover	sp.occu	Dry2	21.78	15.27	ZmixZmax	3.34	0.001
Turnover	sp.occu	Dry3	12.24	4.92	O2	1.67	0.009
Turnover	bFD.index.occu	Rainy1	18.73	9.7	ZmixZmax	2.07	0.009
Turnover	bFD.index.occu	Rainy2	0	0	--	0.00	0
Turnover	bFD.index.occu	Rainy3	0	0	--	0.00	0
Turnover	bFD.index.occu	Dry1	15.6	7.16	zmax	1.85	0.004
Turnover	bFD.index.occu	Dry2	22.77	8.7	Zmax + ZmixZmax	1.62	0.001
Turnover	bFD.index.occu	Dry3	9.33	1.78	DC	1.24	0.094
Turnover	bFD.index.biovol	Rainy1	18.7	9.66	ZmixZmax	2.07	0.004
Turnover	bFD.index.biovol	Rainy2	10.6	3.15	ZmixZmax	1.42	0.004
Turnover	bFD.index.biovol	Rainy3	12.44	5.14	ZmixZmax	1.71	0.018
Turnover	bFD.index.biovol	Dry1	12.23	3.45	PSR	1.39	0.012
Turnover	bFD.index.biovol	Dry2	10.83	3.4	zmax	1.46	0.019
Turnover	bFD.index.biovol	Dry3	0	0	--	0.00	0
Richness.Dif	mFD.index	Rainy1	0	0	--	0.00	0
Richnes.Dif	mFD.index	Rainy2	24.05	10.24	ZmixZmax + DIN	1.74	0.008
Richnes.Dif	mFD.index	Rainy3	0	0		0.00	0
Richnes.Dif	mFD.index	Dry1	11.5	2.65	O2	1.30	0.087
Richnes.Dif	mFD.index	Dry2	0	0	--	0.00	0
Richnes.Dif	mFD.index	Dry3	38.27	30.56	--	4.96	0.005
Richnes.Dif	FG.biovol	Rainy1	15.41	6	ZeuZmax	1.64	0.004
Richnes.Dif	FG.biovol	Rainy2	0	0	--	0.00	0
Richnes.Dif	FG.biovol	Rainy3	0	0	--	0.00	0
Richnes.Dif	FG.biovol	Dry1	0	0	--	0.00	0
Richnes.Dif	FG.biovol	Dry2	10.39	2.92	ZmixZmax	1.39	0.071
Richnes.Dif	FG.biovol	Dry3	12.61	5.33	Zmax	1.73	0.009
Richnes.Dif	FG.occu	Rainy1	0	0	--	0.00	0
Richnes.Dif	FG.occu	Rainy2	0	0	--	0.00	0
Richnes.Dif	FG.occu	Rainy3	0	0	--	0.00	0
Richnes.Dif	FG.occu	Dry1	0	0	--	0.00	0
Richnes.Dif	FG.occu	Dry2	10.38	2.91	DIN	1.39	0.078
Richnes.Dif	FG.occu	Dry3	0	0	--	0.00	0
Richnes.Dif	sp.biovol	Rainy1	12.77	3.1	ZeuZmax	1.32	0.058
Richnes.Dif	sp.biovol	Rainy2	0	0	--	0.00	0
Richnes.Dif	sp.biovol	Rainy3	0	0	--	0.00	0
Richnes.Dif	sp.biovol	Dry1	14.8	6.27	O2	1.74	0.001
Richnes.Dif	sp.biovol	Dry2	0	0	--	0.00	0

Richnes.Dif	sp.biovol	Dry3	11.88	4.54	zmax	1.62	0.019
Richnes.Dif	sp.occu	Rainy1	0	0	--	0.00	0
Richnes.Dif	sp.occu	Rainy2	11.13	3.72	O2	1.50	0.049
Richnes.Dif	sp.occu	Rainy3	0	0	--	0.00	0
Richnes.Dif	sp.occu	Dry1	12.41	3.66	O2	1.42	0.062
Richnes.Dif	sp.occu	Dry2	0	0	--	0.00	0
Richnes.Dif	sp.occu	Dry3	0	0	--	0.00	0
Richnes.Dif	bFD.index.occu	Rainy1	0	0	--	0.00	0
Richnes.Dif	bFD.index.occu	Rainy2	34.7	29.26	DIN	6.38	0.002
Richnes.Dif	bFD.index.occu	Rainy3	36.67	25.15	Zmax + DC	3.19	0.007
Richnes.Dif	bFD.index.occu	Dry1	22.73	15	DIN	2.94	0.029
Richnes.Dif	bFD.index.occu	Dry2	0	0	--	0.00	0
Richnes.Dif	bFD.index.occu	Dry3	26.84	20.74	DIN	4.40	0.021
Richnes.Dif	bFD.index.biovol	Rainy1	0	0	--	0.00	0
Richnes.Dif	bFD.index.biovol	Rainy2	0	0	--	0.00	0
Richnes.Dif	bFD.index.biovol	Rainy3	0	0	--	0.00	0
Richnes.Dif	bFD.index.biovol	Dry1	35.51	28.95	pH	5.48	0.001
Richnes.Dif	bFD.index.biovol	Dry2	0	0	--	0.00	0
Richnes.Dif	bFD.index.biovol	Dry3	30.22	24.4	DIN	5.20	0.003

Table A3. Pairwise comparisons among dissimilarity measures for beta-diversity components and adjusted R² during the rainy season. Results are based on estimated marginal means (emmeans) from GLMs (beta regression). Parameter indicates whether the response is beta-diversity values ("Diversity") or environmental explanation ("R² Adjusted"). Estimate is the difference in marginal means (first minus second measure); SE = standard error; df = degrees of freedom; t.ratio = test statistic; p.value = p-values adjusted for multiple comparisons in emmeans. Significant differences (p < 0.05) are highlighted in bold.

Parameter	**Beta diversity component**	**contrast**	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
Diversity	Total	**bFD.index.biovol - bFD.index.occu**	**1.130**	**0.138**	**12**	**8.18**	**<.0001**
		bFD.index.biovol - FG.biovol	-0.386	0.158	12	-2.45	0.259
		bFD.index.biovol - FG.occu	**0.937**	**0.139**	**12**	**6.77**	**0.0003**
		bFD.index.biovol - mFD.index	**0.222**	**0.145**	**12**	**1.53**	**0.7237**
		bFD.index.biovol - sp.biovol	**-0.572**	**0.163**	**12**	**-3.50**	**0.0499**
		bFD.index.biovol - sp.occu	-0.010	0.149	12	-0.07	1
		bFD.index.occu - FG.biovol	**-1.517**	**0.148**	**12**	**-10.26**	**<.0001**
		bFD.index.occu - FG.occu	-0.193	0.127	12	-1.53	0.7267
		bFD.index.occu - mFD.index	**-0.908**	**0.134**	**12**	**-6.80**	**0.0003**
		bFD.index.occu - sp.biovol	**-1.702**	**0.154**	**12**	**-11.07**	**<.0001**
		bFD.index.occu - sp.occu	**-1.140**	**0.138**	**12**	**-8.27**	**<.0001**
		FG.biovol - FG.occu	**1.324**	**0.148**	**12**	**8.93**	**<.0001**
		FG.biovol - mFD.index	**0.608**	**0.154**	**12**	**3.95**	**0.0238**
		FG.biovol - sp.biovol	-0.186	0.172	12	-1.08	0.9219
		FG.biovol - sp.occu	0.376	0.158	12	2.38	0.2831
		FG.occu - mFD.index	**-0.715**	**0.134**	**12**	**-5.34**	**0.0025**
		FG.occu - sp.biovol	**-1.509**	**0.154**	**12**	**-9.79**	**<.0001**
		FG.occu - sp.occu	**-0.947**	**0.138**	**12**	**-6.85**	**0.0003**
		mFD.index - sp.biovol	**-0.794**	**0.16**	**12**	**-4.97**	**0.0045**
		mFD.index - sp.occu	-0.232	0.145	12	-1.60	0.684
		sp.biovol - sp.occu	0.562	0.163	12	3.44	0.0553
	Turnover	bFD.index.biovol - bFD.index.occu	**-0.668**	**0.146**	**12**	**-4.59**	**0.0082**
		bFD.index.biovol - FG.biovol	**-1.917**	**0.141**	**12**	**-13.62**	**<.0001**

		bFD.index.biovol - FG.occu	**-1.237**	**0.141**	**12**	**-8.79**	**<.0001**
		bFD.index.biovol - mFD.index	**-1.396**	**0.14**	**12**	**-9.97**	**<.0001**
		bFD.index.biovol - sp.biovol	**-2.397**	**0.144**	**12**	**-16.62**	**<.0001**
		bFD.index.biovol - sp.occu	**-2.370**	**0.144**	**12**	**-16.50**	**<.0001**
		bFD.index.occu - FG.biovol	**-1.249**	**0.125**	**12**	**-9.96**	**<.0001**
		bFD.index.occu - FG.occu	**-0.569**	**0.125**	**12**	**-4.54**	**0.009**
		bFD.index.occu - mFD.index	**-0.728**	**0.125**	**12**	**-5.84**	**0.0011**
		bFD.index.occu - sp.biovol	**-1.730**	**0.129**	**12**	**-13.40**	**<.0001**
		bFD.index.occu - sp.occu	**-1.702**	**0.129**	**12**	**-13.24**	**<.0001**
		FG.biovol - FG.occu	**0.680**	**0.12**	**12**	**5.68**	**0.0015**
		FG.biovol - mFD.index	**0.521**	**0.119**	**12**	**4.39**	**0.0115**
		FG.biovol - sp.biovol	**-0.481**	**0.123**	**12**	**-3.89**	**0.026**
		FG.biovol - sp.occu	**-0.453**	**0.123**	**12**	**-3.69**	**0.0366**
		FG.occu - mFD.index	-0.159	0.119	12	-1.34	0.8237
		FG.occu - sp.biovol	**-1.160**	**0.124**	**12**	**-9.39**	**<.0001**
		FG.occu - sp.occu	**-1.133**	**0.123**	**12**	**-9.21**	**<.0001**
		mFD.index - sp.biovol	**-1.002**	**0.123**	**12**	**-8.17**	**<.0001**
		mFD.index - sp.occu	**-0.974**	**0.122**	**12**	**-7.98**	**0.0001**
		sp.biovol - sp.occu	0.027	0.127	12	0.22	1
	Richness Difference	**bFD.index.biovol - bFD.index.occu**	**1.178**	**0.254**	**12**	**4.64**	**0.0076**
		bFD.index.biovol - FG.biovol	**1.151**	**0.253**	**12**	**4.55**	**0.0088**
		bFD.index.biovol - FG.occu	**1.652**	**0.268**	**12**	**6.17**	**0.0007**
		bFD.index.biovol - mFD.index	**1.290**	**0.259**	**12**	**4.98**	**0.0043**
		bFD.index.biovol - sp.biovol	**1.529**	**0.262**	**12**	**5.83**	**0.0012**
		bFD.index.biovol - sp.occu	**2.089**	**0.287**	**12**	**7.28**	**0.0001**
		bFD.index.occu - FG.biovol	-0.027	0.257	12	-0.11	1
		bFD.index.occu - FG.occu	0.474	0.271	12	1.75	0.5987
		bFD.index.occu - mFD.index	0.112	0.262	12	0.43	0.9993
		bFD.index.occu - sp.biovol	0.351	0.266	12	1.32	0.8308
		bFD.index.occu - sp.occu	0.911	0.289	12	3.15	0.0893
		FG.biovol - FG.occu	0.501	0.27	12	1.86	0.5399
		FG.biovol - mFD.index	0.139	0.261	12	0.53	0.9977
		FG.biovol - sp.biovol	0.379	0.265	12	1.43	0.7768
		FG.biovol - sp.occu	0.938	0.289	12	3.24	0.0761
		FG.occu - mFD.index	-0.362	0.275	12	-1.32	0.8316
		FG.occu - sp.biovol	-0.123	0.279	12	-0.44	0.9992
		FG.occu - sp.occu	0.437	0.301	12	1.45	0.767
		mFD.index - sp.biovol	0.240	0.27	12	0.89	0.9681
		mFD.index - sp.occu	0.799	0.294	12	2.72	0.1737
		sp.biovol - sp.occu	0.559	0.297	12	1.88	0.5249
R2Adjust	Total	bFD.index.biovol - bFD.index.occu	-0.167	0.348	6	-0.48	0.9983
		bFD.index.biovol - FG.biovol	-0.367	0.34	6	-1.08	0.914
		bFD.index.biovol - FG.occu	-0.365	0.34	6	-1.07	0.9157
		bFD.index.biovol - mFD.index	0.229	0.37	6	0.62	0.9934
		bFD.index.biovol - sp.biovol	-0.002	0.357	6	-0.01	1
		bFD.index.biovol - sp.occu	-0.126	0.35	6	-0.36	0.9997
		bFD.index.occu - FG.biovol	-0.200	0.331	6	-0.60	0.9941
		bFD.index.occu - FG.occu	-0.198	0.331	6	-0.60	0.9943
		bFD.index.occu - mFD.index	0.395	0.362	6	1.09	0.9101
		bFD.index.occu - sp.biovol	0.164	0.348	6	0.47	0.9984
		bFD.index.occu - sp.occu	0.041	0.342	6	0.12	1

	FG.biovol - FG.occu	0.002	0.322	6	0.01	1
	FG.biovol - mFD.index	0.595	0.354	6	1.68	0.6485
	FG.biovol - sp.biovol	0.364	0.34	6	1.07	0.916
	FG.biovol - sp.occu	0.241	0.333	6	0.72	0.9854
	FG.occu - mFD.index	0.593	0.354	6	1.68	0.6512
	FG.occu - sp.biovol	0.362	0.34	6	1.07	0.9177
	FG.occu - sp.occu	0.239	0.333	6	0.72	0.9859
	mFD.index - sp.biovol	-0.231	0.37	6	-0.62	0.993
	mFD.index - sp.occu	-0.355	0.364	6	-0.97	0.9431
	sp.biovol - sp.occu	-0.124	0.35	6	-0.35	0.9997
Turnover	contrast	estimate	SE	df	t.ratio	p.value
	bFD.index.biovol - bFD.index.occu	-0.612	0.261	6	-2.35	0.3507
	bFD.index.biovol - FG.biovol	**-0.973**	**0.188**	**6**	**-5.17**	**0.0188**
	bFD.index.biovol - FG.occu	-0.699	0.195	6	-3.59	0.0917
	bFD.index.biovol - mFD.index	**-1.083**	**0.199**	**6**	**-5.44**	**0.0148**
	bFD.index.biovol - sp.biovol	**-0.906**	**0.189**	**6**	**-4.78**	**0.0271**
	bFD.index.biovol - sp.occu	**-1.082**	**0.186**	**6**	**-5.82**	**0.0105**
	bFD.index.occu - FG.biovol	-0.360	0.234	6	-1.54	0.7208
	bFD.index.occu - FG.occu	-0.087	0.24	6	-0.36	0.9996
	bFD.index.occu - mFD.index	-0.471	0.243	6	-1.93	0.5243
	bFD.index.occu - sp.biovol	-0.294	0.236	6	-1.25	0.8534
	bFD.index.occu - sp.occu	-0.470	0.233	6	-2.02	0.4842
	FG.biovol - FG.occu	0.274	0.157	6	1.74	0.6199
	FG.biovol - mFD.index	-0.110	0.163	6	-0.68	0.9894
	FG.biovol - sp.biovol	0.066	0.151	6	0.44	0.9989
	FG.biovol - sp.occu	-0.110	0.146	6	-0.75	0.9826
	FG.occu - mFD.index	-0.384	0.171	6	-2.25	0.3867
	FG.occu - sp.biovol	-0.207	0.159	6	-1.30	0.8307
	FG.occu - sp.occu	-0.383	0.155	6	-2.48	0.3066
	mFD.index - sp.biovol	0.177	0.165	6	1.07	0.9157
	mFD.index - sp.occu	0.001	0.16	6	0.01	1
	sp.biovol - sp.occu	-0.176	0.148	6	-1.19	0.8769
Richness Difference	**bFD.index.occu - FG.biovol**	**1.760**	**0.1196**	**4**	**14.718**	**0.0006**
	bFD.index.occu - mFD.index	**1.182**	**0.0975**	**4**	**12.123**	**0.0013**
	bFD.index.occu - sp.biovol	**2.445**	**0.1582**	**4**	**15.453**	**0.0005**
	bFD.index.occu - sp.occu	**2.259**	**0.1461**	**4**	**15.454**	**0.0005**
	FG.biovol - mFD.index	-0.578	0.1421	4	-4.068	0.0665
	FG.biovol - sp.biovol	0.685	0.189	4	3.626	0.0947
	FG.biovol - sp.occu	0.498	0.179	4	2.784	0.1961
	mFD.index - sp.biovol	**1.263**	**0.1759**	**4**	**7.184**	**0.0093**
	mFD.index - sp.occu	**1.077**	**0.1651**	**4**	**6.521**	**0.0132**
	sp.biovol - sp.occu	-0.187	0.2068	4	-0.904	0.8825

Table A4. Pairwise comparisons among dissimilarity measures for beta-diversity components and adjusted R^2 for the dry season. Results are based on estimated marginal means (emmeans) from GLMs (beta regression). Parameter indicates whether the response is beta-diversity values ("Diversity") or environmental explanation ("R^2 Adjusted"). Estimate is the difference in marginal means (first minus second measure); SE = standard error; df = degrees of freedom; t.ratio = test statistic; p.value = p-values adjusted for multiple comparisons in emmeans. Significant differences ($p < 0.05$) are highlighted in bold.

Parameter	Beta diversity component	contrast	estimate	SE	df	t.ratio	p.value

Diversity	Total	bFD.index.biovol - bFD.index.occu	**0.8521**	**0.167**	**12**	**5.093**	**0.0036**
		bFD.index.biovol - FG.biovol	-0.3629	0.185	12	-1.961	0.4819
		bFD.index.biovol - FG.occu	**0.7314**	**0.167**	**12**	**4.37**	**0.0118**
		bFD.index.biovol - mFD.index	**0.7197**	**0.168**	**12**	**4.275**	**0.0138**
		bFD.index.biovol - sp.biovol	-0.4814	0.188	12	-2.554	0.2223
		bFD.index.biovol - sp.occu	-0.2412	0.182	12	-1.329	0.8267
		bFD.index.occu - FG.biovol	**-1.215**	**0.177**	**12**	**-6.875**	**0.0003**
		bFD.index.occu - FG.occu	-0.1207	0.158	12	-0.765	0.9844
		bFD.index.occu - mFD.index	-0.1325	0.159	12	-0.834	0.9761
		bFD.index.occu - sp.biovol	**-1.3336**	**0.18**	**12**	**-7.4**	**0.0001**
		bFD.index.occu - sp.occu	**-1.0934**	**0.173**	**12**	**-6.324**	**0.0006**
		FG.biovol - FG.occu	**1.0944**	**0.177**	**12**	**6.19**	**0.0007**
		FG.biovol - mFD.index	**1.0826**	**0.178**	**12**	**6.092**	**0.0008**
		FG.biovol - sp.biovol	-0.1185	0.197	12	-0.603	0.9955
		FG.biovol - sp.occu	0.1217	0.19	12	0.64	0.9938
		FG.occu - mFD.index	-0.0118	0.159	12	-0.074	1
		FG.occu - sp.biovol	**-1.2129**	**0.18**	**12**	**-6.728**	**0.0003**
		FG.occu - sp.occu	**-0.9727**	**0.173**	**12**	**-5.624**	**0.0016**
		mFD.index - sp.biovol	**-1.2011**	**0.181**	**12**	**-6.629**	**0.0004**
		mFD.index - sp.occu	**-0.9609**	**0.174**	**12**	**-5.525**	**0.0018**
		sp.biovol - sp.occu	0.2402	0.193	12	1.242	0.8647
	Turnover	bFD.index.biovol - bFD.index.occu	-0.667	0.246	12	-2.714	0.1754
		bFD.index.biovol - FG.biovol	**-1.951**	**0.226**	**12**	**-8.637**	**<.0001**
		bFD.index.biovol - FG.occu	**-1.406**	**0.23**	**12**	**-6.099**	**0.0008**
		bFD.index.biovol - mFD.index	**-1.06**	**0.236**	**12**	**-4.498**	**0.0095**
		bFD.index.biovol - sp.biovol	**-2.341**	**0.226**	**12**	**-10.369**	**<.0001**
		bFD.index.biovol - sp.occu	**-2.591**	**0.228**	**12**	**-11.362**	**<.0001**
		bFD.index.occu - FG.biovol	**-1.284**	**0.197**	**12**	**-6.512**	**0.0004**
		bFD.index.occu - FG.occu	**-0.738**	**0.202**	**12**	**-3.649**	**0.0391**
		bFD.index.occu - mFD.index	-0.393	0.208	12	-1.893	0.5192
		bFD.index.occu - sp.biovol	**-1.673**	**0.197**	**12**	**-8.498**	**<.0001**
		bFD.index.occu - sp.occu	**-1.923**	**0.2**	**12**	**-9.618**	**<.0001**
		FG.biovol - FG.occu	0.545	0.178	12	3.066	0.1015
		FG.biovol - mFD.index	**0.891**	**0.185**	**12**	**4.827**	**0.0056**
		FG.biovol - sp.biovol	-0.39	0.171	12	-2.273	0.3287
		FG.biovol - sp.occu	**-0.64**	**0.175**	**12**	**-3.665**	**0.038**
		FG.occu - mFD.index	0.345	0.19	12	1.816	0.5621
		FG.occu - sp.biovol	**-0.935**	**0.178**	**12**	**-5.263**	**0.0028**
		FG.occu - sp.occu	**-1.185**	**0.181**	**12**	**-6.555**	**0.0004**
		mFD.index - sp.biovol	**-1.28**	**0.184**	**12**	**-6.948**	**0.0002**
		mFD.index - sp.occu	**-1.53**	**0.187**	**12**	**-8.169**	**<.0001**
		sp.biovol - sp.occu	-0.25	0.174	12	-1.435	0.7746
	Richness Difference	**bFD.index.biovol - bFD.index.occu**	**1.1781**	**0.254**	**12**	**4.64**	**0.0076**
		bFD.index.biovol - FG.biovol	**1.1509**	**0.253**	**12**	**4.55**	**0.0088**
		bFD.index.biovol - FG.occu	**1.6521**	**0.268**	**12**	**6.174**	**0.0007**
		bFD.index.biovol - mFD.index	**1.2899**	**0.259**	**12**	**4.983**	**0.0043**
		bFD.index.biovol - sp.biovol	**1.5294**	**0.262**	**12**	**5.832**	**0.0012**
		bFD.index.biovol - sp.occu	**2.0887**	**0.287**	**12**	**7.282**	**0.0001**
		bFD.index.occu - FG.biovol	-0.0272	0.257	12	-0.106	1
		bFD.index.occu - FG.occu	0.474	0.271	12	1.752	0.5987

		bFD.index.occu - mFD.index	0.1118	0.262	12	0.427	0.9993
		bFD.index.occu - sp.biovol	0.3513	0.266	12	1.32	0.8308
		bFD.index.occu - sp.occu	0.9107	0.289	12	3.146	0.0893
		FG.biovol - FG.occu	0.5012	0.27	12	1.855	0.5399
		FG.biovol - mFD.index	0.139	0.261	12	0.532	0.9977
		FG.biovol - sp.biovol	0.3785	0.265	12	1.431	0.7768
		FG.biovol - sp.occu	0.9379	0.289	12	3.244	0.0761
		FG.occu - mFD.index	-0.3622	0.275	12	-1.318	0.8316
		FG.occu - sp.biovol	-0.1227	0.279	12	-0.44	0.9992
		FG.occu - sp.occu	0.4367	0.301	12	1.45	0.767
		mFD.index - sp.biovol	0.2395	0.27	12	0.886	0.9681
		mFD.index - sp.occu	0.7988	0.294	12	2.721	0.1737
		sp.biovol - sp.occu	0.5594	0.297	12	1.882	0.5249
R2Adjust	Total	bFD.index.biovol - bFD.index.occu	0.3481	0.222	6	1.568	0.7056
		bFD.index.biovol - FG.biovol	0.5552	0.229	6	2.421	0.3251
		bFD.index.biovol - FG.occu	0.7654	0.267	6	2.863	0.2025
		bFD.index.biovol - mFD.index	0.3666	0.223	6	1.646	0.6662
		bFD.index.biovol - sp.biovol	0.423	0.225	6	1.884	0.5483
		bFD.index.biovol - sp.occu	0.5384	0.229	6	2.354	0.3482
		bFD.index.occu - FG.biovol	0.207	0.218	6	0.948	0.9492
		bFD.index.occu - FG.occu	0.4173	0.258	6	1.618	0.6804
		bFD.index.occu - mFD.index	0.0184	0.211	6	0.087	1
		bFD.index.occu - sp.biovol	0.0748	0.213	6	0.351	0.9997
		bFD.index.occu - sp.occu	0.1903	0.218	6	0.874	0.9644
		FG.biovol - FG.occu	0.2102	0.264	6	0.796	0.9768
		FG.biovol - mFD.index	-0.1886	0.219	6	-0.862	0.9666
		FG.biovol - sp.biovol	-0.1322	0.221	6	-0.599	0.9943
		FG.biovol - sp.occu	-0.0167	0.225	6	-0.074	1
		FG.occu - mFD.index	-0.3988	0.258	6	-1.544	0.7176
		FG.occu - sp.biovol	-0.3424	0.26	6	-1.317	0.8243
		FG.occu - sp.occu	-0.227	0.264	6	-0.861	0.9667
		mFD.index - sp.biovol	0.0564	0.214	6	0.264	0.9999
		mFD.index - sp.occu	0.1719	0.218	6	0.788	0.9779
		sp.biovol - sp.occu	0.1155	0.22	6	0.524	0.9972
	Turnover	bFD.index.biovol - bFD.index.occu	-0.307	0.516	6	-0.595	0.9945
		bFD.index.biovol - FG.biovol	-0.8326	0.519	6	-1.605	0.6869
		bFD.index.biovol - FG.occu	-0.2914	0.561	6	-0.519	0.9973
		bFD.index.biovol - mFD.index	-0.8661	0.486	6	-1.782	0.5981
		bFD.index.biovol - sp.biovol	-0.9556	0.482	6	-1.982	0.502
		bFD.index.biovol - sp.occu	-0.9556	0.482	6	-1.982	0.502
		bFD.index.occu - FG.biovol	-0.5255	0.432	6	-1.215	0.8663
		bFD.index.occu - FG.occu	0.0156	0.483	6	0.032	1
		bFD.index.occu - mFD.index	-0.5591	0.393	6	-1.424	0.7757
		bFD.index.occu - sp.biovol	-0.6486	0.388	6	-1.672	0.6531
		bFD.index.occu - sp.occu	-0.6486	0.388	6	-1.672	0.6531
		FG.biovol - FG.occu	0.5412	0.485	6	1.116	0.902
		FG.biovol - mFD.index	-0.0336	0.394	6	-0.085	1
		FG.biovol - sp.biovol	-0.123	0.389	6	-0.316	0.9998
		FG.biovol - sp.occu	-0.123	0.389	6	-0.316	0.9998
		FG.occu - mFD.index	-0.5747	0.45	6	-1.278	0.8408
		FG.occu - sp.biovol	-0.6642	0.445	6	-1.491	0.7433

	FG.occu - sp.occu	-0.6642	0.445	6	-1.491	0.7433
	mFD.index - sp.biovol	-0.0895	0.344	6	-0.26	0.9999
	mFD.index - sp.occu	-0.0895	0.344	6	-0.26	0.9999
	sp.biovol - sp.occu	0	0.339	6	0	1
Richness Difference	bFD.index.biovol - bFD.index.occu	0.4912	0.427	6	1.151	0.89
	bFD.index.biovol - FG.biovol	1.8907	0.576	6	3.282	0.1282
	bFD.index.biovol - FG.occu	2.1168	0.805	6	2.631	0.2603
	bFD.index.biovol - mFD.index	1.0985	0.478	6	2.298	0.369
	bFD.index.biovol - sp.biovol	1.6499	0.543	6	3.037	0.1674
	bFD.index.biovol - sp.occu	1.9493	0.77	6	2.531	0.2896
	bFD.index.occu - FG.biovol	1.3995	0.593	6	2.361	0.346
	bFD.index.occu - FG.occu	1.6256	0.816	6	1.991	0.4974
	bFD.index.occu - mFD.index	0.6073	0.5	6	1.216	0.866
	bFD.index.occu - sp.biovol	1.1587	0.561	6	2.064	0.4647
	bFD.index.occu - sp.occu	1.4581	0.783	6	1.863	0.5584
	FG.biovol - FG.occu	0.2261	0.893	6	0.253	1
	FG.biovol - mFD.index	-0.7922	0.627	6	-1.263	0.8472
	FG.biovol - sp.biovol	-0.2409	0.673	6	-0.358	0.9997
	FG.biovol - sp.occu	0.0586	0.864	6	0.068	1
	FG.occu - mFD.index	-1.0182	0.841	6	-1.211	0.868
	FG.occu - sp.biovol	-0.4669	0.875	6	-0.534	0.9969
	FG.occu - sp.occu	-0.1675	1.029	6	-0.163	1
	mFD.index - sp.biovol	0.5513	0.598	6	0.921	0.9552
	mFD.index - sp.occu	0.8507	0.809	6	1.052	0.9223
	sp.biovol - sp.occu	0.2994	0.845	6	0.354	0.9997
	sp.biovol - sp.occu	0.2994	0.845	6	0.354	0.9997

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