



# The invasive tropical tanner grass decreases diversity of the native aquatic macrophyte community at two scales in a subtropical tidal river

Rayana Yumi Sato<sup>1</sup> , Ana Paula Lula Costa<sup>1, 2</sup>  and Andre Andrian Padial<sup>1, 2, 3, 4\*</sup> 

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## ABSTRACT

The tropical tanner grass, *Urochloa arrecta*, is one of the worst aquatic plant invaders in Brazilian freshwater ecosystems. This study aimed to compare beds of macrophytes dominated and without *U. arrecta* in the Guaraguaçu River, a subtropical tidal river in South Brazil, to analyze effects that this invasive grass has on the biodiversity of native macrophytes at two spatial scales. We compared macrophyte beds dominated by tanner grass to macrophyte beds without, considering species richness, composition, and beta diversity at two scales of variation: among-beds and within-beds. We expected that beds dominated by tanner grass would have lower biodiversity, thus promoting macrophyte biotic homogenization. Our results confirmed our hypotheses, highlighting the lower species richness in beds dominated by tanner grass. Species composition differed among beds. In general, nestedness among beds dominated by *U. arrecta* was more related to variation in species composition. Beds dominated by tanner grass had lower turnover and higher nestedness within beds. This study indicates a prominent sign of biotic homogenization promoted by *U. arrecta*, and highlights the degree of biotic homogenization among and within beds.

**Keywords:** biological invasion, biotic homogenization, beta diversity, ecosystem engineers, floodplain, non-native macrophytes, *Urochloa arrecta*

## Introduction

The introduction and establishment of exotic invasive species often leads to species loss and imbalance in natural ecosystems (Simberloff *et al.* 2013). Biological invasions are one of the main causes of changes in our society, impacting our way of life, mostly on the environmental and economic perspective. In addition, impacts by invasive species are one of the main causes of species extinction in the last centuries, and one of the main current threats to global biodiversity (Early *et al.* 2016). Environmental changes due

to invasive species result in the 'Biotic Homogenization' process, a complex phenomenon of increasing similarity amongst communities due to biological invasions and extinctions of species in which few winner species replace many losers in the next mass extinction event (McKinney & Lockwood 1999). This phenomenon, although not formally defined, was first described by the prominent Charles Elton's book *The Ecology of Invasion by Animals and Plants* (published in 1958) and it is suggested that an occurrence at a global scale will cause an intense decrease in the beta diversity of natural ecosystems (Olden *et al.* 2018).

<sup>1</sup> Laboratório de Análise e Síntese em Biodiversidade, Departamento de Botânica, Setor de Ciências Biológicas, Universidade Federal do Paraná, 81531-990, Curitiba, PR, Brazil

<sup>2</sup> Setor de Ciências Biológicas, Programa de Pós-graduação em Ecologia e Conservação, Universidade Federal do Paraná, 81531-990, Curitiba, Paraná, Brazil

<sup>3</sup> Departamento de Botânica, Setor de Ciências Biológicas, Programa de Pós-graduação em Botânica, Universidade Federal do Paraná, 81531-990, Curitiba, PR, Brazil

<sup>4</sup> Núcleo de Pesquisa em Limnologia, Ictiologia e Aquicultura, Programa de Pós-graduação em Ecologia de Ambientes Aquáticos Continentais, Universidade Estadual de Maringá, 87020-900, Maringá, PR, Brazil

\* Corresponding author: aapadial@gmail.com



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In freshwater ecosystems, aquatic macrophytes have a great structuring role and affect ecosystem functioning disproportionately (e.g., Thomaz & Cunha 2010). Fast vegetative and reproductive growth combined with high colonization ability allow some macrophytes to proliferate in an undesired and accentuated way mainly in environments altered by human activities, making them powerful invasive species in aquatic ecosystems (Mormul *et al.* 2011; Hussner *et al.* 2017). The nuisance growth of aquatic macrophytes jeopardizes aquatic ecosystems, increasing biodiversity loss and impacting ecological processes in multiple fashions (Michelan *et al.* 2010). Not surprisingly, aquatic macrophytes are among the worst invasive species in the aquatic realm (Mormul *et al.* 2011; Hussner *et al.* 2017).

In Brazilian freshwaters, several invasive macrophyte species deserve particular attention (Ferreira *et al.* 2016) such as the African exotic invasive species *Urochloa arrecta*, popularly known as tropical tanner grass (formerly tropical signalgrass, see Michelan *et al.* 2010). The sad history of tropical tanner grass in Brazil comes from accidental introduction through its use as a mattress for slaves in slave ships (see also Ferreira *et al.* 2016). Subsequently, this species was brought again to Brazilian ecosystems for establishment of pastures, particularly in wetlands. In such areas, tropical tanner grass spreads quickly given their plasticity and adaptation ability in varied environmental conditions (Ferreira *et al.* 2016). Since then, tropical tanner grass has been causing significant negative effects on the diversity of other aquatic macrophytes in reservoirs, lakes and rivers (Michelan *et al.* 2010; Fernandes *et al.* 2013).

Tropical tanner grass has intensively invaded the Guaraguaçu River, a subtropical tidal river in the Coastal basin of Paraná State, South Brazil (Reis *et al.* 2015). The environmental changes caused by this invasive species likely impact susceptible native species, such as endemic birds that use native macrophyte species as perches (Reinert *et al.* 2007). However, little is known about the effects of tropical tanner grass on native macrophyte diversity in this region. As an ecosystem engineer, it is expected that tropical tanner grass may affect multiple facets of biodiversity at multiple scales, such as local species richness and compositional variation. Understanding the scales in which invasive species have a major effect is crucial. Indeed, local and regional diversity may be affected differently by invasive species, which reflects on different facets of biodiversity (Powell *et al.* 2013). For instance, invasive species can promote an increase in species richness, but decreases in beta diversity and consequent biotic homogenization (Nielsen *et al.* 2019), a pattern well explained in Vellend's "Biodiversity Conservation Paradox" (Vellend 2017).

Beta diversity, estimated using dissimilarity measurements that account for differences in community composition, can be partitioned in two different aspects: turnover and nestedness (Baselga 2010; Legendre 2012; Hill *et al.* 2017). Turnover refers to dissimilarity given

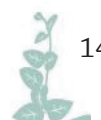
species substitution amongst local communities; nestedness refers to the compositional changes due to the differences between species richness amongst local communities, *i.e.*, the local communities with lower species richness is a subset of the local communities with higher species richness in a nested meta-community (Baselga 2012). The aim of our study was to analyze the effect of the invasive macrophyte *U. arrecta* on the native biodiversity of the Guaraguaçu River by comparing beds either dominated by or without the presence of tropical tanner grass. We hypothesize that the beds dominated by the invasive macrophyte will have lower biodiversity and different composition of species than the beds with native species only. We also predict that nestedness will be relatively more important than turnover to explain beta diversity of beds dominated by *U. arrecta* compared to beds dominated by native macrophytes.

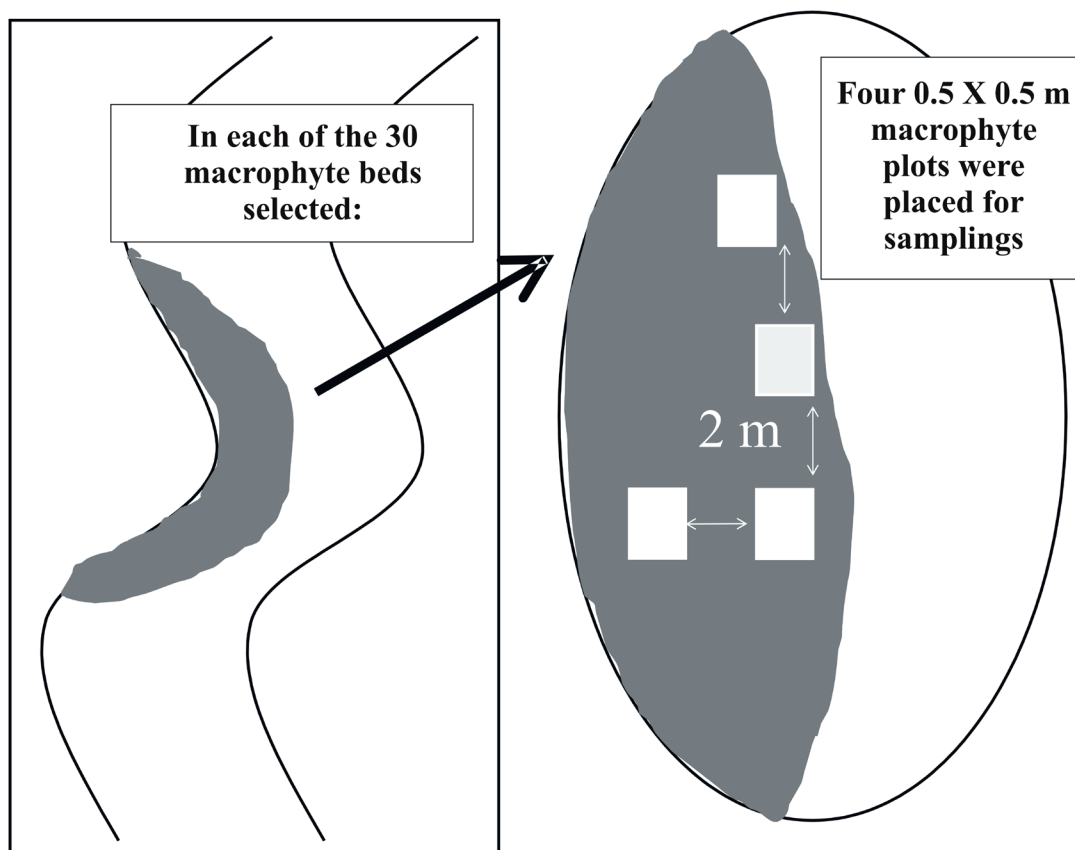
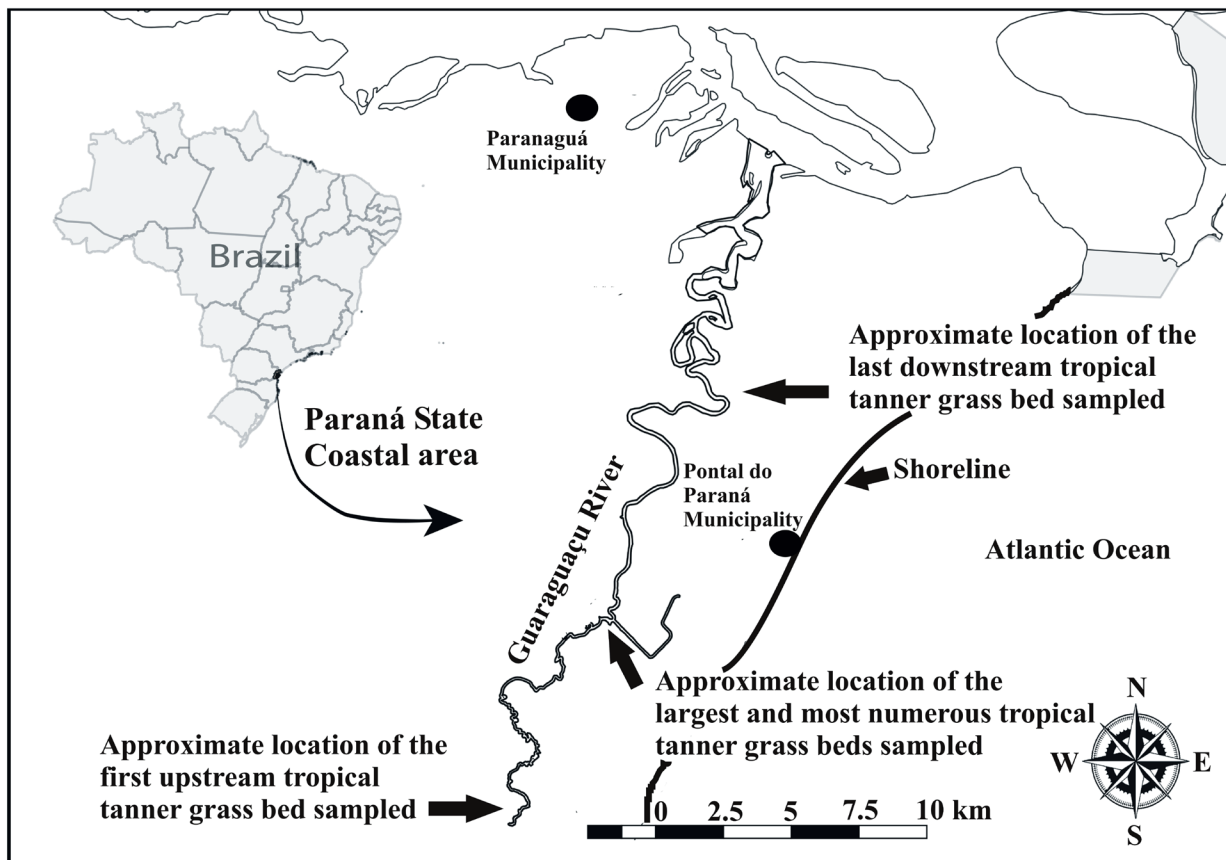
## Materials and methods

### Study area

The study was carried out in the Guaraguaçu River, located in the coastal hydrographic basin of Paraná State, South Brazil (Fig. 1). This river is highly invaded by the African tropical tanner grass *Urochloa arrecta* (Hack. Ex t. Durand & Schinz) Morrone & Zuloaga (Araújo *et al.* 2021). The Guaraguaçu River is a subtropical tidal aquatic ecosystem that is highly dynamic considering the two daily tidal changes in water level; reaching c. 3 m in extreme maritime conditions and depending on the moon phase (personal observation), which means that flora and fauna are subject to such varying water level conditions. Also, ecological conditions in this river vary seasonally mainly considering rainfall, nutrient input and temperature (Vitule 2008). Such temporal variation can affect biodiversity and likely the effects of nuisance macrophytes in biodiversity. Just after summer, macrophyte beds are particularly highly developed (Araújo *et al.* 2021) likely attributed to the high temperatures and leaching of nutrients in water following a combination of frequent rainfall and high human occupation during summer holidays that attract tourists to coastal cities (Vitule 2008).

The Guaraguaçu River is extremely important considering ecosystem services. A large portion of municipal populations on the shoreline of Paraná State use the river as a water supply (Paraná 2020). Moreover, this is the main river of the Lagamar region in Paraná State. 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/>). Guaraguaçu River is the largest river on the hydrographic basin, with a drainage area of approximately 395.5 km<sup>2</sup> within the Atlantic Forest (Vitule 2008; Reis *et al.* 2015). Along its course, the Guaraguaçu River flows through several regions of well-preserved forest





**Figure 1.** Location of the Guaraguau River (above) and sampling design of species in macrophyte beds (below).



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and conservation units, such as the 'Estação Ecológica do Rio Guaraguaçu' (Vitule 2008; Reis *et al.* 2015). Nevertheless, the river continuously receives untreated domestic effluents from municipalities on the coastal shore of Paraná State (Singo *et al.* 2020). Thus, increases in human occupation during summer vacations also increases nutrient inputs in the Guaraguaçu River, which justifies an expectation that effects of invasive macrophytes vary over time, mainly related to differences between summer and winter. Independently of the seasonal variation, human occupation along the river margins has been increasing near the roadside, which also coincides with a region with high input of untreated sewage leachate from a landfill (Singo *et al.* 2020), and with intense tropical tanner grass invasion (see Fig. 1), although this invasive species occurs along most of the navigable stretch of this river (Araújo *et al.* 2021). Apart from the impacted sites, the Guaraguaçu River waters are naturally transparent and black-red due to the large amounts of organic matter and humic compounds received from the forests, which acidify the waters, particularly in the rainiest periods (Vitule 2008). In addition, it presents a meandering aspect influenced by the tidal regime that, as the body of water approaches the mouth of the river, freshwater gradually mixes with salt water from the ocean, diluting it, characterizing an estuarine environment (Oliveira & Marins 2011).

### Data sampling

Samplings occurred at different beds, in March and September of 2018, in a navigable stretch of c. 30 km of the Guaraguaçu River, passing through the most impacted areas (see Fig. 1). Such sampling dates were selected as an effort of sampling repetition and generalization over more than one 'photographic' sampling. Indeed, given the seasonal variations in ecological features described in the introduction, it is necessary to evaluate if effects of invasive species are consistent over time. Surely, a complete evaluation of seasonality would require long-term data, but the samplings in March and September of 2018 are suitable to represent the two periods with extreme distinct situations for macrophytes. March is the end of summer; temperatures are still high in this subtropical area, as well as nutrient input given the intense human occupation in shore cities during summer vacations combined with the period of higher precipitation. The historical accumulated precipitation in summer months is c. 700 mm and the mean temperature is c. 26 °C, although temperature and precipitation levels in summer of 2018 were higher than the historical average (IAPAR 2018). Therefore, macrophytes beds have suitable conditions for intense growth in March whereas in September, conditions are opposite, with low temperature, precipitation and nutrient inputs. The historical accumulated precipitation in winter months is c. 250 mm and the mean temperature is c. 17 °C, however the precipitation level in 2018 was lower than expected by the historical average (IAPAR 2018).

More than varying over time, ecological conditions also vary over the spatial gradient of the river. The upstream area of the river comprises a more preserved area, with less anthropic impacts and also with lower influence of the tidal regime. Following the river gradient, it is possible to observe a more damaged landscape and a higher influence of human activities (see approximate locations in Fig. 1), such as higher organic matter and garbage deposition. The downstream of the river have a high influence of tidal regime and water salinity. Therefore, to avoid effects of spatial autocorrelation in biodiversity patterns, we selected 30 paired beds along all stretches of the river with *U. arrecta* invasion (see approximate locations of the first and the last *U. arrecta* bed in Fig. 1) for samplings in each sampling period. Beds were not the same between sampling periods, but exact locations of all 60 beds sampled were unfortunately not recorded. In each sampling period, 15 beds represented communities dominated by *U. arrecta*, while the other 15 represented paired-communities without its presence, i.e., the nearest macrophyte beds without tropical tanner grass. A distance of 10 to 20 m separated paired beds. Beds sampled had a minimum of 5.5 m length and 3 m in width, always parallel to the river course; however beds varied widely in size, reaching more than 200 m in length and 50 m in width at the largest of *U. arrecta* dominated beds (see [Fig. S1 in supplementary material](#)). In each bed, four 0.5 x 0.5 m square plots (0.25 m<sup>2</sup>) were used to record the species composition (see Fig. 1 and [Fig. S2 in supplementary material](#)). The chosen plot size was based on Downing & Anderson (1985) who showed that most macrophyte studies use plots with an average value of 0.25 m<sup>2</sup>. Thus, 120 plots were sampled in each sampling period; each plot was used as the sampling unit to demonstrate sampling sufficiency based on a species accumulation curve (see [Fig. S3 in supplementary material](#)).

The four plots sampled in each bed were separated from each other by exactly two meters, as shown in Figure 1. For that, we used a two meter straight pipe, graduated every half meter. Three plots were arranged horizontally along the bed's edge and parallel to the course of the river ('on the edge' hereafter), and the last one was positioned vertically into the macrophyte bed, so perpendicular to the course of the river ('far from the edge' hereafter; see plot design in Fig. 1). This design was to capture species variation within macrophyte beds, given that species had both vertical zonation from the margin, and also clustered distribution along the macrophyte bed (*e.g.* Pokorný & Björk 2010), and to allow access by the small boat used for samplings, as it was very difficult to reach more than three meters within the dense beds of the invasive tropical tanner grass. Although not all variation may be represented in this design, we believe that it allows comparison among beds dominated by and without the presence of tropical tanner grass. All species recorded in the four plots (a total sampled area of 1 m<sup>2</sup> in each bed) comprised our effort to estimate the species composition of the entire bed. Species were



identified following specialized literature (for a checklist of macrophyte species in this river, see Araújo *et al.* 2021). The classification of phanerogamic botanical families was based on APG IV (2016) and revised names according to REFLORA (Flora do Brasil 2020).

### Data analysis

We compared beds using values obtained at two spatial scales considering the sampling unit size: for each bed (summing values of all four plots) and for each plot within beds. All analyses were done separately for each sampling period, even though beds sampled were different between periods, as described in methods. We decided to use sampling efforts separately given our main goal was to evaluate if tropical tanner grass were persistent over these two distinct sampling periods, and not to investigate the formal role of temporal variation in biodiversity, which would be suitable only in a long term monitoring.

Considering bed-scale analyses, we first tested if the species richness of macrophyte species differed between beds dominated by and without the presence of tropical tanner grass, considering all plots in each bed. For that, we used a paired *t*-test, given the sampling design was done with paired macrophyte beds as explained above, as well as to avoid effects of spatial autocorrelation in species richness. A Permutational Multivariate Analysis of Variance with 999 permutations (PERMANOVA, Anderson 2001) was then carried out to test for differences in species composition among beds dominated by and without the presence of tropical tanner grass. In this case, tropical tanner grass was removed from the species table as its occurrence was the classification criterion itself. If significant, the differences were visualized using the Principal Coordinate Analysis applied in a Sorensen dissimilarity matrix (PCoA, Gower 1966), and species with high association with and without tropical tanner grass were defined using an analysis of 'species indicator value' (IndVal, Dufrene & Legendre 1997). A measurement of total compositional variation, *i.e.* beta diversity, among beds was compared between the set of beds dominated by and without the presence of tropical tanner grass using a permutation test (Anderson *et al.* 2006). Three beta diversity estimates were estimated using the "betadisper" approach, which is also based on a PCoA. For that, we used three dissimilarity matrices considering the indexes of Sorensen, turnover and nestedness. In this case, turnover represents the replacement of species between communities, while nestedness is the subsequent loss of species richness between these communities (Baselga 2010).

The above mentioned dissimilarity indexes were also used to estimate a multiple sites variation index following Baselga (2012) for the plot-scale analysis described as follows: first we used Baselga's indexes to obtain a value for the variation between plots on the edge and far from it in each bed, then both plot-scale variation indexes of beta diversity calculated in each bed were compared between beds

dominated by and without the presence of tropical tanner grass using paired *t*-tests. The mean difference was calculated as 'With' (*i.e.* dominated by) minus 'Without' tropical tanner grass. So, if the mean difference (D in results summarized in Figure 4) is negative for a particular beta diversity index, it indicates lower variation in beds dominated by *U. arrecta* compared to beds without *U. arrecta*. We reinforce that because sampling design was done in paired beds, spatial autocorrelation was not an issue to be addressed either in comparisons made at bed-scale and at plot-scale. Indeed, in a paired design, the spatial extent between compared situations is the same, and tests are done considering respective pairs of samples.

Before performing the paired *t*-tests, the normality of the data was tested with a Shapiro-Wilk test, and homogenization of variances was tested with a Levene test. For data that did not show normality, a log-transformation was applied. If the homogeneity of the variances has not been reached, the *t*-tests were calculated considering heterogeneous variances. Significant results were considered when the probability of type I error was less than 5%. The analyses were performed for each sample period separately. All analyses were performed using software R 3.5.1 (R Development Core Team 2018), using packages "vegan" (Oksanen *et al.* 2018), "betapart" (Baselga *et al.* 2018), "car" (R Development Core Team 2018) and "labdsv" (Roberts 2016).

## Results

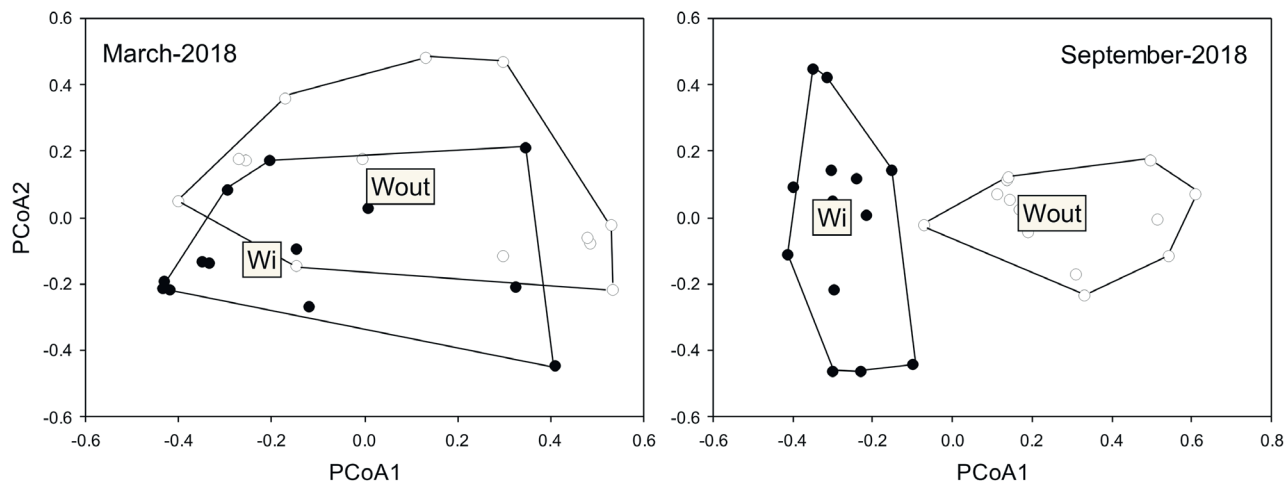
We identified 25 species of aquatic macrophytes, distributed in 21 families and 24 genera (Tab. 1). During both sampling efforts, species accumulation curves indicated good sampling sufficiency (see [Fig. S3 in supplementary material](#)). The macrophyte species richness was significantly lower in beds dominated by the tropical tanner grass in both sampling efforts (Tab. 2).

There were also significant changes in the species composition amongst beds dominated by and without the presence of tropical tanner grass (Tab. 3 and Fig. 2). The most representative species in beds without tropical tanner grass were *Schoenoplectus californicus* (C.A.Mey.) Soják (popularly known as "piri") and *Crinum americanum* L. (popularly known as "crino-americano" or "açucena") in both sampling efforts, and *Nymphaea caerulea* Savigny (popularly known as "lótus") in March-2018 (Tab. 3). The species that commonly indicated beds dominated by the tropical tanner grass were *Salvinia biloba* Raddi. ("orelhade-tigre") and *Hydrocotyle leucocephala* Cham. & Schltdl ("agrião-selvagem"), both in September-2018 (Tab. 3).

Significantly higher nestedness was observed in beds dominated by tropical tanner grass in March-2018, but no difference was observed in September-2018 (Fig. 3). Even so, absolute values of turnover were always higher,



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**Figure 2.** Sorensen macrophyte community composition variation in March and September of 2018, summarized by a Principal Coordinate Analyses and classified between bed dominated by the invasive species *Urochloa arrecta* (Hack, ex T. Durand & Schinz) Morrone & Zuloaga (black circles); and without *U. arrecta* (open circles). ‘With’ (Wi) and ‘Without’ (Wout) indicate the centroid of community distribution with and without the invasive species, respectively.

**Table 1.** Recorded macrophyte species in the 60 macrophyte beds sampled in March and September of 2018 in the Guaraguaçu River. Families, genus and life forms (following Pedralli 1990) are also provided for each species.

Family	Species	Life form
Alismataceae	<i>Echinodorus cordifolius</i> (L.) Griseb	Emergent
	<i>Echinodorus grandiflorus</i> (Cham. & Schltld.) Micheli	Emergent
Amaranthaceae	<i>Alternanthera philoxeroides</i> (Mart.) Griseb	Amphibian
Amaryllidaceae	<i>Crinum americanum</i> L.	Emergent
Apiaceae	<i>Hydrocotyle leucocephala</i> Cham. & Schltld.	Free-floating
Araceae	<i>Lemna valdiviana</i> Phil	Free-floating
	<i>Pistia stratiotes</i> L.	Free-floating
Commelinaceae	<i>Murdannia nudiflora</i> (L.) Brenan	Amphibian
Cyperaceae	<i>Rhynchospora corymbosa</i> Britton	Emergent
	<i>Schoenoplectus californicus</i> (C.A.Mey.) Soják	Amphibian
Haloragaceae	<i>Myriophyllum aquaticum</i> (Vell.) Verdc.	Fixed-submerged
Heliconiaceae	<i>Heliconia</i> sp.	Amphibian
Hydrocharitaceae	<i>Egeria densa</i> Planch.	Fixed-submerged
Lentibulariaceae	<i>Utricularia gibba</i> L.	Free-submerged
Malvaceae	<i>Talipariti tiliaceum</i> (L.) Fryxell	Amphibian
Mayacaceae	<i>Mayaca fluviatilis</i> Aubl.	Fixed-submerged
Nymphaeaceae	<i>Nymphaea caerulea</i> Savigny	Fixed-floating
Onagraceae	<i>Ludwigia peruviana</i> (L.) H.Hara	Amphibian
Plantaginaceae	<i>Bacopa monnieri</i> (L.) Pennell	Emergent
Poaceae	<i>Hymenachne amplexicaulis</i> (Rudge) Nees	Emergent
	<i>Urochloa arrecta</i> (Hack.) Morrone & Zuloaga	Emergent
Polygonaceae	<i>Polygonum hydrodiperoides</i> Michx.	Emergent
Pontederiaceae	<i>Pontederia (Eichhornia) crassipes</i> (Mart.) Solms-Laub.	Free-floating
Ricciaceae	<i>Ricciocarpos natans</i> (L.) Corda	Free-floating
Salviniaceae	<i>Salvinia biloba</i> Raddi	Free-floating

**Table 2.** Results of paired *t*-tests for differences in species richness in macrophyte beds with and without dominance of the invasive macrophyte *Urochloa arrecta* (Hack, ex T. Durand & Schinz) Morrone & Zuloaga. Shown are the average difference means the mean species richness difference With – Without *U. arrecta* and the *P* values.

Period	Average difference	t-value	P-value
March-2018	-0.259	-2.20	0.045
September-2018	-2.267	-2.19	0.046





**Table 3.** Results of Permanova (see Anderson 2001) testing compositional differences among macrophyte beds with and without the dominance of the invasive species *Urochloa arrecta* (Hack, ex T. Durand & Schinz) Morrone & Zuloaga for both periods. Significant Indicator Species according to IndVal index (see Dufrene & Legendre 1997) are shown for beds with and without the dominance of *U. arrecta* in both periods.

Period	Permanova F and P	Indicator Species Value and P value	
		With	Without
March-2018	F = 3.53 P = 0.011	Any species had significant Indicator Value in this period	<i>Scirpus californicus</i> (IndVal = 0.50; P = 0.01) <i>Nymphaea caerulea</i> (IndVal = 0.49; P = 0.01) <i>Crinum americanum</i> (IndVal = 0.31; P = 0.05)
September-2018	F = 19.03 P = 0.001	<i>Salvinia biloba</i> (IndVal = 0.50; P < 0.01) <i>Hydrocotyle leucocephala</i> (IndVal = 0.36; P = 0.01)	<i>Scirpus californicus</i> (IndVal = 0.88; P < 0.01) <i>Crinum americanum</i> (IndVal = 0.88; P < 0.01) <i>Ludwigia peruviana</i> (IndVal = 0.44; P = 0.02)

and nestedness always lower, in beds without tropical tanner grass, although differences could not be considered significant given a relatively high type I error (Fig. 3).

At the plot-scale, turnover and Sorensen index were higher within beds without tropical tanner grass considering the variation of plots on the edge of the bed. Turnover was also higher within beds without tropical tanner grass for variation between plots from the edge and from the interior of the bed. Such differences were observed only in March-2018. In September-2018, there were differences considering nestedness for plot-scale variation considering both plots located at the edge and far from the edge of the bed; in all cases, there was higher nestedness within beds dominated by tropical tanner grass (Fig. 4).

## Discussion

Our results evidenced the complexity and overwhelming invasion potential of the exotic species *U. arrecta* - the tropical tanner grass - on the native communities of macrophytes in a subtropical tidal river. A pattern of local increase in species richness and decrease in regional biodiversity is common as a result of biotic homogenization phenomenon driven by invasive species (e.g., Vellend 2010; Peoples *et al.* 2020). Even so, previous papers considered variation within a watershed as a 'local-scale' analysis, and variation amongst watersheds as a 'regional scale' analysis (see Daga *et al.* 2020; Peoples *et al.* 2020). Here, we evaluated the effects of the tropical tanner grass at two spatial scales (among plots within beds, and among beds) within the same watershed and found consistent negative effects of the tropical tanner grass on native macrophytes. We emphasize that this pattern occurred even though biotic homogenization is not easily found within the same watershed, considered by many to be a small spatial scale (Daga *et al.* 2020; Padial *et al.* 2020). Following this rationale, comparing plots within beds would be an extremely small spatial scale, but we argue that is an informative strategy given the structuring role of macrophytes, and given the fact that many invertebrates perceive the habitat at very local scales (Thomaz & Cunha 2010). Complementarily, comparing beds over the spatial

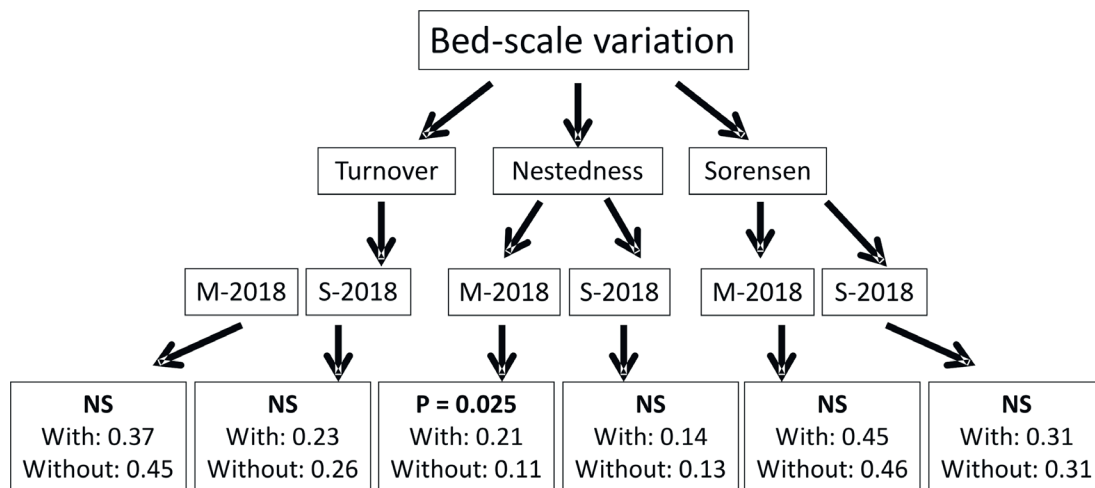
gradient of the river (the other scale addressed here) may inform how the invasive plant changed the regionalization along the river, which is indeed very observable in the Guaraguaçu River for multiple biological groups (Vitule 2008; Araújo *et al.* 2021). By digging further within our data, we argue that effects observed depended on the beta diversity facet (*i.e.*, turnover and nestedness, see also Angeler 2013), and may also depend on sampling period, which demonstrates the complexity in describing impacts of invasive species. Compared to a recent checklist reporting 47 species for this basin (Araújo *et al.* 2021), our samplings did not fully represent the aquatic community of the river. This can be explained by the fact that only paired and well-developed beds were sampled in our study, excluding unique macrophytes that commonly colonize several small patches of the river margins.

The fact that macrophyte beds dominated by tropical tanner grass harbored less macrophyte species has already been demonstrated (Michelan *et al.* 2010; Fernandes *et al.* 2013). Such consistent patterns indicate a simplification of the structuring role of macrophyte communities in the environment, possibly having cascading effects on the numerous ecosystem functions that macrophytes provide (Thomaz & Cunha 2010; Michelan *et al.* 2010; Zhang *et al.* 2018). We must assume however, that simplification of the ecosystem would be better estimated by measuring relative abundance of species. Although not formally measured, it was visually observed that the macrophyte beds dominated by tropical tanner grass had an overwhelming presence of the grass (see [Figs. S1, S2 in supplementary material](#)), which only highlights the homogeneity of the structuring role promoted by the invasive species (see also Valley & Bremigan 2002). Indeed, Fernandes *et al.* (2013) had already shown that *U. arrecta* produces and accumulates large amounts of biomass, which may prevent the establishment of native macrophytes. This relationship was also explained by Michelan *et al.* (2010), who showed that there is an inverse relationship between species richness and biomass of the invasive grass.

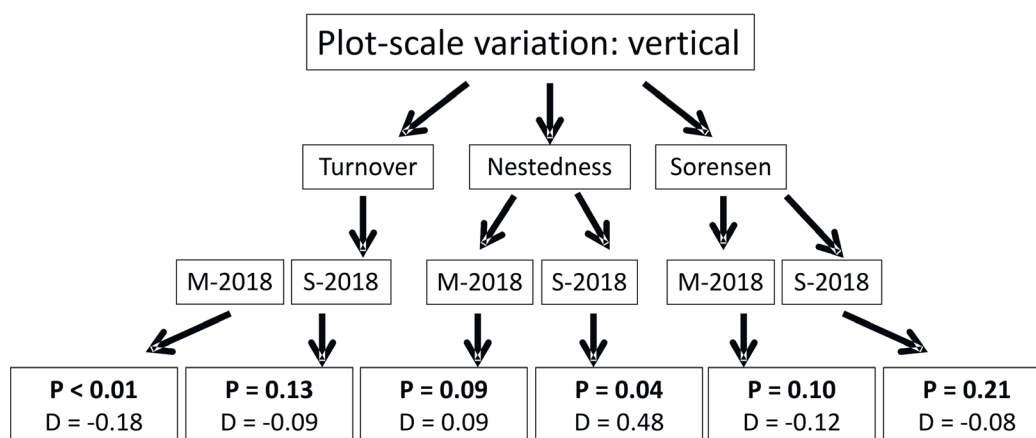
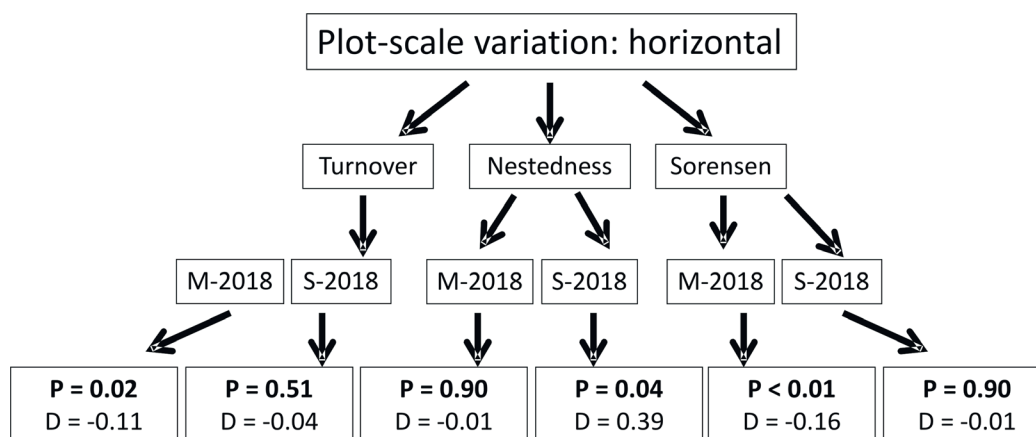
Moreover, we also demonstrated that the effect of tropical tanner grass in the native macrophyte community composition is directional, promoting higher occurrence



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**Figure 3.** Summary of permutation tests for differences in bed-scale compositional variation (see description in methods) considering different beta diversity indexes for samplings in March (M-2018) and September (S-2018) of 2018. *P* values are shown only for significant differences (Nestedness in March-2018). NS = non-significant differences. Values for ‘With’ and ‘Without’ are the mean distance to centroid distribution (following *betadisper* approach in Anderson *et al.* 2006) with and without the invasive species *Urochloa arrecta* (Hack, ex T. Durand & Schinz) Morrone & Zuloaga.



**Figure 4.** Summary of paired *t*-tests for differences in plot-scale horizontal and vertical compositional variation (see description in Materials and methods) considering different beta diversity indexes for samplings in March (M-2018) and September (S-2018) of 2018. *P* values are shown for all comparisons. *D* indicates the difference in beta diversity indexes With – Without the invasive species *Urochloa arrecta* (Hack, ex T. Durand & Schinz) Morrone & Zuloaga. Therefore, negative values indicate that the index is higher without than with *U. arrecta*.



probability of certain opportunistic species - predominantly free-floating ones - in agreement with Michelan *et al.* (2010). The species that most frequently co-occurred with the tropical tanner grass was a free-floating fern with high invasive potential, *Salvinia biloba* (see <https://www.invasive.org/species/aquatic.cfm>), likely due to the fact that small free-floating species anchor easily in the dense tropical tanner grass beds (Camargo & Henry-Silva 2006). On the other hand, among the macrophytes typical from beds without tropical tanner grass were *Schoenoplectus californicus* and *Crinum americanum*. These two widespread species in the coastal basin of Paraná State have an important role for several ecological processes, e.g. shelter and perches for endemic birds (Reinert *et al.* 2007). The fact that native macrophyte beds had low or no presence of *U. arrecta* also corroborates with the biotic resistance theory, which says that communities with higher diversity have a major niche occupation and resource utilization, which decreases the opportunity of establishment by new colonizers (Elton 1958, Fernandes *et al.* 2013). Although native beds may impede the dominance of *U. arrecta*, it is unlikely that biotic resistance alone can stop its spread and invasion (Levine *et al.* 2004; Jeschke *et al.* 2012; Taucare-Ríos & Brescovit 2019). It may be only a matter of time until tropical tanner grass is able to develop over more native macrophyte beds, restricting these native beds to sites with very harsh conditions for tropical tanner grass colonization (e.g., high flow and margins with high forest cover).

Most likely, the expansion of tropical tanner grass beds in the Guaraguaçu River will eliminate most native macrophyte beds and may have serious ecological consequences for the Lagamar region – currently a high priority conservation area in the Atlantic Forest hotspot (see UNESCO ‘Atlantic Forest South-East Reserves’ in <https://whc.unesco.org/en/list/893/>). Indeed, the substitution of tidal-swap forming *S. californicus* by tropical tanner grass has already been reported by the ecological plan of ‘Estação Ecológica do Guaraguaçu’, the main conservation unit along the river (IAP 2006). A previous study has also demonstrated that *U. arrecta* have rapid evolution responses to salt - a filter for macrophyte occupation in the biologically unique mangroves of Guaraguaçu River (Bora *et al.* 2020). Thus long-term monitoring and controlling efforts is an urgent avenue for future studies.

The difference of beta diversity results between sampling periods can be explained by the strong difference in environmental features relevant for development of macrophytes. March is just after summer when, due to the vacation period, coastal cities of Paraná State receive over a million tourists, instead of the few hundred thousand inhabitants during winter. The combination of high temperature, higher precipitation causing leaching and consequent nutrient input due to domestic effluents and sewage promote higher development in abundance of macrophytes (Dhir 2015) including tropical tanner

grass (Alves *et al.* 2015). This combination is typical in coastal environments of Paraná State. With higher biomass production, impact of dominant macrophytes on biodiversity may be enhanced (see also Moura-Júnior *et al.* 2019).

The introduction of exotic invasive species and consequent replacement of native species, as well as other environmental changes, can increase species similarity at a local scale and contribute to biotic homogenization over time (Rahel 2002). We compared macrophyte beds dominated by tropical tanner grass with nearby beds dominated by native macrophytes to infer about biotic homogenization in a space-for-time substitution approach. In this point of view, our study did demonstrate biotic homogenization promoted by tropical tanner grass; macrophyte beds dominated by this invasive species did have lower species richness and beta diversity at two spatial scales depending on the index used.

At the largest spatial scale studied here – variation amongst macrophyte beds – we found that tropical tanner grass beds promoted higher nestedness in March-2018. High nestedness is related to species loss in impacted sites (see also Heino *et al.* 2015), and thus tropical tanner grass expansion may result in an impoverishment of beta diversity across the river. The consequences will likely extend to the diversity of ecological functions provided by macrophytes in a scenario of decreasing turnover and increasing nestedness. Indeed, the effect of tropical tanner grass seems to be particularly evident considering functional homogenization (see Michelan *et al.* 2010).

Our results innovated by shedding light on the effects of tropical tanner grass at a very local scale, *i.e.*, within macrophyte beds. Indeed, most other aquatic organisms inhabiting macrophyte-areas perceive the environment in a very small scale (Thomaz & Cunha 2010). Both results on variation following the watercourse (along the edge of the bed) and in direction to the margin (between the edge and the interior of the bed) indicated that tropical tanner grass beds decreased turnover and increased nestedness. This pattern was more clearly observed in March-2018, and is consistent with a pattern of decreasing beta diversity, *i.e.*, biotic homogenization (Baeten *et al.* 2012). The anchorage of free-floating species in dense tropical tanner grass beds (Camargo & Henry-Silva 2006) may indicate functional and taxonomic redundancy of plants along the bed, reducing turnover and increasing nestedness.

Biotic homogenization is a trending phenomenon that involves several facets (Olden *et al.* 2018). The set of analyses carried out in the present work allowed us to infer that the exotic invasive macrophyte *U. arrecta* is indeed a species with a high invasive potential, responsible for several changes in macrophyte native community, such as species loss and biotic homogenization. Our interpretations are in line with studies demonstrating negative effects of this African grass in Brazilian freshwaters (Fernandes *et al.* 2013; Michelan *et al.* 2013; Ferreira *et al.* 2016). Although the main concern of negative impacts were consistent, it



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seems that the degree of effects are variable over the year; and the likely increase in human interference in ecosystems may enhance even more the extent of tropical tanner grass effects on the biotic homogenization phenomenon. Constant monitoring and long-term studies are extremely necessary in this region. Our study used data on a key ecosystem for conservation and used different facets of biodiversity to reinforce the overwhelming effects of human activities promoting the biotic homogenization phenomenon during the Anthropocene. Such events have been used to define the Homogocene era (see also Padial *et al.* 2020), in which biotas are reshuffled and cause ecological and evolutionary consequences (Olden *et al.* 2004), the human creation of a highly connected 'New Pangaea' (Rosenzweig 2001) world without dispersal barriers for a selected number of species accompanying human movements. Our results indicate that tropical tanner grass is one of such species, with the aggravating scenario of being an ecosystem engineer species in aquatic ecosystems that promote simplification of macrophytes at multiple scales.

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