Community stability and seasonal biotic homogenisation emphasize the effect of the invasive tropical tanner grass on macrophytes from a highly dynamic neotropical tidal river

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Abstract

We described the spatial and temporal dynamics of aquatic macrophytes in a Neotropical coastal estuarine river, and identified the negative effects associated to the presence and dominance of the invasive tanner grass. We compared macrophyte beds along the Guaraguaçu River (South Brazil) over four years, using taxonomic and functional dimensions. Biodiversity descriptors were higher in the driest periods compared to the rainiest, although this difference seems to be decreasing over the studied years. Moreover, the spatial organization of biodiversity and community structure slightly changed over time. Such spatial community stability was highlighted by the dominance of the highly invasive tanner grass. In beds dominated by the invasive species, the biodiversity was reduced. As aquatic macrophytes represent an important group in water bodies, the long-term loss of seasonal differences in community structuring is of concern, mainly regarding its potential to impact other groups and ecosystem functioning. By analysing data from standardized monitoring, we were able to identify a poorly discussed facet of biotic homogenisation—the seasonal homogenisation. We also discussed the impact of massive development of invasive species and its consequences for biodiversity in a Neotropical river of outmost importance for biological conservation.

Introduction

A myriad of interactive ecological factors contributes to explain biodiversity in ecosystems. It is well established for aquatic macrophytes that spatial and temporal changes in species composition are explained by a combination of processes, including seasonal changes, dispersion, hydrological variation and environmental filtering (Lacoul and Freedman

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2006; Bornette and Puijalon 2011; Fritz et al. 2017; Ceschin et al. 2017). At larger scales, dispersion and landscape (including hydrology) are common drivers of the diversity of aquatic plants (Rolon et al. 2010). Within an ecosystem without barriers for dispersal, environmental filtering of species is the predominant factor. Characteristics such as nutrient concentrations (Lacoul and Freedman 2006) and salinity are important drives of macrophyte communities (Alahuhta et al. 2020) and, in this sense, precipitation is expected to be a key factor shaping macrophyte communities (Pavão et al. 2017), given it can directly control nutrient load, physicochemical characteristics, and also affect species' dispersion particularly in environments with seasonal differences in rainfall and with geographic features that highlight effects of rain in hydrology.

At long term, there is a growing consensus that anthropogenic changes in the abiotic and biotic characteristics of a system is the most important underlying cause for species distributions (Pozo et al. 2011; Elo et al. 2018). Among the consequences of anthropogenic impacts is the promotion of invasive species. Negative impacts associated with invasive species are well described (Simberloff et al. 2013), particularly in aquatic systems (Thomaz et al. 2015). In this respect, the dominance of invasive macrophyte species is probably the most emblematic anthropogenic impact on aquatic macrophyte communities at ecosystem scale (Havel et al. 2015; Bolpagni et al. 2020). To illustrate the importance of this impact, the Brazilian hyacinth *Pontederia crassipes* Mart. is considered one of the world's worst invasive species (Lowe et al. 2000). Interestingly, in some Brazilian aquatic environments in which *P. crassipes* is native, one of the most successful invasive species is the African tropical tanner grass *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga (see Amorim et al. 2015). This species was introduced in many countries as a robust and resilient pasture grass, a former common practice in coastal areas of South Brazil (Araújo et al. 2021). In Brazil, the sad history of *Urochloa* species invasion is also associated to accidental introduction given its use as mattress for slaves in slave ships (Sato et al. 2021). The high growth rate, wide physiological tolerance and rapid evolutionary responses of this species result in a very aggressive invader in aquatic macrophyte communities (Michelan et al. 2010; Bora et al. 2020). It is well documented that *U. arrecta* dominates aquatic macrophyte beds and replaces native plant species (Amorim et al. 2015). Nonetheless, this response may depend on the richness and biomass of the native species (Michelan et al. 2013). Therefore, one can expect that different facets of biodiversity will be distinctly affected by the occurrence and dominance of *U. arrecta* in macrophyte beds.

Biodiversity is increasingly being assessed using a functional approach in addition to the usual taxonomy-based ecological indices, such as species richness and diversity

(Vecchia et al. 2020). Indeed, it has been recognized that functional diversity might help to understand the relationship between the biota and ecosystem functioning, as well as the effects of disturbances on the ecosystem's stability and resiliency (Petchey and Gaston 2006; Cadotte et al. 2011; Flynn et al. 2011). Similarly, functional diversity may also be a better proxy for the effects of anthropogenic drivers on the phenomenon of biotic homogenisation (or 'biotic homogenization', see Olden et al. 2018). Management actions that could serve to maintain or even increase diversity over time and space are better defined if the functional role of species in ecosystems is taken into consideration (Song et al. 2014). In this sense, it is important to highlight the need for long-term monitoring programs in order to capture the major temporal and spatial patterns occurring in the different components of biodiversity (Hussner 2014); particularly given that nuisance control of macrophytes is extremely difficult (Hussner et al. 2017). Beyond that, long-term monitoring can help to detect effects of environmental changes, and can provide evidences of biotic homogenisation as a result of species invasions (Strayer et al. 2006).

Here, we described the spatial and temporal dynamics of aquatic macrophyte diversity (both taxonomic and functional) in the Guaraguaçu River, a subtropical coastal tidal river in southern Brazil that has been highly invaded by *U. arrecta* (Araújo et al. 2021). We hypothesized that the main drivers of macrophyte diversity are: i) seasonal pattern of precipitation driving the temporal variation, and ii) the presence and dominance of the invasive tropical tanner grass and, the changes in environmental conditions along the river, leading to spatial variation. Yet, regarding the spatial variation, we expected lower values of taxonomic and functional diversity associated to increased *U. arrecta* dominance, and in sites near the mouth of the river, given that salinity is a limiting factor for aquatic plant colonization (Haller et al. 1974).

Materials and methods

Study area

The Guaraguaçu River (25° 37′ 36.4″ S, 48° 30′ 29.2″ W, Fig. 1) is a tropical river with a strong tidal influence (it discharges into the Paranaguá Bay) and strong salinity gradient (in the last sampling, the salinity ranged from 53.1 to 7460 μS/cm in the first and last sites sampled, respectively). Also, there is conspicuous longitudinal variation, with distinct microhabitats along the course of the river (Lana et al. 2001). It is colonized by aquatic macrophytes along its entire length. The river has a linear total extent of about 60 km and is the largest river of the coastal basin of Paraná State, South Brazil. It is located in one of the best preserved reminiscent

Fig. 1 Geographical location of the macrophyte beds sampled in Guaraguaçu River, Paraná, Brazil. The regions along the river considering the environmental characteristics and anthropic pressure are: pristine "caixetal"—P1–P4; intermediate and human disturbed—P5–P12; mangrove area—P13–P16
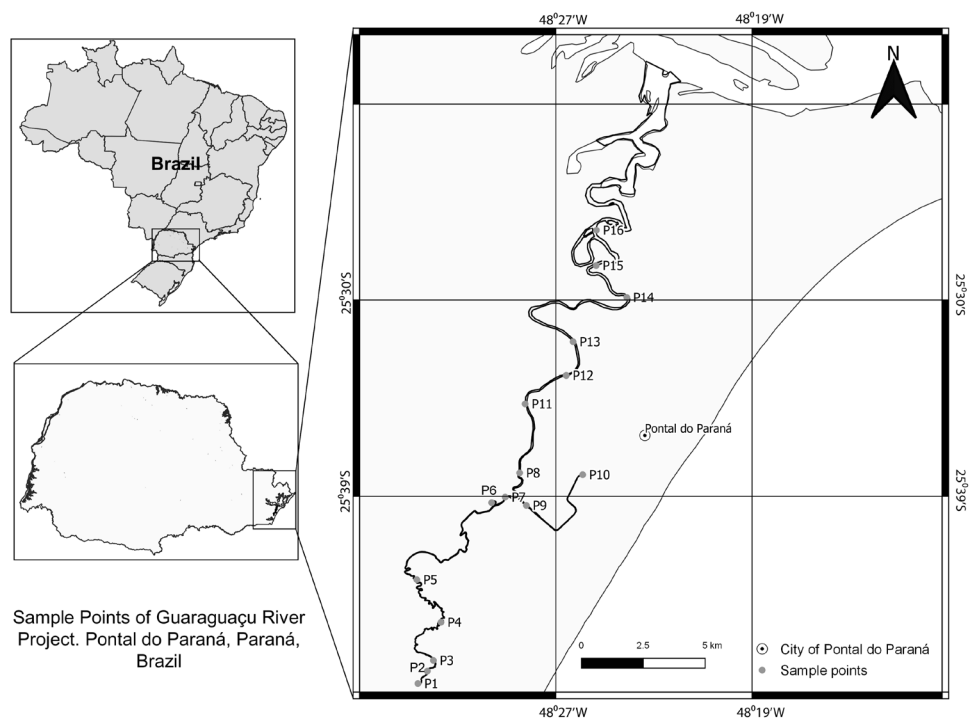
of the Atlantic Forest biodiversity hotspot (Myers et al. 2000), known as Lagamar. Lagamar is the set of estuaries in South-Southeast Brazil (mainly Paraná and São Paulo States) with extremely high importance for conservation, considered as a Biosphere Reserve and World Heritage Site (<https://whc.unesco.org/en/list/893/>). Its headwaters include multiple streams located in the Serra da Prata/Serra do Mar range at an elevation of 766 m above sea level, inside the Saint-Hilaire/Hugo Lange National Park. The region has a tropical and super-humid climate. The average accumulated rainfall is 2300 mm year^{-1}. The rainfall is distributed throughout the year, but there are marked differences between summer and winter: the rainiest season occurs in summer, with an accumulation of about 800 mm year^{-1}, and the driest season occurs in winter, with an accumulation of about 280 mm year^{-1} (Vanhoni and Mendonça 2008). Given the geographic layout of Guaraguaçu river (formed by mountain streams and flowing in the coastal plain), water flow and material leaching is severely affected by extreme rainfall events that occur mainly during the rainiest season in the mountain chains that harbours the headwater streams (Pinto et al. 2012). The mean temperature is between 17 and 21 °C (Vitule et al. 2006).

Considering the changes in environmental characteristics and the nature of anthropic pressures along the river, there are three clearly distinct zones: the upstream near-pristine region known as "caixetal" [i.e., an ecosystem characterized by the high abundance of the amphibious endangered tree *Tabebuia cassinoides* Lam. (DC.) (Bignoniaceae)] (Araújo et al. 2021); the intermediate zone marked by the strong

degradation in water quality associated with anthropic occupation (e.g., wastewater discharge); and the downstream brackish waters marked by less environmental degradation. This gradient has been shown to be important in the determining the structure of the fish association (Contente et al. 2011a).

In the intermediate region, there are two rectified channels used for public water supply, besides the mentioned reception of domestic wastewater. In this region, macrophyte species occur that are considered potentially invasive, such as *U. arrecta* (Fig. S1 in Appendix) and *P. crassipes* Mart. (even though native, *P. crassipes* can achieve invasive status in Brazilian waters, see Michelan et al. 2013; Pavão et al. 2017). The *U. arrecta* beds in this part of the river can reach hundreds of meters long, and dozens of meters large (A.A.P personal observation, see also Fig. S1 in Appendix); in contrast to its small occupation in sites nearby. In the upstream portion of the river, this invasive species is absent, as well as in most part of the mangrove at the river mouth (see Bora et al. 2020).

In addition, there are records of several non-native fish and invertebrate species, such as *Clarias gariepinus* (Burchell, 1822), *Ictalurus punctatus* (Rafinesque, 1818), *Salminus brasiliensis* (Cuvier, 1816), tilapias and Malaysian giant shrimp (Faria et al. 2021).

Data sampling

Sixteen macrophyte beds were selected and georeferenced along the navigable stretch of the river (Fig. 1). Samplings

followed a standardized protocol for continuous monitoring (see details and metadata in <https://lasbufprbio.wixsite.com/home>) and occurred twice a year—in April, ending summer; and in September, ending winter—from 2016 to 2019. Unfortunately, data was not available for 2020 given samplings were cancelled after Sars-COV-2 pandemic. Taxonomic classification and trait measurements were performed in all sampling efforts. April and September were the chosen sampling months given the possible accumulative effects of summer and winter seasons on community structuring. Summer and winter are extremes not only in temperature, but also in precipitation and nutrient input in Guaraguaçu River. Precipitation in summer is substantially higher (Lana et al. 2001) as well as the input of domestic sewage in tributaries of the Guaraguaçu River given the high human density in coastal and touristic cities in the shoreline (IPARDES 2013).

We followed the conventional methods of collection and herborization of aquatic macrophytes (Pedrali 1990) in all macrophyte beds. Specimens of each species in the reproductive stage were collected, herborized, and indexed in the scientific collection of the Botany Department Herbarium of the Federal University of Paraná (UPCB-UFPR). The minimum extent of each macrophyte bed selected was 50 m, so all macrophyte species within the georeferenced 50-m stretch were recorded—an adaptation for aquatic macrophytes of the RAPELD protocol (see Magnusson et al. 2005). The distances between macrophytes beds were never lower than 1 km. We estimated the abundance of each species recorded in macrophyte bed using Braun-Blanquet abundance classes, considering the occupancy of each species in the 50-m extension of macrophyte beds ($0 = 0\%$; $1 =$ less than 5%; $2 = 5–25\%$; $3 = 25–50\%$; $4 = 50–75\%$; $5 =$ greater than 75% of occupancy).

Aquatic macrophytes are modular organisms with common vegetative reproduction. So, three modules (we consider a module a repeated part of the plant containing all vegetative organs) of each species recorded were selected from each macrophyte bed to measure the following functional traits: root length (cm), leaf length (cm), leaf width (cm), leaf area (cm^2), petiole length (cm), stem width (cm) and herbivory degree (using the same Braun-Blanquet classes described above when considering the percentage of leaf area showing herbivory). Averages of each trait from all samplings were then used to calculate functional diversity (see 'Data analysis'). We selected the most different modules possible in each macrophyte bed (the largest, the smallest and one common-sized intermediate) in an attempt to represent most trait variation of a species within a macrophyte bed. However, due to clonal and vegetative reproduction, it is very likely that modules of a same bed are from a same clonal individual. We consulted specialized bibliographies (APG 2009; Pott and Pott 2000; Moura-Junior et al. 2015)

to determine the life form (emergent, rooted floating, free floating, rooted submerged, free submerged, amphibious, epiphyte) for each species. Functional traits abovementioned are commonly used in studies of aquatic macrophytes (e.g. Fu et al. 2014) and provide important information on biological responses to environmental variation, since they might affect critical stages of colonization and establishment, as well as the adaptive value of species (Violle et al. 2007; Cavalli et al. 2014).

Because of the close association of *U. arrecta* with degraded habitats (Araújo et al. 2021), we considered its presence to be an indicator of environmental quality. Therefore, we separated the aquatic macrophyte beds into three classes based on the abundance of *U. arrecta*: "Absent", "Dominant" and "Not dominant". A fourth class was used to designate the downstream Mangrove zone, where *U. arrecta* poorly occur, probably due the higher salinity (Bora et al. 2020).

Data analysis

We calculated the popular indices of local taxonomic (species richness, Pielou's evenness and Shannon–Wiener) and functional (functional richness—FRic, functional divergence—FDiv, functional dispersion—FDis, functional evenness—FEve and Rao's quadratic entropy—RaoQ; Laliberté and Legendre 2010) diversity (hereafter alpha diversity) for each sampling site in each sampling. The functional diversity indices were calculated using averages of all measurements of the traits. To assess the effect of seasonal rainfall on taxonomic and functional indices as evidence of a seasonal pattern, we ran a linear model, with permutations when the residuals were not normal. The mean diversity index was the response variable and the cumulative rainfall for the 15 days previous the start of field sampling was the explanatory variable indicative of seasonal effects. To calculate the cumulative rainfall, daily rainfall data was summed until the date of the sampling. These data were collected from the National Institute of Meteorology website <https://mapas.inmet.gov.br/>; the meteorological station is approximately 8 km from the Guaraguaçu River in straight line. The accumulated rainfall was also contrasted according to the month of sampling and according to the season (i.e., summer and winter) by performing an ANOVA.

The functional alpha diversity indices were compared among samplings using tests that account for repeated measures of the sites. In cases where a site or sample did not contain the minimum number of species necessary to calculate a particular diversity index, the index was not calculated. Incomplete data and the normality of its distribution were conditions driving the statistical analysis performed for each index: FRic, FEve and FDiv—Durbin Test, post hoc Conover Iman Test; FDis—linear mixed effects model, post

hoc Tukey Test; RaoQ—Friedman Test, post hoc Conover Iman Test.

We then assessed the spatial variation along the river by contrasting the number of shared species pairwise with the distance among the respective sites, using an ordinary linear model or a linear model with permutations when the residuals were not normal. The dependent variable was the number of shared species and the independent variable was the distance. The distance was manually calculated by connecting the sites in QGis software version 3.10.4 (QGIS.org 2021).

The number of species at each site shared with the other sites was evaluated in relation to accumulated rainfall and between the samplings. In the first case, we used the sum of shared species in the sampling period as the dependent variable and the rainfall as the independent variable. In the second case, we used the Friedman test, considering the pairwise differences as the blocks. Post hoc pairwise comparisons were performed by Conover–Iman test.

Temporal changes in community composition were assessed using two approaches. First, we used the temporal beta diversity index (TBI; Legendre 2019). In TBI, a dissimilarity index is calculated for the same sites between two moments or times, and through permutations the sites which had an extraordinary level of dissimilarity in relation to the others are identified. The analysis can also provide the components loss (B) and gain (C) of the dissimilarity index, and they can be differentiated through a permuted paired t test. Therefore, the analysis can inform us if there were more losses or gains in abundance-per-species and/or species occurrences between the distinct times or dates. The second approach was the *betadisper* function (Anderson et al. 2006), intended to inform about the whole dissimilarity (using a Bray–Curtis dissimilarity index) of the river compared between each sampling. In summary, the *betadisper* approach calculates the dispersion around the centroid of a given group (i.e. variance) using a dissimilarity matrix, and then compares the dispersion among groups. In our case, the *betadisper* approach informed us if there was any sampling period with higher or lower taxonomic variation among the sites sampled in the river. Also, compositional

changes were evaluated through Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001). The TBI and *betadisper* approaches were also performed using the community-level weighted means of trait values (CWM), in order to analyse temporal changes in traits. For that, the Euclidean distances were applied to standardized CWM values. The CWM is the average value of a trait in the community, considering the relative abundances of each species. Therefore, CWM represents the dominant value of a given trait in the community.

We used the categories of dominance of *U. arrecta* to evaluate its possible effects on the functional and taxonomic indexes. Then, we compared the indices from each dominance category in each sampling using ANOVA. *Betadisper* was used with the dominance categories as the groups for comparisons of the homogeneity of variances, both with the taxonomic and CWM matrices. We also performed a comparison of the dominance categories using data from all samplings. In this case, we performed a linear mixed effects model (distances to centroid ~ category of dominance, random = ~ 1|sampling) and used Tukey Test for post hoc pairwise comparisons. Finally, we used the analysis of Indicator Value (IndVal, Dufrene and Legendre 1997) to evaluate if and which species were typical for each class of *U. arrecta* dominance. We called the species significantly associated with the classes as the indicator species. We used these analyses as well to explore indicator species of sampling sites and periods (summer and winter, see Table S1 in Appendix).

All analyses and graphing were performed in R software, version 4.0.2 (R Core Team 2020; see Table S1 in Appendix to specific functions and packages used). For all tests, we considered significant differences when type I error was lower than 5%.

Results

The accumulated rainfall differed between summer (mean 998.25 ± 305.03 mm) and winter (mean 159.42 ± 135.86 mm; $F_{1,6} = 25.24$, $P = 0.00239$; Fig. 2a).

Fig. 2 Average accumulated rainfall and standard deviations of **a** the whole summer and winter seasons; and **b** of the 15 days before the samplings. Different letters represent statistical difference. Dates for the selection of data were: summer–December-21th–March-20th; winter: June-21th–September-21th

a Season accumulated rainfall

b Accumulated rainfall of 15 days before sampling
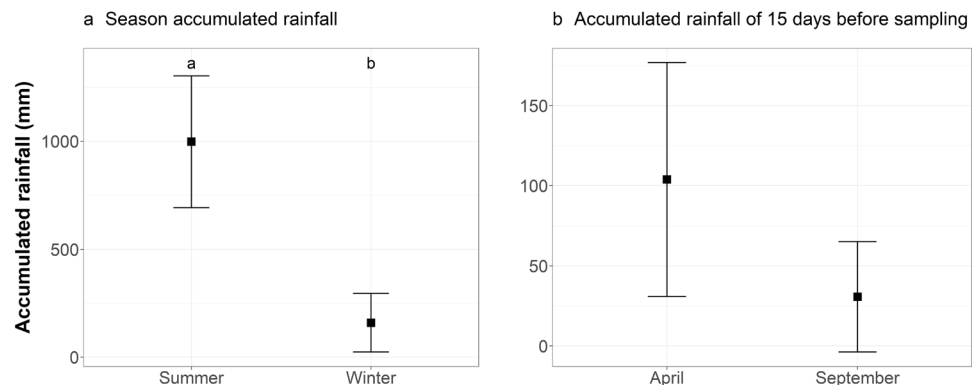
However, the accumulated rainfall of the 15 days before the sampling was not different between April (mean 103.9 ± 72.95 mm) and September (mean 30.7 ± 34.49 mm; $F_{1,6} = 3.291$, $P = 0.12$; Fig. 2b).

A total of 39 species were identified. According to the species accumulation curve (Fig. S2 in Appendix), these were a good representation of the aquatic macrophyte community of the Guaraguaçu River. The maximum number of species sampled in one macrophyte bed was 20, in September 2018 at sampling site 11. The minimum of one species was recorded in site 16 (i.e., the last mangrove site) in five samplings (April 2017 and September of all years), and at sites 15 and 9 at September 2016. The minimum and maximum values of Shannon–Wiener index were 0.60 and 2.85. The maximum was associated with the same site and sampling period where the maximum richness was found; the minimum value was at sampling site 1 in September 2016. The highest Pielou index value was recorded at site 10 in April 2017, and the lowest non-zero value was recorded at site 16 in September 2016. The site 15 in April 2016 and September 2017 reached the value of 1 for Pielou, but as it was a bias of the reduced number of species, we did not consider it as the maximum.

Spatial and temporal patterns in alpha diversity

There was no relationship between the 15 days accumulated rainfall before the samplings and the alpha taxonomic species richness, averaged Shannon–Wiener index and averaged Pielou index in any of the samplings (Fig. S3 in Appendix).

The sum of shared species among pairs of sites was not dependent on the rainfall accumulated 15 days before the samplings (Fig. 3), although more species were shared in summer than in winter in 2018 and 2019 (chi-squared = 307.52, $P < 0.001$; Fig. 4). On the other hand, the number of shared species in pairs of sites was dependent on the distance between sites in all periods (see Fig. S4 in Appendix), confirming that more species are shared between nearby sites. There is clear spatial autocorrelation consistent to river-continuous dependency.

Similar to the results regarding the taxonomic indexes, the averaged functional alpha diversity indices were not related to the accumulated rainfall during the 15 days previously the samplings (Fig. S5 in Appendix). However, Fric, Fdis and RaoQ entropy differed between the samplings. In general, there was a trend of higher values in April in comparison to September, and this pattern of increase in April and decrease in September was more consistent in Fric (Fig. 5 and Fig. S6 in Appendix). In relation to the spatial distribution of functional diversity indices, elevated values were, in general, associated with sites 5 and 6 (Fig. S7 in Appendix).

The temporal beta diversity is shown in Fig. 6, both as abundance-per-species and occurrence data. Sites that
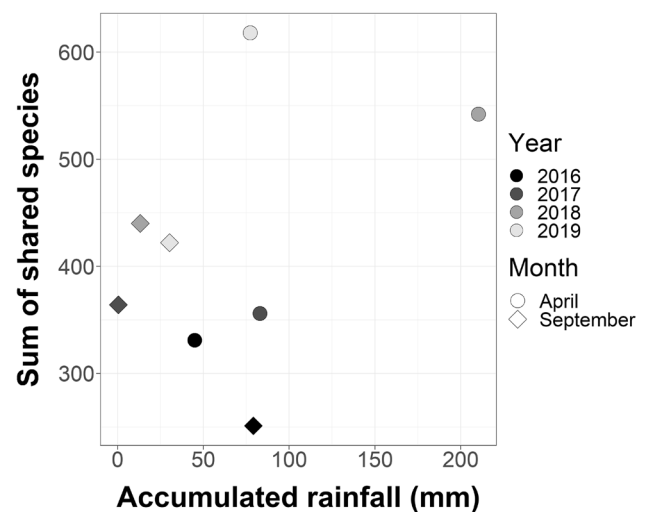

Fig. 3 Scatterplot of the sum of shared species among pairs and accumulated rainfall (15 days before the survey) from each sampling. There was no relationship between the variables ($F_{1,6} = 1.05$, $P = 0.345$)

changed significantly between the samplings were only detected using the occurrence data, in the comparisons April/18-Sep/18—site 15, Sep/18-April/19—site 16 and April/19-Sep/19—site 16. Yet, on some occasions, the gain and loss components of TBI differed, and gains in abundance-per-species and number of species were associated with transition from winter to summer (Table 1 and asterisks in Fig. 6). Irrespective of the type of the data, abundance-per-species or occurrence, a trend toward a reduction in the mean dissimilarity can be observed. Thus, during the period studied, the sites reduced the seasonal variability between summer and winter.

No differences in the distances to the centroids among the sampling periods using *betadisper* approach were found (PERMUTEST: $F_{7,120} = 0.5655$; $P = 0.7913$; Fig. 7a, c); meaning that the dissimilarities in community composition in the river were the same during the studied period. Also, no significant changes in species composition occurred (PERMANOVA: $F_{7,120} = 1.1068$; $P = 0.2943$).

The analysis of temporal functional beta diversity, i.e., application of the TBI approach on the CWM matrix, revealed the same pattern as the taxonomic data: a reduction in the mean dissimilarity between consecutive seasons experienced by the sites over the four-years studied period (Fig. 8). Variations in the B (reduction) and C (increase) of traits' values were not significant; only at sites 9 (April/16–Sep/16) and 16 (April/19–Sep/19) was the dissimilarity exceptionally higher than at the other sites. In all comparisons (except April/19–Sep/19), at least one trait varied significantly (Table S2 in Appendix). The two clearest patterns of increase and reduction over time are associated with leaf length and leaf width, in opposite directions. In winter, the length of the leaves
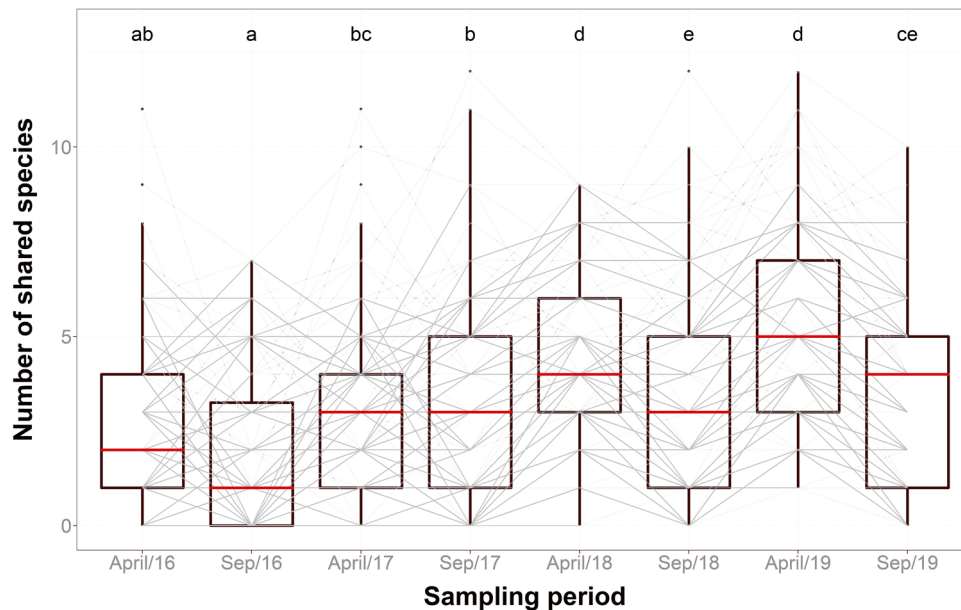
Fig. 4 Boxplots of the number of shared species pairwise of each site and in each sampling. The lines represent the temporal evolution of each site. Intensity in the color of lines represent overlap of data, i.e., sites with the same number of shared species. Different letters on the top represent differences in median among the samplings, obtained by the Conover–Iman test after running Friedman test. The red line in the boxes represent the median, and the limits of the box the first and third quartiles. The whiskers represent the lowest and highest values in the range determined by 1.5 times the difference between the inter-quartiles, and the points are outliers. April/16–April/19 indicate April 2016–April 2019; and Sep/16–Sep/19 indicate September 2016–September 2019

Fig. 5 Boxplots of functional richness index calculated in each sampling. Different letters indicate differences among the samplings, obtained by the Conover–Iman test after performing Durbin Test (chi-square $=67.562$, $P<0.001$). April/16–April/19 indicate April 2016–April 2019; and Sep/16–Sep/19 indicate September 2016–September 2019. The limits of the box represent the first and the third quartiles. The line inside the box is the median, and the whiskers represent the lowest and highest values in the range determined by 1.5 times the difference between the interquartiles. Points represent outliers
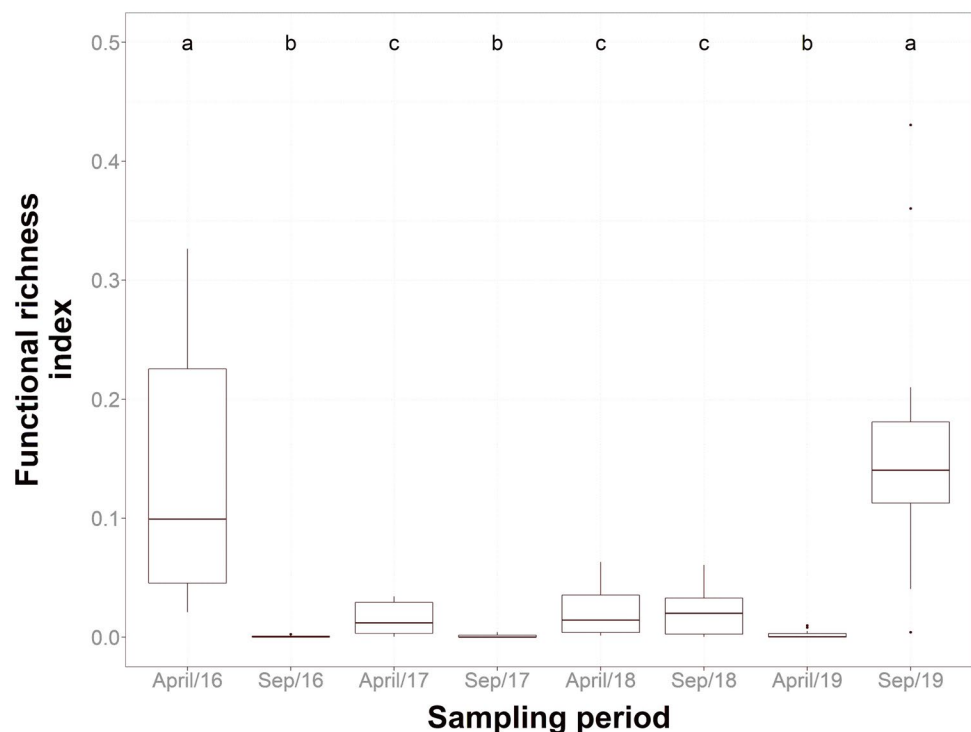
usually increased and the width decreased. The stem width increased in winter and foliar area in summer, but this was not as consistent as the leaf patterns. Regarding the variability in traits among sites, the variances were the same in all samplings (PERMUTEST: $F_{7,120}=0.8794$, $P=0.5242$, Fig. 7b, d).

Fig. 6 Mean dissimilarity (i.e., TBI) over time (comparisons between consecutive samplings). Distinct colors represent the TBI and its components loss (B) and gain (C). Standard deviation of mean dissimilarity is shown. Asterisks indicate when loss and gain components were different, after permuted paired *T*-test. April/16–April/19 indicate April 2016–April 2019; and Sep/16–Sep/19 indicate September 2016–September 2019
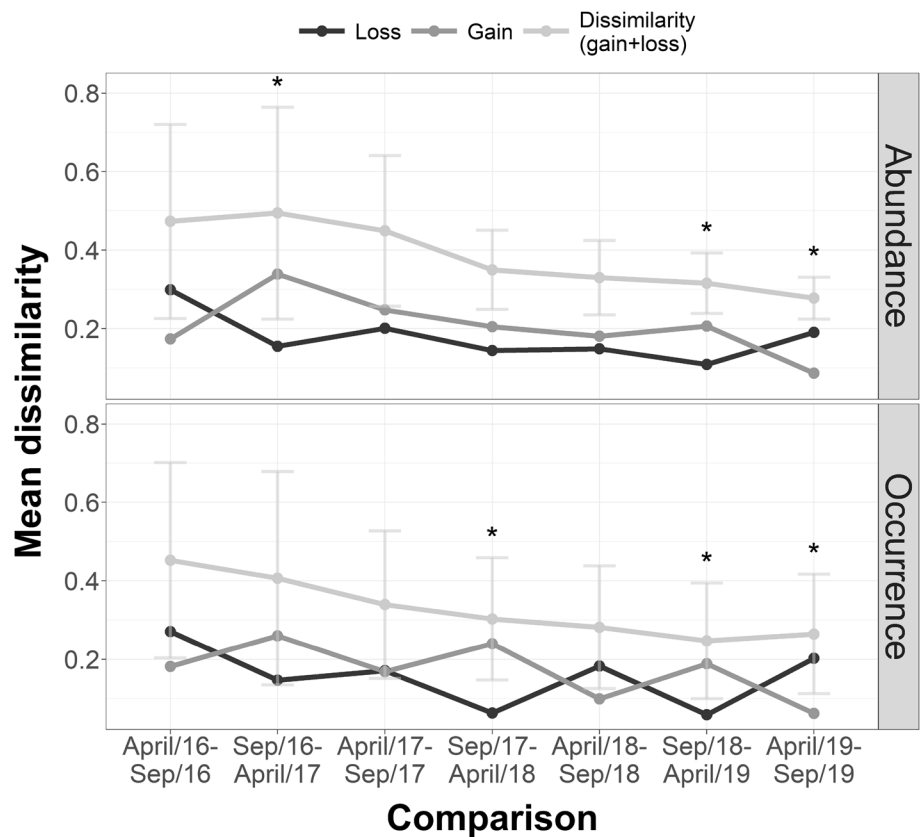
Table 1 Number of sites (*n* = 16) that had a loss (B) and a gain (C) in abundance-per-species and occurrence data (separated by '/'), from the comparison between subsequent sampling periods

	Comparison between subsequent sampling periods						
	A16–S16	S16–A17	A17–S17	S17–A18	A18–S18	S18–A19	A19–S19
B (−)	8/6	**3/5**	6/7	**5/1**	6/9	**3/1**	**14/11**
C (+)	6/7	**11/9**	9/7	**9/14**	8/6	**13/12**	**1/1**
No change	2/3	**2/2**	1/2	**2/1**	2/1	**0/3**	**1/4**

The loss and gain are components of the TBI. Numbers in bold indicate differences in loss and gain obtained by permuted paired *T*-test (*P* < 0.05). A16–A19 indicate April 2016–April 2019; and S16 to S19 indicate September 2016–September 2019

Effects of the invasive tanner grass

In none of the analyses, the abundance of *U. arrecta* was related to either 15 days of accumulated rainfall before sampling or sampling period. It is important to mention that almost all sites where *U. arrecta* was absent are located in the upper area of the river, the 'Caixetal' ecosystem, and in monitored sites of the mangrove area. Therefore, the distribution of this species along the river is between the sites 5 and 14.

Changes in alpha taxonomic indexes were found when contrasting the *U. arrecta* dominance categories and the mangrove. In most cases, the difference was between the

Mangrove and the categories of dominance of *U. arrecta* (see Table S3 in Appendix for averages and standard deviations).

Analysing the relation of *U. arrecta* dominance and the functional diversity indices in each sampling period, we found 21 occasions (in a total universe of 40, because: 5 indexes × 8 sampling periods) when the indices differed in respect to the categories of dominance (Figs. S8–S12 in Appendix). On 17 occasions, reduced values were from the category 'dominant'; increased values from the category 'absent' occurred on 10 occasions. Regarding the sensibility of the indexes, Fdis, Fdiv and RaoQ entropy had differences
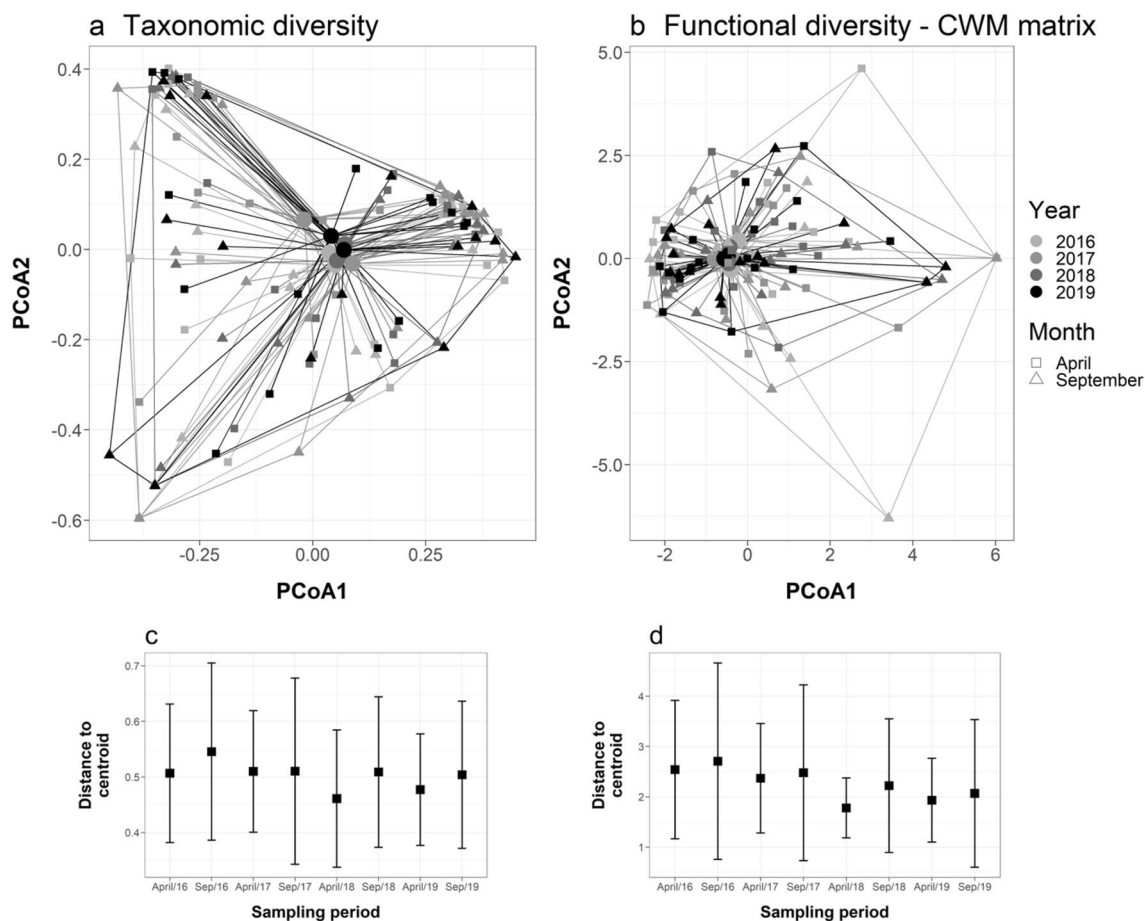
Fig. 7 Top: compositional (**a**) and functional (**b**) dispersion of each period. The central circles are the centroids. Distinct colors and symbols indicate the year and month of samplings, respectively. Bottom: mean ± standard deviation of distances to centroid in each sampling, taxonomic (**c**) and functional (**d**). April/16–April/19 indicate April 2016–April 2019; and Sep/16–Sep/19 indicate September 2016–September 2019
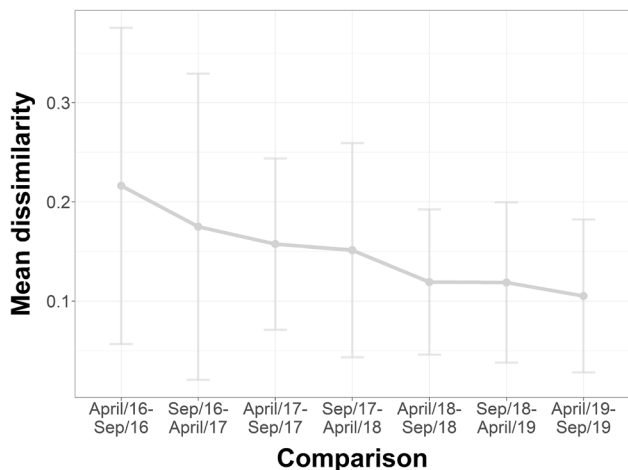

Fig. 8 Temporal mean functional TBI calculated from CWM matrix data. The bars indicate standard deviation. No differences between the increase and decrease components of TBI were found by permuted paired *t*-test. April/16–April/19 indicate April 2016–April 2019; and Sep/16–Sep/19 indicate September 2016–September 2019

among dominance categories in five occasions, Feve in four and Fric in one.

The dominance of *U. arrecta* also effected the distances to centroid, both taxonomic ($F_{1,3} = 19.7941$, $P < 0.0001$) and functional ($F_{1,3} = 7.9309$, $P = 0.0001$). After pooling the data, and controlling by the sampling period, sites without *U. arrecta* had higher variances among themselves than the sites where *U. arrecta* was dominant (Fig. S13 in Appendix). When testing for the effects of *U. arrecta* abundance on the community's variance for each sampling period separately, there were elevated distances to the centroid associated with sites without *U. arrecta* in all samplings that took place in winter, and none in summer, for taxonomic data (Fig. 9). The CWM matrix data also showed differences among categories of dominance but only in Sep/16 and Sep/17, between 'dominant' and 'mangrove' categories, and 'dominant' and the other categories, respectively (Fig. S14 in Appendix).

The indicator species associated with each dominance category are shown in Table 2. In general, the species

Fig. 9 Taxonomic dispersion among sites according to the *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga dominance classes (see methods). The asterisks represent $P < 0.05$ in unequal variances according to PERMUTEST, centroids are highlighted using larger-sized symbols. April/16–April/19 indicate April 2016–April 2019; and Sep/16–Sep/19 indicate September 2016–September 2019
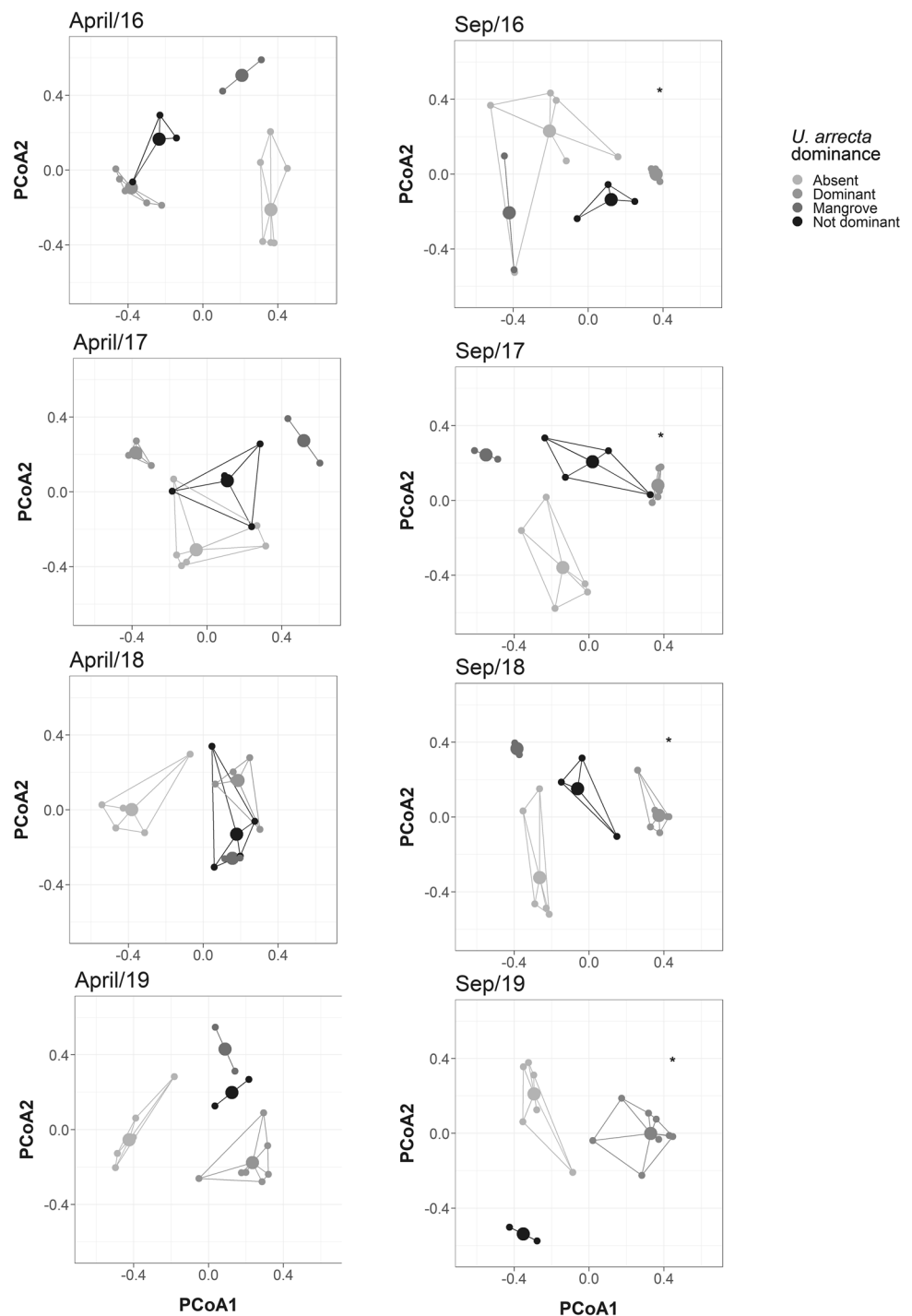
associated with sites where *U. arrecta* was absent were emergent; those associated with sites where *U. arrecta* was dominant were free floating. The most diverse class regarding life form was the 'not dominant', where emergent, submersed floating, emergent floating and epiphyte species were associated.

Discussion

Here, we conducted an investigation of spatial and temporal variation of macrophyte taxonomic and functional diversity in a subtropical tidal river, and revealed interesting patterns. Although seasonality in this subtropical environment is well marked, macrophytes respond in a very complex way to seasonal variation. Neither community composition

Table 2 Results of the indicator value analysis for species associated to the *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga dominance classes (see methods)

Classes	Species	Sampling period	Life form
Absent	*Pontederia crassipes*	A19	Free floating
	Hymenachne amplexicaulis	A18, A19	Emergent
	Ludwigia peruviana	A16, S18	Emergent
	Ichnanthus sp.	A19	Emergent
	Polygonum hydropiperoides	A18	Emergent
	Rhyncosphora corimbosa	A18, A19	Emergent
Dominant	*Hydrocotyle leucocephala*	A16, S16, S18, A19, S19	Free floating
	Lemna sp.	A17, S17, S18, A19, S19	Free floating
	Pistia stratiotes	S16, A17, S17, S18, S19	Free floating
Not dominant	*Echinodorus tenellus*	S18	Emergent
	Egeria densa	A17	Submerged floating
	Ludwigia peploides	S17	Emergent floating
	Oxycaryum cubense	S18	Epiphyte
Mangrove	*Crinum americanum*	A16, A17, S17, A18, S18, S19	Emergent

The table lists only species significantly ($P < 0.05$) associated to classes, as well as the period(s) of the association and the macrophyte life form. A16–A19 indicate April 2016–April 2019; and S16–S19 indicate September 2016–September 2019

nor compositional variation differed between seasons when compared to the whole river. Instead, dissimilarity between subsequent seasons seems to be decreasing over the four-years of standardized monitoring, both for taxonomic and functional facet of the macrophyte metacommunity. Even so, one seasonal pattern was observed: the spatial differences in community composition were high after winter. Yet, some spatial patterns were consistent over time: community structure had a clear river-continuum autocorrelation, and consistently differed according to the invasive *U. arrecta* dominance in this tidal coastal river.

The seasonal changes in rainfall also summarize differences regarding total nutrient input (Mizerkowski et al. 2012), particularly given the higher human impacts in summer holidays associated to enhanced population density. As a subtropical environment, temperature obviously has a seasonal pattern, but it is unlikely that relatively lower temperatures in winter affect plant growth, given the average values at coldest months is c. 18 °C (Vanhoni and Mendonça 2008). Even though rainfall data had a seasonal pattern, accumulated rainfall data from 15 days before the field survey had no relationship with biodiversity.

The occurrence of seasonal variation in macrophyte community was expected based on the above-mentioned seasonality in rainfall. In summer, the resulting community may probably be shaped by a higher dispersion of individuals and changes in establishment, due the higher rainfall and temperature, and the increased amounts of nutrients in the water. The higher dispersion and nutrient input in the water would be especially important for floating species (Trindade et al. 2018; Hussner et al. 2021). The patterns in traits highlighted by the use of TBI approach on CWM matrix data

corroborate our hypotheses. The increase in leaf width in summer might be a result of nutrient stimulus to growth, as larger leaves allow the capture of more sunlight and, therefore, increased biomass production (Chambers et al. 2008); or a response to enhanced water flow (Franklin et al. 2008). The increase in foliar area usually seen in summer is consistent with this idea, although the pattern of increases and decreases was not as consistent as that for leaf width. The level of herbivory on leaves did not change with time, suggesting that other interactions and factors are probably more important in the temporal dynamics of these communities, such as physical and chemical conditions of water (e.g. Lindholm et al. 2020) or underwater herbivory (e.g., Bakker et al. 2016). The increased stem width associated, in general, with winter is a difficult trait to associate to possible seasonal changes, because it is a species-specific response (Puijalon and Bornette 2004) and can be associated to other factors, such as water flow (Bociąg et al. 2009) and nutrients (Lamberti-Raverot and Puijalon 2012), in opposite directions; but it may also mean a trade-off of less investment in leaves and more investment in storage after the relatively harsher conditions of winter (see also Cornelissen and Makoto 2014). Even though our empirical data allow us to speculate, only detailed environmental data and experiments would determine exactly which factors are influencing seasonal differentiation in traits (Jiang et al. 2008; Stefanidis and Papastergiadou 2019).

The variability of functional indexes of alpha diversity reinforces the results of other studies using more than one approach to evaluate the biodiversity (Heino et al. 2007; Villéger et al. 2012; Trigal et al. 2014). Beyond choosing the right index—according to its formulation, purpose and

sensitivity—, we argue that uncovering which specific traits vary or remain the same is a very useful link between environmental conditions, species response and ecosystem functioning. In our experience, the TBI approach applied to the CWM matrix was promising and showed interesting patterns discussed above and below.

The seasonal effects described above are also corroborated by considering together the trend of increase in number of shared species and reduction in the variance (i.e., distances to centroid) among sites in summer, and the increase in the gain component (C) of TBI in transitions from winter to summer. This high similarity associated to summer is expected considering the homogenising effects when the ecosystem has disturbances (see Thomaz et al. 2007), which in our case are those associated to increased rainfall.

As stated before, even with the increase in abundance and number of species in summer, it was still possible to observe a spatial structuring of the river into different sectors. Taking into consideration the interplay between spatial and temporal dynamics, we suggest that, after winter, the local factors spatially structuring the river probably increase in importance. The rationale for that is the reduction in homogenisation and nutrient supply in the water, promoting differentiation between the communities as the environmental conditions become more dissimilar (Thomaz et al 2007). An interesting issue to be studied in the future is how long does it take for these seasonal variations to occur. One might hypothesize that the changes from winter to summer are faster than changes from summer to winter because the populations may respond quicker to increased temperature, nutrients and light (see also Lindholm et al. 2020).

It was interesting to describe the complex temporal changes: whereas the *betadisper* approach did not show temporal changes, the TBI indicated that the sites, individually, had a reduction in diversity during the studied period. This temporal reduction, despite the absence of any clear evidence of changes in general trend of rainfall during the studied period (Fig. S15 in Appendix), might indicate a trend toward biotic homogenisation. Biotic homogenisation was firstly introduced as a continuous temporal trend of decreasing biodiversity due to many 'loser' and few 'winner' species (McKinney and Lockwood 1999). As research evidence accumulated, different facets of biotic homogenisation phenomenon were reported (Olden et al. 2018; Padial et al. 2020). Here, we present another interesting facet: the temporal decrease in seasonal variation, i.e., the seasonal homogenisation. We suggest that this is a concerning facet of biotic homogenisation, given that other organisms that depend on seasonal variation of macrophytes may also be affected, decreasing the biodiversity at long term. Moreover, we also found that spatial differences among the classes of *U. arrecta* dominance (discussed in details below) also depend on seasonality. If macrophyte community organization and

biodiversity became more similar between seasons, so a higher constancy in the effects of the invasive *U. arrecta* may also be expected.

Effects of the invasive tanner grass scrutinized

In addition to the well-known impact of the gradient in environmental conditions along the river on the structure of the communities, our results clearly demonstrated that distribution of species and biodiversity indexes respond to the dominance of an invasive species. Indeed, the effect of *U. arrecta* on aquatic macrophytes in Guaraguaçu River showed clear spatial and temporal components. The spatial effects include the, until now, absence of this invasive species in the 'Caixetal' (upper river) and Mangrove (down river) ecosystems. In the particular case of the 'Caixetal', we do not know whether physiological tolerances, the lack of opportunities (dispersion of enough propagules upward the river) and/or the more preserved terrestrial vegetation prevent its establishment in this area (Evangelista et al. 2017; Teixeira et al. 2016; but see Pott et al. 2011 reporting *U. arrecta* invasion in presence of *Tabebuia insignis* (Miq.) Sandw.). This component of spatial structure makes it more complicated to disentangle which are the main factors promoting the higher dissimilarities among the sites without *U. arrecta*: if it is its absence or other factors (e.g., physical and chemical conditions) that we did not measure. Even so, a previous study comparing neighbouring macrophyte beds have also demonstrated that *U. arrecta* decreased biodiversity and promoted compositional changes at different spatial scales (Sato et al. 2021). The analyses on our monitoring data reinforce this conclusion and add that *U. arrecta* effects extend to the entire river length. This is of particular concern given that a previous study has demonstrated that this invasive species can show rapid adaptive responses to cope with increased salinity (Bora et al. 2020), so the overwhelming effect of the invasive species can extend toward the mangrove, central areas for conservation in the Lagamar region (Araújo et al. 2021). After nuisance growth, management and control efforts are complex and in most cases, not effective (Hussner et al. 2017).

It is interesting to note that the temporal dimension of the effects of *U. arrecta* on the system is the variation of the distances to centroid in a direction opposite to that seen in the sites where *U. arrecta* is absent. In winter, the sites categorized as 'dominant' are more similar to each other than in summer. This opposite direction of increase and decrease between sites where *U. arrecta* is dominant and where it is absent, probably explains why the significant differences in distance to centroids among these categories occurred in winter and not summer. This indicates that more than affecting spatial community structuring (Sato et al. 2021) the invasive tanner grass can also change the temporal

dynamics of macrophyte communities. We hypothesized two main factors, acting in conjunction, for the enhanced similarity among sites where *U. arrecta* dominates in winter. The first is the supposedly more frequent removal of beds of *U. arrecta* because of higher water flows due to rainfall in summer, releasing space for the establishment of other plants. In this scenario, the main limiting resource macrophytes are competing for would be space. The second is the known and widely reported high tolerance and rapid evolution of *U. arrecta* to a wide range of environmental conditions (Bora et al. 2020). This high tolerance, together with its high growth rate (Amorim et al. 2015; Michelan et al. 2010; Thomaz et al. 2009, 2012), make this species one of the most potentially invasive plant species known (Michelan et al. 2010). Indeed, traits related to nutrient absorption in invasive species, for instance, are commonly associated to invasiveness (Hussner et al. 2021). In winter, the total nutrient load in the river is lower due to the reduced water flow (Mizerkowski et al. 2012). Under this likely limiting condition in winter, the invasive *U. arrecta* could have an advantage over the other aquatic macrophytes, in addition to shaping the beds' local environmental features that could reduce the chances of establishment of other species. One example of seasonal change is the progression of its biomass towards the pelagic zone, resulting from its growth above its own biomass, leaving no space in the littoral zone for other emergent plants (Bao et al. 2015). The presence of free-floating species on beds where *U. arrecta* is dominant corroborates this rationale. Yet, the decomposition of *U. arrecta* biomass and the diminished circulation of water between its stems, could favour an accumulation of nutrients in the adjacent water, allowing the free-floating plants to prosper after ending up trapped by the extensive *U. arrecta* macrophyte beds (e.g., Dainez-Filho et al. 2019). Furthermore, the dominance of the established *U. arrecta* can hamper the recolonization of other species (Michelan et al. 2018), promoting a positive feedback.

Our results corroborate many previous studies that reported a negative impact of *U. arrecta* on the diversity of plant communities (Thomaz and Cunha 2010; Fernandes et al. 2013; Bao et al. 2015; Sato et al. 2021), and show that even the beds dominated by *U. arrecta* are subjected to some seasonal variation. Even so, it is important to mention that the main homogenising effect of *U. arrecta* was probably observed in the first years after its establishment in the river (see e.g. Vitule et al. 2007). Since the first sampling period, the extensive *U. arrecta* beds were already established over all river (A.A.P. personal observation; see also Araújo et al. 2021). It is important to highlight though that expansions towards other river stretches such as the mangrove is possible, since this species demonstrates rapid evolutionary responses to salinity (Bora et al. 2020). We here reinforced the threat to biodiversity promoted by *U. arrecta* and the seasonal component of this threat. The continuing monitoring is central to reveal how metacommunities will evolve in Guaraguaçu River ecosystem (see also Hussner 2014).

Conclusions

Results summarized in this study are the first from a long-term monitoring program in Guaraguaçu River. A temporal pattern in biodiversity was found, in which more species are shared among the sampled sites in summer than in winter. As a consequence, the traits of the communities also tended to vary more in winter than summer. We suggest the rainfall accumulated over the seasons is the main driver of changes in environmental conditions, which will shape locally the communities over time. We hypothesize that in winter, the communities are under more limiting conditions, and local specific characteristics become more important, favouring higher differentiation among the communities. This alternation or fluctuation in aquatic environments is a key factor driving the food web in these environments (e.g. Contente et al. 2011b), and changes in the patterns can impact the whole ecosystem (Maltchik et al. 2007). Thus, by understanding the temporal dynamics of the Guaraguaçu River communities and the dominance of *U. arrecta*, impacts of future scenarios, such as severe events (e.g., droughts) or changes in the distribution of rainfall during the year, can be estimated. In particular, it will be important to assess how individuals will respond to the interaction of different environmental cues, such as a result of climate change (e.g., Fukushima et al. 2021). Finally, we showed the negative effects of the invasive *U. arrecta* are also influenced by the season, and its effects are more evident in winter, although observed in all periods. Studying the consequences for the invasive *U. arrecta* is necessary to explain community and ecosystem modification related to other biological groups and process important to humans and future generations.

Declarations

Conflict of interest Authors declare no conflict of interest.

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