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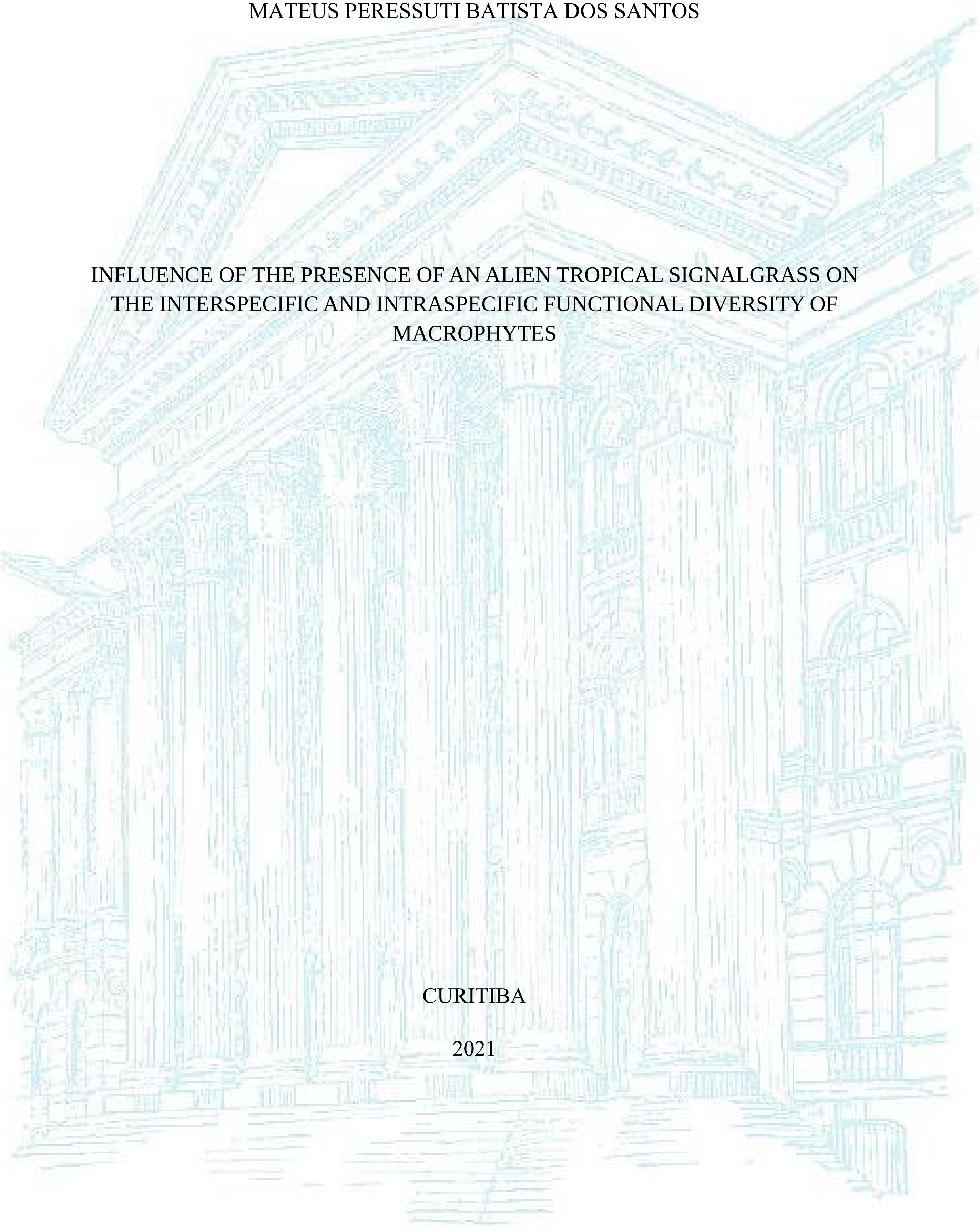
MATEUS PERESSUTI BATISTA DOS SANTOS



INFLUENCE OF THE PRESENCE OF AN ALIEN TROPICAL SIGNALGRASS ON THE INTERSPECIFIC AND INTRASPECIFIC FUNCTIONAL DIVERSITY OF MACROPHYTES

CURITIBA

2021

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Orientador: Prof. Dr. André Andrian Padial.

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em BOTÂNICA da Universidade Federal do Paraná foram convocados para realizar a arguição da Dissertação de Mestrado de **MATEUS PERESSUTI BATISTA DOS SANTOS** intitulada: **Influence of the alien invasive tropical signalgrass on the interspecific and intraspecific functional diversity of macrophytes.**, sob orientação do Prof. Dr. ANDRE ANDRIAN PADIAL, que após terem inquirido o aluno e realizada a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

Curitiba, 23 de Fevereiro de 2021.

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Dedico esse trabalho a todos
que acreditam na ciência e
combatem o obscurantismo.

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RESUMO

A invasão de espécies é um dos impactos ambientais mais comuns em ambientes aquáticos, sendo uma delas a *Urochloa arrecta (*Hack. Ex. T. Durand & Schinz) Morrone & Zuloaga, uma gramínea que vem sendo um problema em diversos ambientes aquáticos brasileiros, em diversas formas, inclusive no rio Guaraguaçu, situado na planície litorânea do estado do Paraná e que tem um gradiente de impactos antrópicos. Uma das formas de avaliar como a invasão de espécies afeta as espécies nativas é através da diversidade funcional, que avalia como características dos ecossitemas afetam características específicas das espécies, os atributos funcionais. Porém, na maior parte das pesquisas, inclusive envolvendo macrófitas aquáticas, não se leva em consideração a diversidade dentro das espécies, portanto, algo que deveria ser explorado. Os objetivos deste trabalho eram avaliar se a espécie invasora afetava a diversidade funcional das macrófitas do rio Guaraguaçu, se a diversidade funcional mais afetada seria a diversidade intraespecífica ou a intraespecífica e se a diversidade se alterava durante o tempo, sendo que o método do cálculo de diversidade funcional intraespecífica é através do Rao intraespecífico. Nos resultados percebe-se que a diversidade funcional é menor na presença de *U. arrecta* e a diversidade intraespecífica é a mais afetada na maioria dos atributos funcionais analisados, porém, poucos resultados foram significativos. Isso significa que outros fatores necessitam ser avaliados, como o fato da causa dessa alteração de diversidade funcional ser outra, como o gradiente de impactos antrópicos, ou seja, ainda precisam ser avaliados outros fatores que causam a alteração dessa diversidade funcional, além de avaliar a possibilidade de *U. arrecta* ser uma engenheira de ecossistemas, algo levantado durante este estudo.

Palavras-chave: *Urochloa arrecta*, comunidades aquáticas; diversidade funcional, hidrófitas; plantas aquáticas; variação intra-específica, variação interespecífica.

ABSTRACT

Species invasion is one of the most common environmental impacts in aquatic environments, one of them being *Urochloa arrecta* (Hack. Ex. T. Durand & Schinz) Morrone & Zuloaga, a grass that has been a problem in several Brazilian aquatic environments, in various forms, including the Guaraguaçu River, located in the coastal plain of the state of Paraná and that has a gradient of anthropogenic impacts. One way to assess how invasive species affect native species is through functional diversity, which evaluates how characteristics of ecosystems affect specific characteristics of species, the functional attributes. However, in most research, including that involving aquatic macrophytes, diversity within species is not taken into consideration, thus something that should be explored. The objectives of this study were to evaluate whether the invasive species affected the functional diversity of the macrophytes of the Guaraguaçu River, whether the functional diversity most affected was the intraspecific or the intraspecific diversity, and whether the diversity changed over time. The method for calculating intraspecific functional diversity is through the intraspecific Rao. In the results it can be seen that functional diversity is lower in the presence of *U. arrecta* and intraspecific diversity is the most affected in most of the functional attributes analyzed, but few results were significant. This means that other factors need to be evaluated, such as the fact that the cause of this change in functional diversity is another, such as the gradient of anthropic impacts, i.e., other factors that cause the change in functional diversity still need to be evaluated, in addition to evaluating the possibility of *U. arrecta* being an ecosystem engineer, something raised during this study.

Keywords: *Urochloa arrecta*, aquatic communities, functional diversity, hydrophytes, aquatic plants, intraspecific variation, interspecific variation.

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LISTA DE ABREVIATURAS

CWM - Community-weighted trait means

FD – Functional diversity

SLA – Specific Leaf Area

ANOVA - Analysis of variance

NS – Non-significant

UPCB-UFPR - Botany Department Herbarium of the Federal University of Paraná

AM – amphibious
EM - emergent
EP - epiphyte
FF - free floating
FS - free submerged
RF - rooted floating
RS - rooted submerged.
WA - water caption station
RC - rectified channels
DG - a damping ground
FD – Functional diversity

Mn abs - mean index of beds where *U. arrecta* was absent;
Sd abs -standard deviation of index of beds where *U. arrecta* was absent;
Mn Pres - mean index of beds where *U. arrecta* was present;
Sd abs - standard deviation of index of beds where *U. arrecta* was absent
RL- root length

LA - leaf area

PL - petiole length

SW - stem width

H - herbivory

SUMÁRIO

Introdução geral

A dissertação apresentada é por um único capítulo, que discute a influência da espécie invasora *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone and Zuloaga nas diversidades intraespecífica e interespecífica das macrófitas do rio Guaraguaçu, no espaço e no tempo, estruturado como um artigo submetido à revista Aquatic Botany (Qualis A2).

A área de estudo está situado no no bioma Mata Atlântica, um hotspot de biodiversidade mundial e que vem sofrendo com impactos antópicos (Arroyo-Rodríguez et al., 2015). Uma boa forma de avaliar impactos da biodiversidade é através da diversidade funcional, que se define como uma forma de avaliar como características biológicas dos organismos (atributos funcionais) são afetados através de características dos ecossistemas (Tilman, 2001), sendo que esses atributos funcionais devem impactar indiretamente a aptidão física através de seus efeitos no crescimento, reprodução e sobrevivência (Violle et al., 2007). Porém a diversidade funcional, na maioria das análises, é avaliada apenas a diferença entre as espécies, não levando em consideração a variação dentro das espécies (McGill et al,2006), mas é algo que não pode ser descartado, já que há evidências de variação dentro das espécies (Cornwell e Ackerly, 2009).

Entre os principais impactos do ser humano nos ecossistemas está a invasão de espécies (Fares et al., 2020) e entre as principais espécies invasoras em ambientes aquáticos do Brasil está a gramínea *Urochloa arrecta*, nativa da África e que invadiu ambientes aquáticos em todo o Brasil (Fares et al., 2020) sendo introduzida desde a época da escravidão (Parsons, 1972). Como espécies invasoras podem ser prejudiciais na composição de espécies, na heterogeneidade ambiental e diversidade funcional (Sodhi et al., 2019). E neste tipo de ambiente é interessante a avaliação de macrófitas aquáticas, também chamadas de hidrófitas, grupo compreende as formas macroscópicas de vegetação aquática, incluindo macroalgas, briófitas, pteridófitas e angiospermas, que vivem em diversos ambientes aquáticos (Pitelli et al., 2008; Thomaz & Bini, 2003; Pott & Pott, 2000). As macrófitas são boas indicadoras ambientais e tem alta plasticidade individual ecom grandde importância ecológica (Havel et al., 2015; Grimaldo et al., 2016), portanto ideias para esse estudo.

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Influence of the alien invasive tropical macrophyte on the interspecific and intraspecific functional diversity

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ABSTRACT

Macrophyte invasive species in Brazilian continental waters, such as *Urochloa arrecta* (Hack. Ex. T. Durand & Schinz) Morrone & Zuloaga, end up damaging the establishment and development of native macrophyte species and promoting biotic homogenization. The functional diversity indices are metrics that indicate the relationship between biodiversity and ecosystem function, based on the variation of specific characteristics - which vary among species and within species - of organisms essential to the survival of individuals and species, called functional traits. This work aimed to evaluate if the *U. arrecta* causes a decrease in the functional diversity of aquatic plants, and to evaluate its impact considering the variation of characteristics among species and within species, using data sampled in the different periods of a coastal river within the Atlantic Forest, South of Brazil. The results show that most of the traits, including the joint analysis of all the characteristics present there, there is a decrease in functional diversity on the margins where the *U. arrecta* is present, both in different macrophyte beds and analysed periods, especially the functional diversity between species, although it also decreases within the species,in addition to a decrease in the intraspecific variability of trait values in these beds. However, in most of these analyses there were no significant results, i.e., it is not necessarily because of *U. arrecta* that there were these changes. Therefore, new analyses are needed, with other possibilities, to observe what affects the functional diversity of these communities.

Keywords: *Urochloa arrecta*, tanner-grass, functional diversity, intraspecific variation, variation interspecific, aquatic communities, hydrophytes.

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2.Introduction

Freshwaters are fundamental to maintaining biodiversity but are among the most threatened habitats in the world (Geist, 2011). Among the main threats, invasions of exotic freshwater species are increasingly being recorded worldwide, causing deep and widespread effects on ecosystem functioning (Fares et al. 2020). Impacts such as pollution, eutrophication and biological invasions involve changes in biotic interactions, such as predation, competition for resources; spread of diseases, and habitat changes (Gallardo et al., 2016). There is also the worrisome fact that low-diverse and more disturbed communities are more susceptible to biological invasion, because of by establishing itself in environments where it has a competitive advantage and exploits the resources present (David et al., 2017). Understanding effects of biological invasions in natural communities are crucial, given an impacted ecosystem by exotic species also threatens the use of natural resources for anthropic activities (Thomaz et al. 2009), in addition to being able to increase species richness at low human pressure, but it generally promotes species loss when human intervention is high (Michelan et al., 2010), and with effects depending on a myriad of characteristics, such as the macrophyte's way of life, the severity of anthropic impacts, the extent and nature of natural environmental gradients, water quality and other ecosystem variables associated with anthropic influence (Fontanarrosa et al., 2019).

The impact of invasive species in Neotropical continental waters on functional diversity is not well understood, considering the conservation and functionality of ecosystems. Functional diversity is the range of biological characteristics of organisms that affect ecosystem functioning and are affected by environmental characteristics (Tilman, 2001), not always being proportional to species richness and being a much more complex and informative measure than species richness (Gallagher and Leishman 2012). The relationship of specific functional diversity to ecosystem functioning is based on the fact that biological characteristics, known as functional traits, characterize the niche and indicate how species respond to environmental gradients in space and time (Jaryzina and Jetz, 2016). The reasoning is that species (and individuals) can establish themselves in a community because they have proper functional characteristics (Cornwell and Ackerly, 2009). As a result, studies on plant and animal resource-based approaches to predict responses at the community level have increased considerably. Morphological traits of macrophytes comprise, for example, morphological traits that indicate nutrient uptake and removal, as well as the strategies of biomass conversion and storage (Chmara et al. 2019). The ecosystemic processes efficacy varies as functional traits vary between species and between individuals of the same species (Cornwell and Ackerly, 2009). Consequently, the estimation of functional diversity, both among species and within species, is essential to represent how biodiversity affects ecosystem functioning. This kind of results should be more informative than taxonomic diversity indices (especially the richness) and even general indices that estimate the entire community's functional space without detailed information on functional traits (Cadotte, 2011). An example of a well-known functional trait approach is community weighted trait means (CWM; Lavorel et. al. 2008), an analysis whose main goal is to assess changes in functional trait values from the ecosystem, unlike most other indices, which take into account the variation of these functional traits. We used CWM values to express the effect, for instance, density-dependent competition (Leps et al., 2011).

A convergence of functional traits is one of the patterns that arise, mainly at larger scales, when species with similar traits predominate in specific habitat conditions given habitat filtering (Cornwell and Ackerly, 2009). In habitat filtering, the formation of the realized niche through the relationship between abiotic factors and interactions occurs in the environment where the species lives. This filter determines the attributes of the individuals in the local pool (McGill et al., 2006). Habitat filtering restricts the range of possible trait values to suit the abiotic and biotic conditions prevailing in a site, leading to the restriction - or sub-dispersion – of trait values within communities (McGill et al., 2006). On the other hand, competition may prevent the establishment of functionally similar species, generating trait divergence patterns at smaller scales.

However, it is increasingly evident that a complete understanding of trait variation cannot rely solely on the values of functional diversity among species - which are the most used in functional ecology research - to represent the community's total functional diversity (de Bello et al., 2011). For example, considering the average values of traits per species, one underestimates the phenotypic plasticity of individuals of a species to support the presence of others in a community and, finally, minimize the degree of differentiation and facilitation of the niche among species (Albert et al. 2010), something that can be resolved with intraspecific diversity since this plasticity is a response to environmental factors (Chmara et al. 2019). Indeed, intraspecific functional diversity has been recognized among the critical factors for species' habitat suitability, the dynamics of co-occurrence of different species, and the total functional diversity and functioning of ecosystems (Albert et al. 2010). An excellent model community to evaluate such issues in freshwater ecosystems is aquatic macrophytes, which have high dynamics into the populations in these environments (Araújo, 2017).

Moreover, there is the temporal variation of functional diversity because all the abiotic and biotic components that affect functional diversity may vary over time, being necessary for assessing functional diversity (Lewis et al., 2014). There are also influence of seasonality, with factors such as rainfall and temperature affecting functional diversity during the year (Le Bagousse-Pinguet et al.,2017). The seasonality affects functional groups, biomass, nutrient absorption, and macrophyte species turnover (Le Bagousse-Pinguet et al., 2017) and, consequently, affects functional diversity (Leps et al., 2011). Another relatively common factor is the oscillation of diversity in the periods (Coladello et al., 2020). It is also contributed to decrease both the interspecific variation and the interspecific variation(Sodhi et al., 2019). However, the temporal variation in functional diversity, especially over the years, is also poorly evaluated compared to variation in spatial gradients, even though there is evidence of changes in functional diversity in the long term due to various anthropic impacts, such as changes in the conditions of the environment. ecosystem or introduction of invasive species (Lewis et al., 2013).

Among the aquatic organisms, macrophytes are good models to indicate these impacts, given their high sensitivity to changes in the aquatic environment (Michelan et al., 2010). The tropical tanner grass *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz; Fig S1) Morrone and Zuloaga, belongs to the Poaceae familly*,* is an alien plant that invaded aquatic environments in the South, Southeast, North and Northeast Brazil (Fares et al. 2020). It is a perennial grass native to Africa, presenting high resource use efficiency, rapid growth, and resistance to temporary flooding (Carniatto et al., 2013). This grass is highly population establishment and growing in tropical environments, given its foliar anatomy and C4 metabolism, highly efficient in capturing sunlight in tropical systems and with high solar incidence. (Sandel et al., 2016). It was initially introduced in Brazil given its' fodder potential, mainly for buffalo, although it is considered toxic for most cattle cultivated in Brazilian pastures (Thomaz et al., 2009);

the sad history of its invasion in Brazil also comes from slavery ships that used the tropical tanner grass as matches for slaves coming from Africa to Brazil (Veldman and Putz, 2011). *U. arrecta* is a high-risk invader due to: i) its high power of competition and homogenization (average of 19% relative abundance in the last four years, reaching more than 50% in a bed of macrophytes); ii) its C4 metabolism (Spasojevic et al., 2010), causing a greater performance in macrophyte beds; and iii) its effect as an ecological filter (with the *U. arrecta* changing the environment from local to regional scale by the fact an African plant in the Atlantic rainforest), which reduces the total functional diversity of local habitat, together with intense changes in local abiotic conditions; iv) *U. arrecta* on ecosystems is the decrease in taxonomic, and morphological diversity of native macrophyte species (Michelan et al., 2010), caused by factors such as preventing the pollination of other macrophytes, spreading disease vectors, (Hofstra, et al., 2020). v) it promotes the homogenization of the habitat, caused by the growth and greater individual plasticity of invasive species (Wang et al. 2016). There is the fact that the functional diversity, especially intraspecific diversity, has not yet been addressed in the case of the influence of *Urochloa arrecta* on this diversity, especially if one takes into account studies in the Neotropics.

In this research, we sampled functional traits of aquatic plants in several macrophyte beds over four years and had as main hypotheses: i) The presence of a dominant invader *Urochloa arrecta* to reduce functional diversity; ii) Intraspecific functional diversity would be the most negatively affected in the presence of the alien species; and iii) there would be a tendency for functional diversity to decline over time, especially in the presence of *Urochloa arrecta.*

3. **Material and methods**

3.1. Field of study

The study was conducted in the Guaraguaçu River (S, 25º64'33"; W, 48º61'26"), located on the Paraná Coastal basin, South Brazil, comprising three municipalities: Matinhos, Pontal do Paraná and Paranaguá. The Guaraguaçu River is highly dynamic, as its hydrologic regime depends on the tides. This river presents a seasonal variation, with more significant rainfall and more significant anthropic impact during the summer (especially between December and February), when there is an intense presence of tourists in the resorts whose drainage channels flow to the Guaraguaçu River. A strong and well-defined environmental gradient of anthropic impacts is also characteristic (Araújo, 2017). The upstream region of this river has low anthropic implications since it is not in an urbanized area. Its main characteristic is the presence of the emblematic and amphibious tree species *Tabebuia cassinoides* Lam. (DC.) (Bignoniaceae), popularly known as 'caixeta.' In the intermediate regions, there is a more significant impact of the humans given the occupation in its margins and the presence of a garbage dump and the sewage discharge of some tributaries that flow into this part of the river (Araújo, 2017). In this stretch of the river, there is a high dominance of *U. arrecta* in macrophyte beds. Downstream, t the river ends into an extensive and well-preserved mangrove region, region characterized by the highest salinity (Fig. 1). In the periods observed, *Urochloa arrecta* was almost never recorded in the caixetal and was never recorded in the mangrove. The above mentioned environmental gradient areas makes Guaraguaçu River key for conservation within the 'Lagamar' Region, an estuarine complex in the most preserved region of the Atlantic Forest Biome , considered by UNESCO as a core zone of the Atlantic Forest Biosphere Reserve, and a natural World Heritage Site (Souza and Oliveira, 2016). Indeed, the Guaraguaçu River is a subtropical river with seasonal variation in precipitation and temperature, with extreme temperature, flow, and water level, particularly in summer.

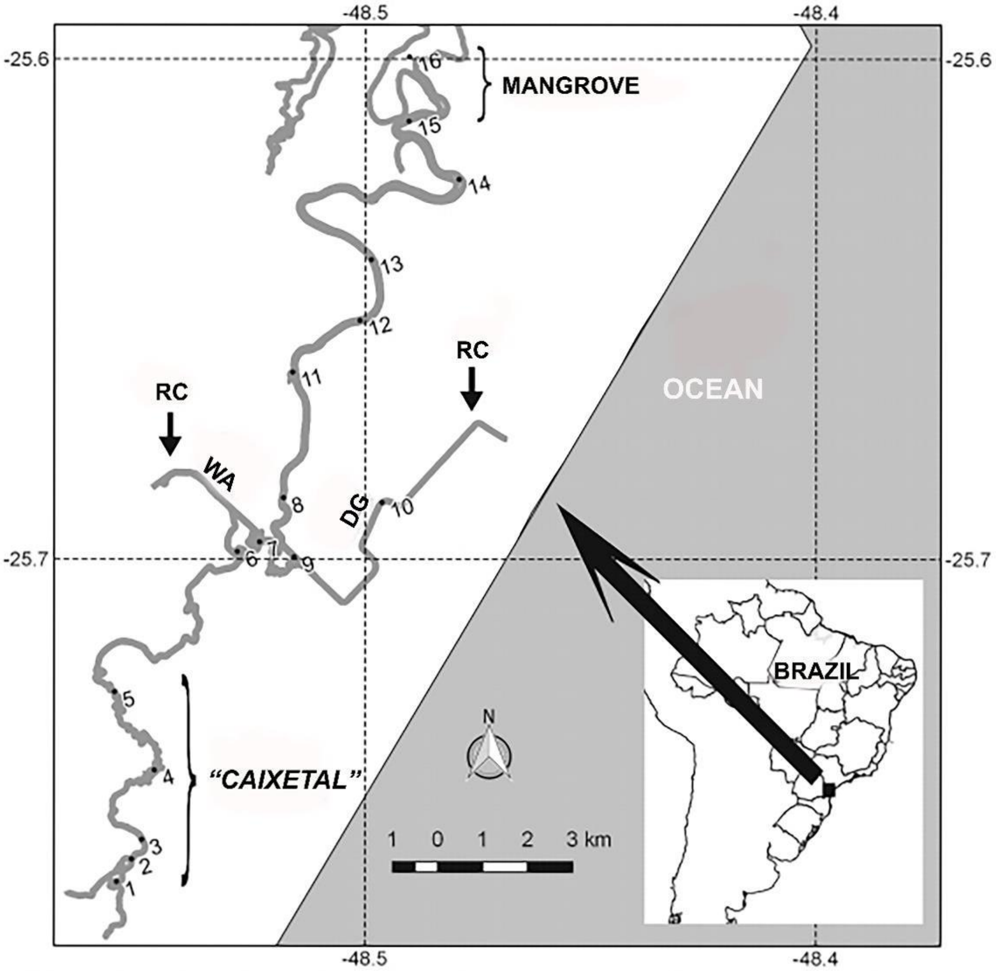


Fig 1: The Guaraguaçu River, sampling sites, and an indication of the stretches described in methods. Sites 1-5 are within the well preserved 'caixetal' area, where *U. arrecta* was rarely present; sites 6-14 are the sites with high anthropogenic impacts, where there is a presence and great dominance of the *U.arrecta* (RC = rectified channel for human use, WA = station for water catchment, DG = dumping ground area); and sites 14-16 are mangrove sites, where *U. arrecta* has never been present.

3.2. Data Collection

Data was gathered in a standardized monitoring protocol derived from the PPBio approach (see < https://ppbio.inpa.gov.br>). The monitoring of aquatic biota (including samples of freshwater macrophyte species) started in 16 georeferenced sampling sites (each sampling site is a macrophyte bed of 50 m length, and 10 m width), five in the "Caixetal," nine in the area with high anthropogenic impact, and two in the mangrove swamp. For this work, we used data from four years of collection between 2016 and 2019, in April and September (complete matrices are freely available for scientific purposes at <https://lasbufprbio.wixsite.com/home>). Three modules (a portion of a plant, in which it contains the root, stem and one leaf at least, some species do not have all the traits and in the case of *Salvinia biloba* species, the modified leaves were considered as roots and in species without stem and with stolon, the stolon was considered as stem) of each species present in the bed were collected, and the emerging macrophyte modules required the use of pruning shears and a macrophyte collector fork in the case of fixed submerged species. In total, 3343 modules and 39 species were measured, 1381 modules and 32 species in the beds without *U. arrecta* and 1962 species and 35 species in the beds with *U. arrecta*. We used vernier calipers (vernier scale = 0.075) to measure macrophytes' traits smaller than 15 cm and metric sewing tapes for larger macrophytes. The functional traits measured were: length of the longest root (cm); length of the largest leaf (cm), leaf width (cm) and leaf area, (cm2), which in the case of this research was the multiplication of the two previous measures; petiole length (cm); stem width (cm); and degree of herbivory in leaves (estimated using Braun-Blanquet index based on the percentage of the leaf area with herbivory signs), evaluated to see how the invasive species affects herbivory interactions and is also the main trait for the evaluation of plant defense (Pearse et al. 2018). In the last sampling period (September of 2019), the specific leaf area (SLA) trait (the ratio of the leaf area for the dry mass; cm^2 g-1) was included as a new trait, given it is common to use to measure functional diversity in plants (Cornwell and Ackerly 2009) (Table 1). These trait was not included in the all traits analysed. For that, the leaves' dry mass content was obtained by drying the fresh mass of the leaves in envelopes within an oven at a constant temperature of 60 °C for 72 h (or until reaching constant mass). The dry mass was then measured on an analytical scale of 0.001g / 510g MARTE®. The relative abundance of species on each macrophyte bed was estimated with Braun-Blanquet classes, converting the percentage of the species' abundance into a number (1<5%; 2=5-25%, 3=25-50%, 4=50-75% and 5>75%; Araújo 2017), bearing in mind that because this research is present in a larger project, this measure of relative abundance was already standardized.

Table 1: Traits used in this research and their biological meaning.

Traits	Biological meaning
Root length	Ability to absorb and cycle water and nutrients (C, P, K, N, etc.) and reveals growth rates
Leaf area (calculated based on leaf lenght x leaf	Ability to capture sunlight for photosynthesis and involvement with

width)	evaporation, perspiration, respiration, maintenance of resources and water balance
Petiole Length	Ability to modify the arrangement of the leaves in relation to sunlight
Stem width	Stability, defense, carbon assimilation capacity and growth potential
Degree of herbivory	Macrophytes' capacity to resist to herbivory Macrophyte response to herbivory
Specific leaf area (SLA) (calculated based on leaf area / leaf dry mass)	Compensation between an investment in the surface area of the sheet to capture the light for photosynthesis and acquisition in the construction of more protected fabrics to avoid dehydration and herbivory

3.3. Intraspecific and interespecific diversities and the comparison between their ratios between macrophyte beds in space and time

The statistical analysis used was based on the approach described by de Bello et al. (2011). The intraspecific, interspecific, and total functional diversity were calculated through Rao's quadratic entropy, taking into account the relative abundance. We calculated each trait's diversity separately and all the united and standardized traits (transforming the data, converting the mean to zero and the standard deviation to two) to no more extended influence the traits with higher measurements. These types of Rao are calculated in the following ways:

$$IntraRao = ra . \sum{}' ed\, indsp \qquad (1)$$

where IntraRao is the intraspecific diversity index, ra is the relative abundance (in percentage, obtained through cross-multiplication through relative abundance in degrees of Braun-Blanquet), and ed indsp are the Euclidean distances of individuals within each species.

$$InterRao = ra . \sum{}' ed\, mdsp \qquad (2)$$

where InterRao is the interspecific diversity index, ra is the relative abundance (%), and ed mdsp is Euclidean distances from the mean of the traits of a species.

$$TotalRao=ra.\sum' ed\ ind \quad (3)$$

where TotalRao is the total functional diversity index, ra is the relative abundance (%), and ed mdsp is Euclidean distances from the mean of the traits all individuals.

In this calculation of functional diversity, two comparisons were made: first between the sampling sites with and without the alien species *U. arrecta* considering its functional contribution in each of the periods. Second calculating these indices, an analysis of the proportion of the intra and interspecific diversity was made for each period, to observe whether it is the intraspecific or interspecific variation that is most affected by exotic species. Afterward, a mean and standard deviation of the intra-specific functional diversity and the proportions of intraspecific and interspecific diversity in relation to total functional diversity of all periods analyzed were made.

Considering that the analyzes above were made for each period, we also investigated whether there is a temporal variation in the relative contribution of the variation of intra and interspecific traits. Through the results of the intraspecific, interspecific and total functional diversities, we performed an ANOVA correlating the results of the different periods with the presence of *Urochloa arrecta* and we see these explanations and the meaning of the intraspecific, interspecific and total indices. These indices were also calculated for each period in all macrophyte beds.

3.4. CWM and functional diversity partition

One of the community trait means (CWM) was calculated, which aims to observe the influence of *U. arrecta* on the trait values. first the CWM of all individuals (CWM whole) represented by the following equation is calculated

$$CWMwhole=ra.\sum' tii \quad (4)$$

where ra is the relative abundance of the species and tii is the functional trait value of each individual (according to Leps et al., 2011) . A specific CWM will also be calculated, represented by the following equation

$$CWMspecific=ra.\sum' tis \quad (5)$$

where ra is the relative abundance (%) of each species and tis is the mean value of a trait in a species in the community (according to Leps et al., 2011). These calculations were done on each macrophyte bed.

The Such ‘whole’ and ‘specific’ functional diversity of each macrophyte bed was then calculated, in order to observe the rates of macrophyte beds, in a similar way to CWM calculations, replacing the average of the species or individual average euclidian distance between two species or two individuals (Carlucci et al., 2015). With this the formulas for these two indices become as follows

$$Raowhole=ra\sum' edind \quad (6)$$

$$Raospecific=ra\sum' edmsp \quad (7)$$

Where ra are the relative abundances (%) of the species, edind are the Euclidean distances between the traits of the individuals, and edmsp are the Euclidean distances between the means of the species traits.

Using the CWM and functional diversity (FD) for the 'integral' and 'specific' approach, we perform a two-way ANOVA. This type of two-way ANOVA separates the effect of intraspecific variability, species turnover and covariation from functional diversity and CWM, assigning significance of these indices based on the specific and whole CWM and specific and whole FD, correlating with the presence (represented by 1 in this ANOVA) and absence of *U. arrecta* (.respresnted by 0).The 'Covariation' effect explains the correlation between species turnover and intraspecific variability, with the total functional divisiveness being subtracted by the effects of turnover and intraspecific variability, with the value being either positive or negative. If 'Covariation' is positive, the correlation between turnover and intraspecific variability is positive, and If negative, the correlation is negative (there being a trade-off between these two effects)(according to the R script of Leps et al. 2011). The calculation of the two-way ANOVA of both the CWM and the FD was done through the CWM and the FD of each bed, with the presence (0) and absence (1) of *U. arrecta* from each bed of macrophytes.

We did all the analyses through the statistical software Rstudio® version 4.0.2 (R Core Team, 2020) and using the packages "vegan” (Oksanen et al., 2013), "car” (Fox and Weisberg, 2019), "ade4" (Dray and Defour, 2007), “FD” (Laliberté and Legendre, 2010), and the files “RaoRel.r” (de Bello et al., 2011) and “e6904_trait-flex-v3.r” (Leps et al., 2011).

4. **Results**

4.1. Intraspecific and interspecific diversities and the comparison between their ratios between macrophyte beds in space and time

During the research period, 39 species were recorded in the Guaraguaçu River, 32 species in the beds without *Urochloa arrecta* (7 macrophyte beds), and 35 in beds with *U. arrecta* (9 beds), with *U. arrecta* having about 16% relative abundance in all beds during all these periods, with almost double the second highest relative abundance of Guaraguaçu (*Schoenoplectus (Scirpus) californicus* with about 9%). Regarding the mean of intraspecific Rao indices over the periods (Fig. 2) , the beds with higher functional diversity were usually those without the alien species: five of seven analyses, each analysis considering a trait or the set of all traits (see methods), and the traits whose intraspecific Rao was greatest in the presence of *U. arrecta* were stem width and degree of herbivory. In relation to mean of interspecific Rao was lower in the presence of *U. arrecta* in six of the seven analyses, the only exception being the specific leaf area analysis. And in relation to mean of total Rao was lower at the points with *U. arrecta* in six of the seven analyses, the only exception being for stem width. In most of these analyses, there are no large differences in the results, and they may have an inverse trend to the mean in some periods, but large differences can also occur between the points with and without *U. arrecta*, as in the intraspecific Rao of leaf area and in the total and interspecific Rao of all standardized traits (Fig. 2).

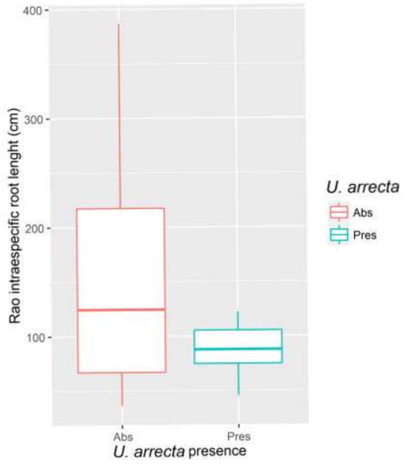
The contribution of intraspecific variation to the functional diversity of the sampling sites where the alien species was present was the largest in most analyses: five of the seven analyses (Fig. 3). Leaf area and specific leaf area was the traits in which the contribution of the beds' intraspecific variation where the alien species was present was lower. In the analysis of all standardized traits analyzed, the beds where the intraspecific functional diversity contribution was more significant proportionally in the beds with *U. arrecta*.

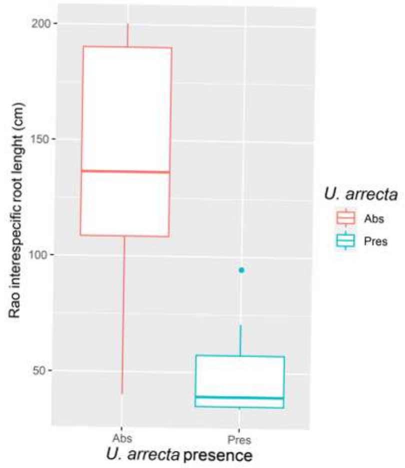
A) Mn abs: 163.000 Mn abs: 139.167 Mn abs: 303.526

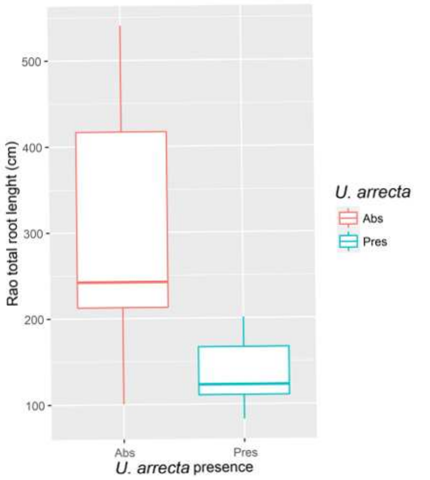
Sd abs: 127.471
Mn pres: 106.365
Sd pres: 40.270

Sd abs: 55.914
Mn pres: 71.825
Sd pres: 30.600

Sd abs: 159.937
Mn pres: 178.190
Sd pres: 66.908



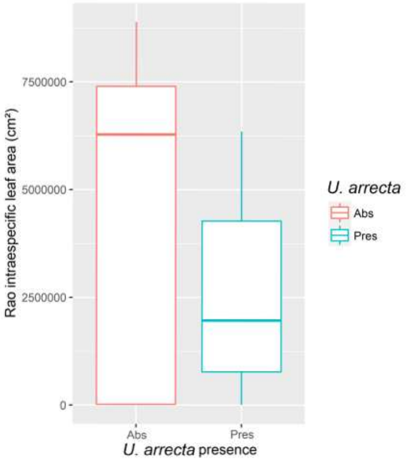


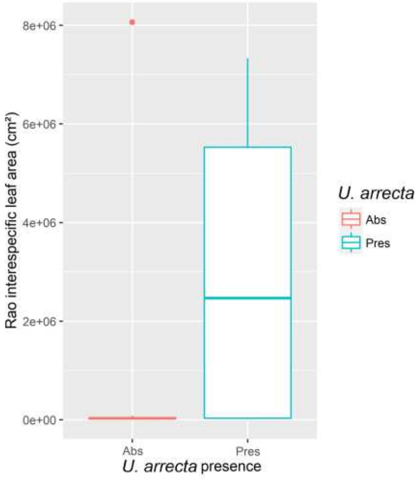


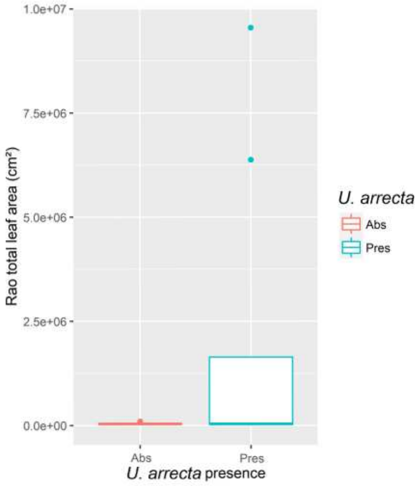
B) Mn abs: 9921.826
Mn abs: 27727.55
Sd abs: 4130.144
Mn pres: 6899.903
Sd pres: 7481.466

Mn abs: 37649.38
Sd abs: 23633.12
Mn pres: 19428.19
Sd pres: 17265.46

Sd abs: 24463.62
Mn pres: 23827.84
Sd pres: 17526.86



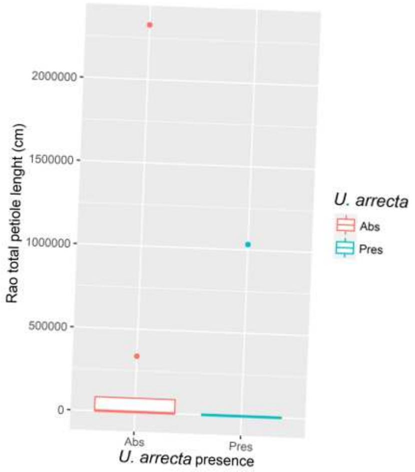


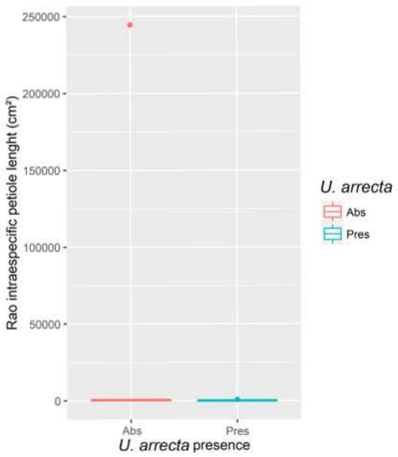


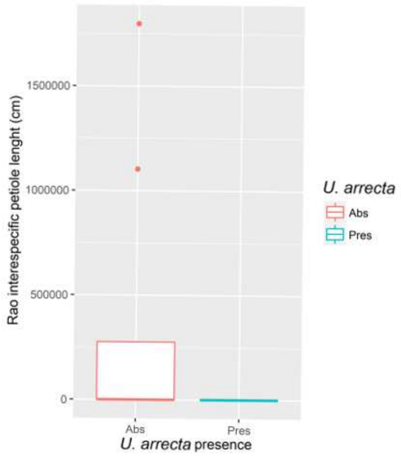
C) Mn abs: 269.236
Sd abs: 247.847
Mn pres: 244.476
Sd pres: 449.857

Mn abs: 556.982
Sd abs: 635.769
Mn pres: 133.847
Sd pres: 107.557

Mn abs: 826.218
Sd abs: 792.270
Mn pres: 378.323
Sd pres: 542.800





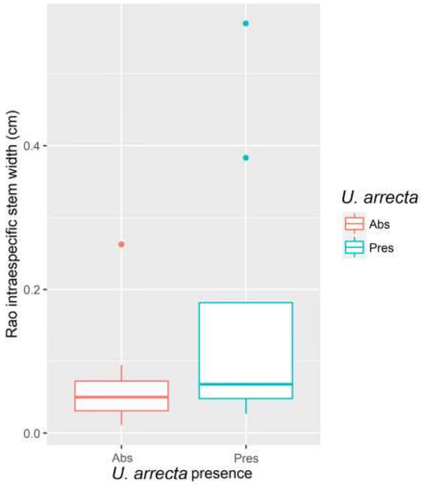


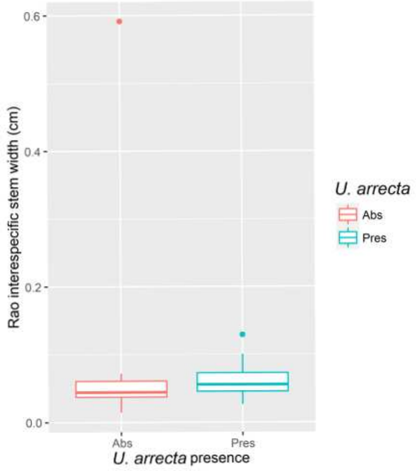
D) Mn abs: 0.074
Mn abs: 0.112
Mn abs: 0.185
Sd abs: 0.081
Sd abs: 0.194
Sd abs: 0.272
Mn pres: 0.212
Mn pres: 0.092
Mn pres: 0.304

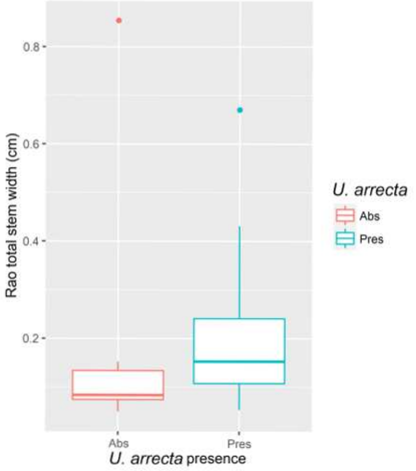
Sd pres: 0.254

Sd pres: 0.051

Sd pres: 0.280



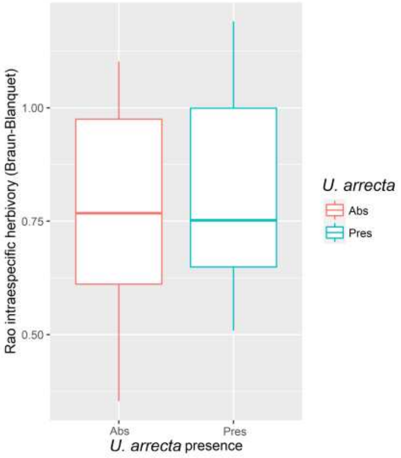


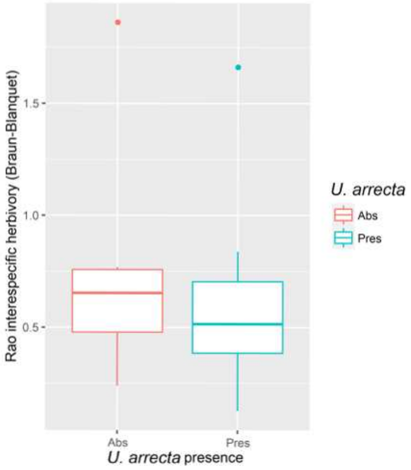


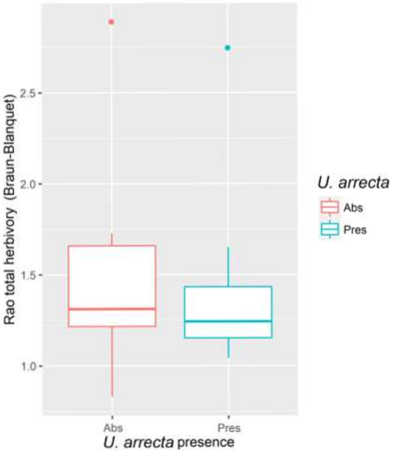
E) Mn abs: 0.774
Sd abs: 0.257
Mn pres: 0.880
Sd pres: 0.212

Mn abs: 0.735
Sd abs: 0.194
Mn pres: 0.592
Sd pres: 0.285

Mn abs: 1.510
Sd abs: 0.623
Mn pres:1.472
Sd pres: 0.361



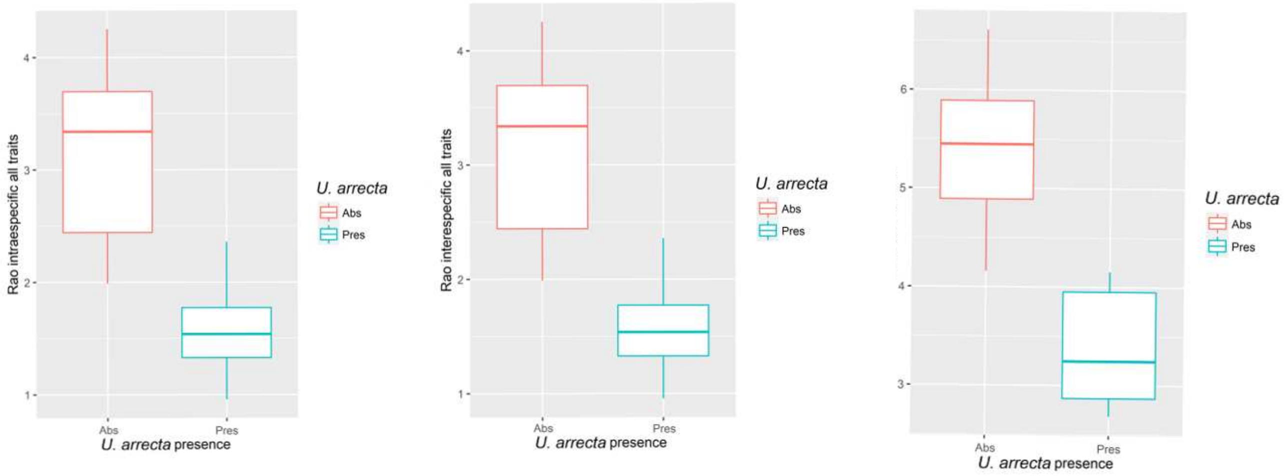




F) Mn abs: 2.225
Sd abs: 0.551
Mn pres: 1.987
Sd pres: 0.485

Mn abs: 3.163
Sd abs: 0.884
Mn pres: 1.802
Sd pres: 0.384

Mn abs: 5.388
Sd abs: 0.884
Mn pres: 3.648
Sd pres: 0.611



G) *

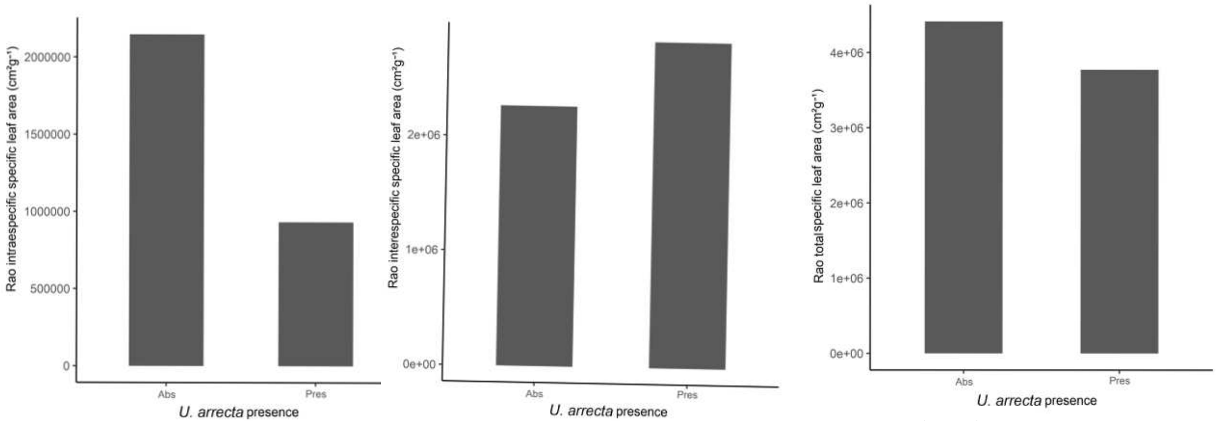
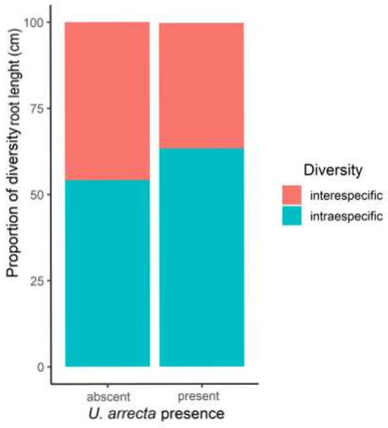
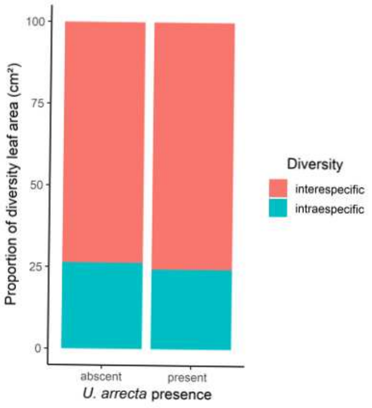


Fig 2: Boxplot of Rao's functional diversity intraspecific (left), interspecific (center) and functional diversity (right) in each period in beds with and without *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga over time of the attributes (A) Root length (cm); (B) Leaf area (cm²); (C) Petiole length (cm); (D) Stem width (cm); E) Degree of herbivory (Braun-Blanquet); (F) All standardized traits; (G) Specific leaf area (SLA; cm²-1). (Mn abs = mean index of beds where *U. arrecta* was absent; Sd abs = standard deviation of index of beds where *U. arrecta* was absent; Mn Pres = mean index of beds where *U. arrecta* was present; Sd abs = standard deviation of index of beds where *U. arrecta* was absent). *Specific leaf area was sampled in only one period, that is, it had no standard deviation.

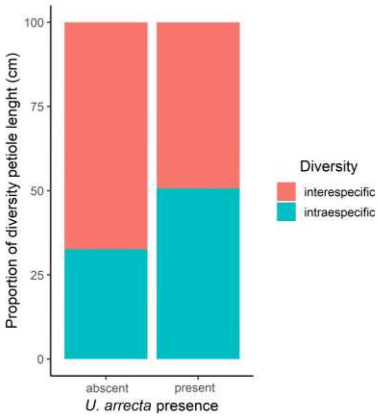
A) Sd abs: 16.93%
Sd pres: 6.21%



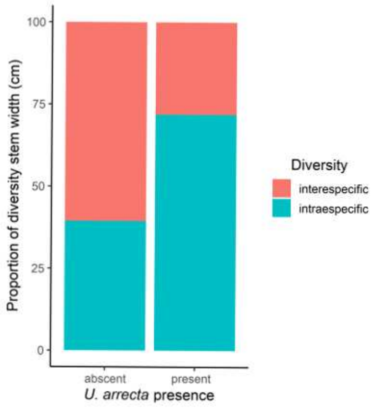
B) Sd abs: 15.79%
Sd pres: 13.08%



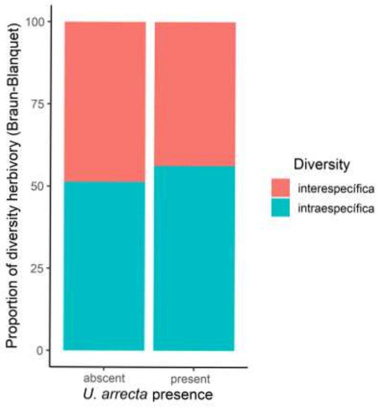
C) Sd abs: 23.89%
Sd pres: 26.57%



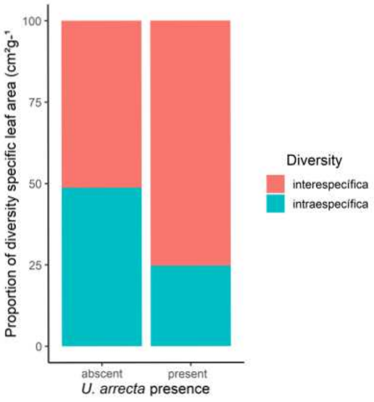
D) Sd abs: 18.70%
Sd pres: 20.35%



E) Sd abs: 13.84%
Sd pres:12.96%



F) *



G) Sd abs: 10.44%

Sd pres: 21.45%

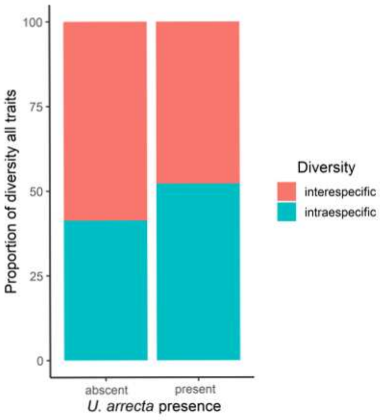


Fig 3: proportion of intraspecific and interspecific functional diversity to total functional diversity, at sites with and without *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga ,of the traits (A) Root length (cm); (B) Leaf area (cm^2); (C) Petiole length; (D) Stem width; (E) Degree of herbivory; (F) Specific leaf area (cm^2-^{1}); (G) All standardized traits. (Sd abs = standard deviation of index of beds where *U. arrecta* was absent; Sd abs = standard deviation of index of beds where *U. arrecta* was absent). *Specific leaf area was sampled in only one period, that is, it had no standard deviation.

4.2. Variation of functional diversities in different periods

There was no clear pattern considering differences between the driest and coldest period (September) compared to the rainiest and warmer period (April) for intraspecific trait variation, with only significant differences between these periods in the intraspecific functional diversity of petiole length and the interspecific functional diversity of leaf area. In the case of functional diversity for all standardized traits, there was a downward trend in the intraspecific functional diversity results, especially in the beds with *U. arrecta* present, a variation with quite a bit of oscillation of the interspecific functional diversity, while in the total functional diversity there is a downward trend in the beds with *U. arrecta* in the last two years, and a small downward trend when taking all beds into account (Fig. 4). In relation to the intraspecific diversity of the other traits, there is a tendency to fall or oscillate on most occasions, since there is a tendency to increase only in the length of the root in banks without *U. arrecta* and oscillation with an index much above normal in September of 2018 of the degree of herbivory in all banks. In interspecific diversity, there is no tendency to increase, only to fall and fluctuate, only to have fewer analyzes with a tendency to fall. There is a case of a much higher index than the others in the width of the stem in banks without *U. arrecta* in September 2017. In relation to total functional diversity, the results were similar to intraspecific diversity, with one of the few differences in the width of the stem of beds without *U. arrecta,* which is similar to the indices of interspecific diversity (Figuras S).

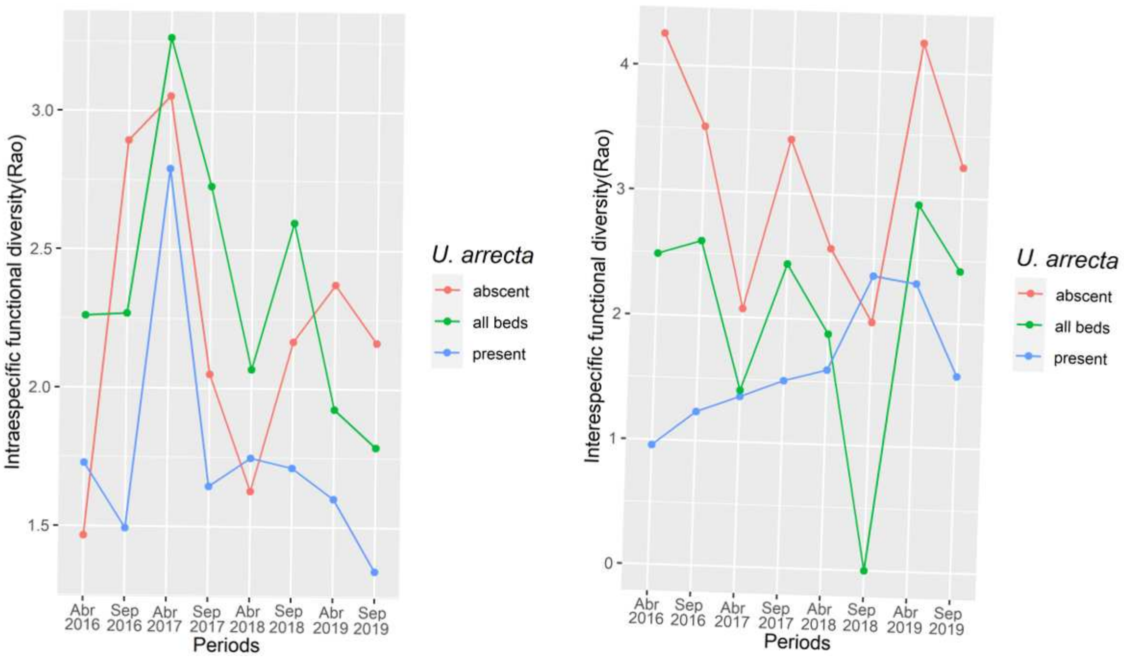
About the effect of *U. arrecta* in the different periods, in the analysis of all standardized traits, the results of intraspecific diversity were not significant ($R^2 = 0.216$; $P = 0.070$), while the results of interspecific diversity ($R^2 = 0.573$; $P = 6.812e\text{-}04$) and total diversity ($R^2 = 0.665$; $P = 1.172e\text{-}04$) were significant. In the other attributes, there was a significant result in the intraspecific functional diversity in none of them. As for the intraspecific diversity of other traits , only the leaf area had a significant result ($R^2 =$

0.322, P = 0.021). Regarding interspecific functional diversity, the length of the root had significant results (R² = 0.566, P = 7.677e-04), something that also occurred in the results of this trait in total functional diversity (R² = 0.406, P = 0.007) (Table 3a).

Table 2: ANOVA results (R^2, P-values and F-values) of the relationship between the trait variation over time and the presence of the *U. arrecta* species (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga.

Traits	R²	P	F
Root length (cm)	Intra: 0.101 Inter: 0.566 Total: 0.406	Intra: 0.230 Inter: 7.677e-04 Total: 0.007	Intra: 1.578 Inter: 18.290 Total: 9.571
Leaf area (cm²)	Intra: 0.322 Inter: 0.121 Total: 0.190	Intra: 0.021 Inter:0.187 Total: 0.092	Intra: 6.653 Inter:1.927 Total: 3.282
Petiole lenght (cm)	Intra: 0.044 Inter: 0.065 Total: 0.042	Intra: 0.433 Inter: 0.340 Total: 0.446	Intra: 0.652 Inter: 0.976 Total: 0.616
Stem width (cm)	Intra: 0.108 Inter: 7.998e-04 Total: 0.059	Intra:0.214 Inter:0.917 Total:0.364	Intra:1.695 Inter:0.011 Total:0.864
Degree of herbivory (Braun-Blanquet Degrees)	Intra: 0.007 Inter: 0.030 Total:0.003	Intra: 0.762 Inter: 0.522 Total: 0.836	Intra: 0.095 Inter:0.223 Total: 0.045
All standardized traits	Intra: 0.216 Inter: 0.573 Total: 0.665	Intra: 0.070 Inter: 6.812e-04 Total: 1.172e-04	Intra: 3.861 Inter: 18.820 Total: 27.830

A) B)



C)

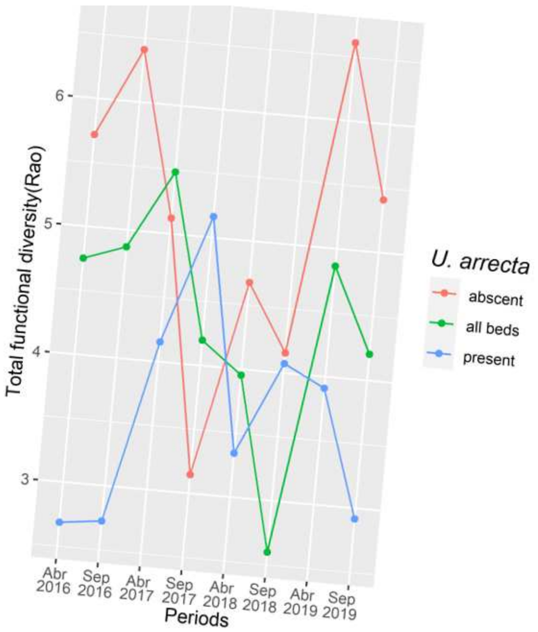


Fig 4 : Functional diversity indices of all standadized traits in beds with (blue) and without *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga (red) and in all beds (green) (A) Intraspecific; (B) Interspecific; (C) Total.

4.3. Functional diversity partitioning

Regarding diversity partitioning in the macrophyte beds, few results were significant. In the analysis of all standardized traits none of the results were significant (table 4A). In relation to the analyses of each trait separately, the only result with significant variation was the intraspecific variability of leaf area, which began to explain more the functional diversity in relation to the turnover in the presence of *U. arrecta*, the inverse that happens in the residues. n this trait the covariation was negative in the effect of the presence of *U. arrecta* and in the residuals. (fig. 5A-F). Besides almost no significant results, the presence of *U. arrecta* contributed little to the functional diversity of the beds (between 0.04% in root length and 15.12% in herbivory degree).

4.4.CWM Partition

In the case of the community weighted mean traits of beds, the community weighted mean traits of the bed, there were also few significant results. All the results of the CWM analyses of all the standardized traits were not significant (table 5B). In the case of the analyses of the septate traits, the only significant results were the turnover and total CWM of the stem width and the intraspecific variability of the degree of herbivory. In the case of stem width the turnover explained by *U. arrecta* was less explained than in the residuals, but the drop in this part of the CWM smaller compared to the drop in intraspecific variability and the covariation is always negative. In the case of herbivory, the explanation of intraspecific variability becomes greater than that of turnover in the presence of *U. arrecta*, the opposite of what occurs in the residuals. Moreover, the covariation that is negative in the residues becomes positive in the presence of *U. arrecta*, that is, the turnover and intraspecific variability are no longer antagonistic to each other (fig. 5G-L). The explanation of the presence of *U. arrecta* in CWM is also relatively small (between 0.04% in leaf area and 11.81% in root length). It should be pointed out that the mean and CWM of the individuals was slightly higher at the points with *U. arrecta*, but with a small difference (Tables S1-S2; Fig. S7).

Table 3: (A) Functional diversity (Rao index) variance breakdown of the community, taking into account all traits. These results were obtained through the two-way ANOVA, which considers the sum of the squares, except ‘covariation’, which is the result of total SS total-(SS tunover+SS intraspecific variability). (B) Variance partitioning of the community weighted mean-traits (CWM) of the community, taking into account all traits considering the effect of the alien species' presence compared to total variation. These results were obtained through the two-way ANOVA, which considers the sum of the squares, except ‘covariation', which is the result of total SS total-(SS tunover+SS intraspecific variability).

A)

	Turnover	Div Intraspec	Covariation	Total
Main effect	R^2=0.469	R^2=0.275	-0.718	R^2= 0.026
Residuals	2.274	2.504	-3.804	0.974
Total	2.743	2.779	-4.522	1.000
P value	0.062	0.165	-------	0.486

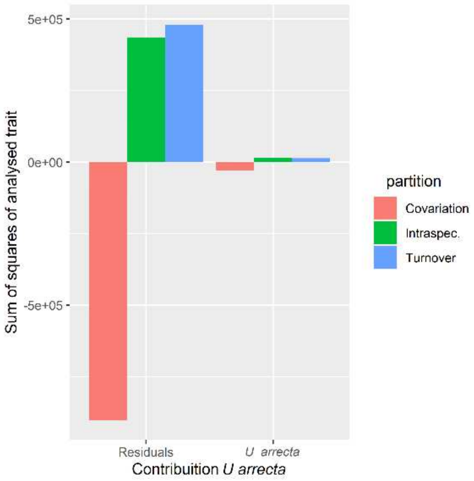
B)

	Turnover	Intraspecific variability	Covariation	Total
Main effect	R^2=3.937e-04	R^2= 0.149	0.015	R^2= 0.165
Residuals	0.072	0.766	-0.002	0.835
Total	0.072	0.915	0.013	1.000
P value	0.750	0.070	------	0.068

A) P turnover= 0.390

P intra= 0.464

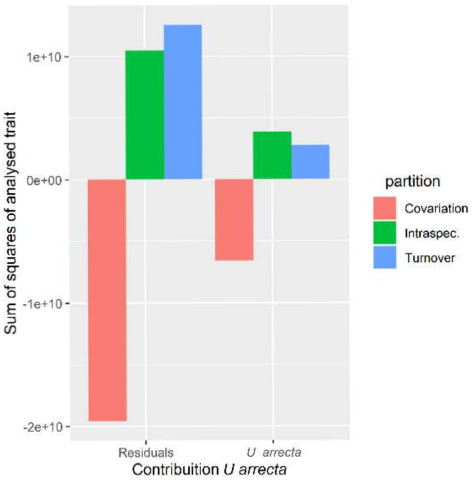
P total=0.360



B) P turnover= 0.045

P intra= 0.018

P total=0.671



C) P turnover= 0.142

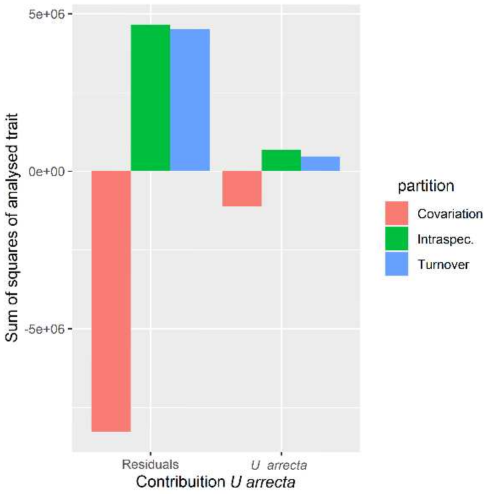
D) P turnover= 0.235

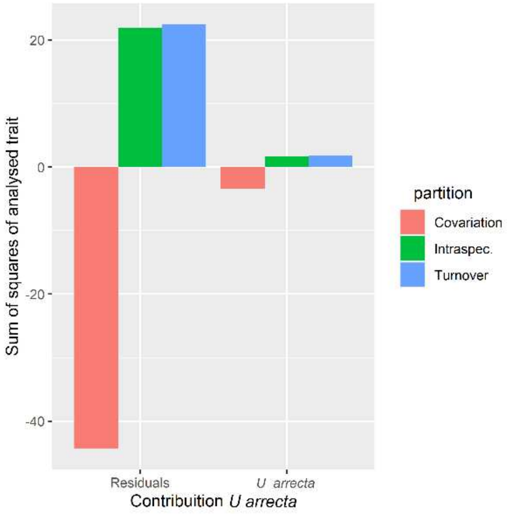
P intra= 0.107

P total= 0.734

P intra= 0.246

P total= 0.090





E) P turnover= 0.330

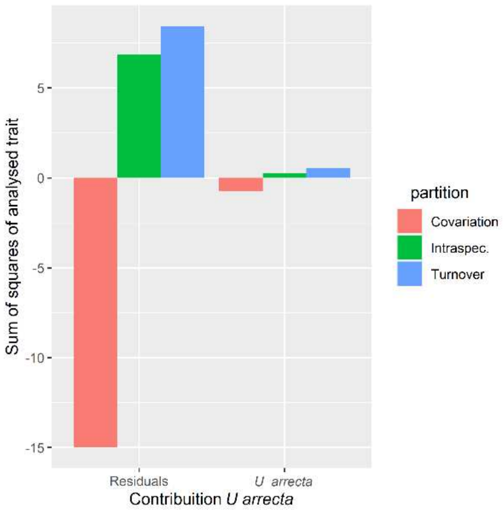
P intra= 0.784

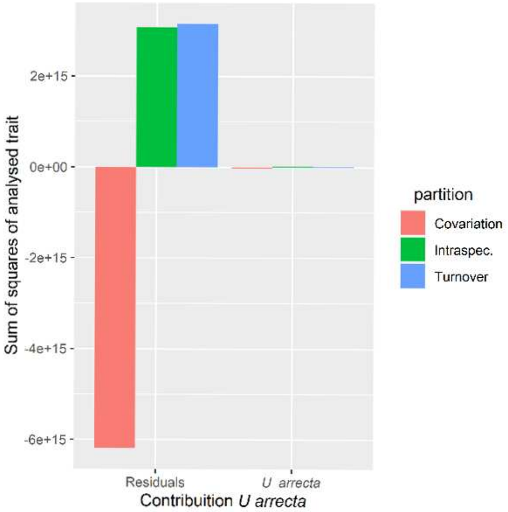
P total= 0.004

F) P turnover= 0.712

P intra= 0.699

P total= 0.915





G) P turnover= 0.402

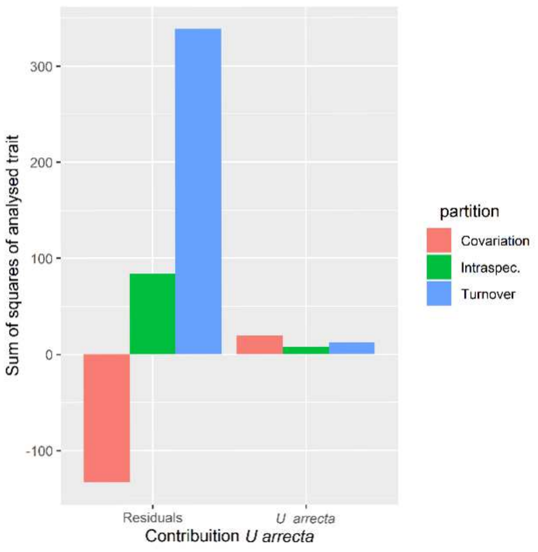
P intra= 0.095

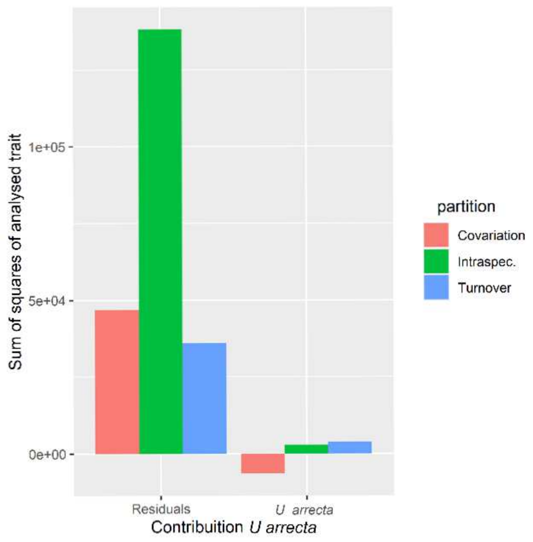
P total= 0.046

H) P turnover= 0.129

P intra= 0.012

P total= 0.303



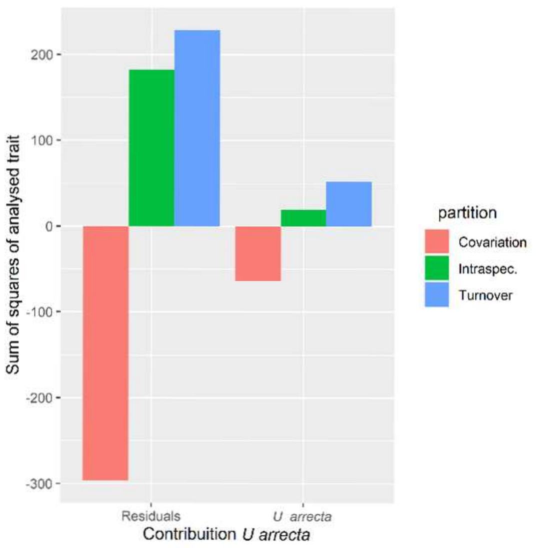


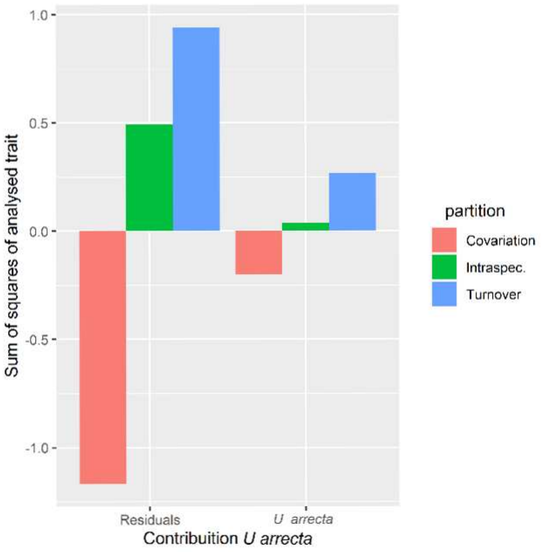
I) P turnover= 0.035
P intra= 0.356

P total= 0.372

J) P turnover= 0.034
P intra= 0.218

P total= 0.015





K) P turnover= 0.614
P intra= 0.059

P total= 0.164

L) P turnover= 0.370
P intra= 0.881

P total= 0.042

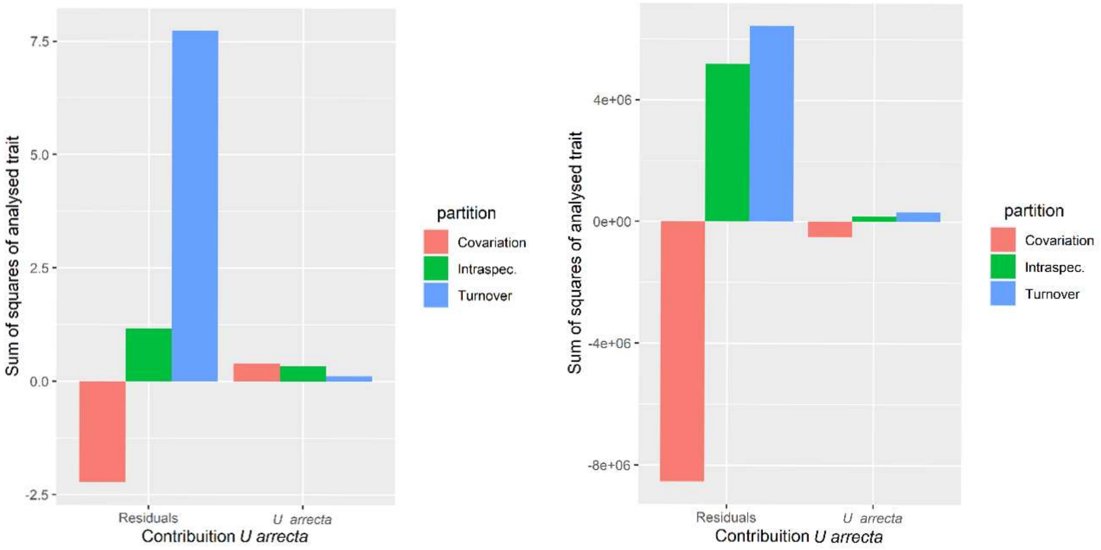


Fig 5: Graphs of the variance partition of the functional diversity (FD) and community weighted means (CWM) variance partition of the Guaraguaçu River macrophytes, taking into account the following traits, and the P values of their total functional variations: (A) FD of Root length (cm), (B) FD of Leaf area (cm^{2}), (C) FD of Petiole length (cm), (D) FD of Stem width (cm), (E) FD of Degree of herbivory (Braun-Blanquet), (F) FD of Specific leaf area (cm^{2}-^{1}), (G) CWM of root length (cm), (H) CWM of leaf area (cm^{2}), (I) CWM of petiole length (cm), (J) CWM of stem width (cm), (K) CWM of degree of herbivory, (L) CWM of Specific leaf area (cm^{2}-^{1}). The columns from left to right correspond to turnover, intraspecific diversity and covariation a. The residuals represent the part of the functional diversity that is not explained by the presence of *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga.

5. Discussion

Most results show that functional diversity, in general, has decreased with the presence of *Urochloa arrecta*, particularly interspecific diversity. These results demonstrate the overwhelming impacts of the *U. arrecta* as an alien species aquatic environment. It influenced the functional diversity and the correlation between turnover and intraspecific variability of CWM. Even so, there is a certain margin for a decrease in the proportion of intraspecific functional diversity in the presence of *U. arrecta*, besides some results in which there was no significant influence of the invasive species, due to the presence of other factors that functional diversity' influence and the calculations of the intra and interspecific Rao indices.

5.1. Functional diversity in space

One of the factors that we believe affected the results, is the fact that exotic species can coexist with some native species as *Panicum aquaticum*, and *Pontederia (Eichhornia) crassipes,* and even previously poorly adapted. Frequently contrasted species (Morais and Reichard, 2018), but the native species present in beds with *U. arrecta* proved to be more similar in traits with this alien species (testar isso). There is also the fact that the interactions of different species identities differ in environmental responses, with intraspecific variability being an essential component in differences in response between species (Albert et al., 2010). Indeed, our results corroborated the idea that the number of species is not always proportional to the functional diversity (Gallagher and Leishman 2012). A lower intra and interspecific functional diversity were estimated in the beds with the invasive species that harbored more species. It is very likely that invasion of *U. arrecta* positively interact with anthropic eutrophication promoting the opportunistic and floating species (Fontanarrosa et al., 2019), such as *Pontederia (Eichhornia) crassipes*, and *Hydrocotyle leucocephala*, well adapted to this type of environment (Machado-Filho, et al. 2021), as well as allowing the establishment of species with similar characteristics, such as other aquatic grass species (Sodhi et al., 2019). In fact, *U. arrecta* beds serve as anchors for such floating species, while the entry of nutrients in impacted sites promotes the growth of floating species, which may characterize this species as an ecosystem engineer, something already described in invasive species, which can modify the concentration of nutrients in its presence, as well as the oxygen and carbon fluctuations of the sites, this modification of conditions may not allow the survival of native species (Ribaudo et al. 2018), which may explain the lower interspecific diversity overall in the sites with *U. arrecta.* Indeed, within a particular species, there can be differences in the capacity to capture nutrients (Barkaoui et al., 2016), which allows a species such as *U. arrecta* to dominate sites with different nutrient avalabilities. Therefore, variability in soil and water nutrient conditions may also explain at least part of the beds' intraspecific diversity where *U. arrecta* dominates (Freschet et al., 2017).

But there was not always a significant change in functional diversity as the traits length of petiole and herbivory. is not present in mangroves, which are environments of high salinity known for their low diversity (functional and taxonomic) and very susceptible to anthropogenic disturbances, especially peoples and exploitation (Leung and Cheung, 2017). The greatest possibility that these changes may be caused by the gradient of anthropogenic impacts in conjunction with salinity in the Guaraguaçu River

(Nunes and Camargo 2017), remembering that environmental data were not evaluated in this research and this is something that still needs to be evaluated.

In the case of root length, functional diversity decreased in the beds with *U. arrecta,* mainly in the interspecific diversity. This fact shows a selection of specific traits for the macrophytes inhabiting *U. arrecta* beds, decreasing their variety, particularly among species with similar resource capture strategies, especially by the high abundance with *U. arrecta*. The root is essential in the resource acquisition competition, mainly because of the hierarchy of competition characteristics, which is the hierarchy of the competitive capacities through the root, something prevalent in grasses (Fort et al., 2014). Therefore, one of the explanations for the homogeneity of traits of *U. arrecta* is that it belongs to the Poaceae family, in which most species generally have a high capacity for absorbing nutrients (Fort et al., 2014).

A trait that corroborated for the most part the hypothesis of lower intraspecific diversity within *U. arrecta* beds was the leaf area (Fu et al., 2015). We thus reinforce that changes caused by anthropogenic impacts (either environmental changes or invasive species) leaf traits' plasticity in wet regions. Given our study design, comparing beds with and without the dominance of *U. arrecta*, we argue that biotic factors such as dominance by an invasive species can modify the leaf area. This fact was already expected since leaf traits are quite sensitive to changes among and within species (Albert et al., 2010), even more so because of the competition for light that is greater in areas with high abundance of individuals, something that affects leaf area (Awan et al., 2015).

The results of the functional diversity of SLA had a greater proportional contribution of the intra-species variation in the *U. arrecta* relatively low SLA species (despite having a higher than standard SLA, like other aquatic grasses), living with high SLA species, which benefit in nitrogen-rich environments (Chmara et al., 2019), there is a decrease in total functional diversity. However, in sure macrophyte beds without *U. arrecta* there are species with an even lower SLA value (such as *Crinum americanum* and *Schoenoplectus (Scirpus) californicus* than *U. arrecta*), especially in mangroves, which contributed to the high interspecific diversity of this characteristic in the absence of *U. arrecta* (Tabela S7). Many ecologists consider the SLA to be one of the most important aspects to evaluate the community's assembly because it measures the ability to convert solar radiation into biomass (Albert et al., 2010; Chmara et al., 2019). The petiole length had similar products with those of the leaf area, even part of the leaf. This result corroborates that it is a trait with intra-specific variation and influenced by environmental factors, especially in different geographic locations in grass species (Sijacic Nikolic et al., 2013), being a result that cannot be dismissed in macrophytes (Araújo, 2017). Concerning the stem, it is one of the traits that are usually related to the plant's growth (Sodhi et al., 2019). Also, the intraspecific variation of this trait can be caused by the gradient or succession (Roeder et al., 2011). Although the intraspecific diversity increases proportionally with exotic species in this research, it is clear that *U. arrecta* selects species with different values of this trait, which can increase the interspecific diversity concerning the intraspecific trait variation (Sodhi et al., 2019).

In the degree of herbivory, *U. arrecta* seems to select species with individuals positively affected by herbivory. Such patterns seem consistent, given that the species had a more similar degree (see also Zhu, 2018). A set of individuals with high herbivory variability can suppress herbivores' performance, caused by many physiological mechanisms (Pearse et al., 2018). Indeed, agricultural systems with many grasses with low functional diversity are more susceptible to pests, promoting greater use of pesticides. Thus, herbivory is the most used trait to evaluate the plant's defense (Pearse et al., 2018). Then, we sugest that the presence of *U. arrecta* also promotes another biological invasion process: the spread of pests (see also Schoelynck and Struyf, 2015). A positive relationship between invasive species is well described in the 'Invasional Meltdown Hypothesis' (Simberloff and Von Holle, 1999). Here, we argue that such positive interaction can be considered another negative impact of *U. arrecta* in the native macrophyte community. It is essential to say that defense against herbivory can reduce the competitive capacity of plants. However, it should be noted that this trait is ordinal and not continuous, like the others, something that ends up causing the variations of the other traits (Sodhi et al. 2019).

5.2. Functional diversity over time

It is essential to mention that seasonality is probably not as important in the rainforest as in temperate regions (Guan et al., 2020) and is the likely explanation that patterns were not observed in all analyses (Table S6).

The leaf area results corroborate some previous studies literature, which already said that the increase in rainfall increases foliar trait values (Le Bagousse-Pinguet et al., 2017). Although we already know that the absence of dominance promotes diversity (functional and taxonomic), it also increases depending on the resource availability, mainly because of changes in the covariation of traits. Besides, in some traits, as the leaf area and the petiole length, there was a tendency to decrease in the beds with *U. arrecta*, especially in April due to invaders' introduction and climate change (Chmara et al., 2019). According to our results, *U. arrecta* selected functional groups with smaller leaves in the stretch of river with higher anthropogenic impact (where *U. arrecta* is present). For example, small free-floating species are usually related to increased nutrient enrichment, such as those of the genera *Lemna* and *Pistia*, which highlights the possibility of the effect of this species as an ecosystem engineer (Ribaudo et al., 2018). Apart from the effects in the leaf area, the decrease in intraspecific diversity of foliar traits may be harmful to the ecosystem since this trait is key to promote stability of ecosystems (Chmara et al., 2019), given it is a trait that usually varies according to the gradient of environmental variables, such as nutrient concentration and pH (Chmara et al., 2019; Le Bagousse-Pinguet et al., 2017). Remembering that interspecific functional diversity can vary positively between periods, as occurred in April 2016 and 2018 in some traits, such as leaf area (Appendix 1). In the case of the traits stem width and petiole length there were no significant results in relation to the presence of *U.arrecta,* but as and these traits are related to the leaf size that had a significant result, it may be that these variations are related to that (Sijacic Nikolic et al., 2013; Roeder et al., 2011).

The functional diversity in root length values did not depend on time precisely because the species allows different species to occur, besides the high availability of nutrients, over time through environmental and anthropic factors, which influence these changes (Chmara et al., 2019 ; Fontanarrosa et al., 2019).

About the herbivory, the variation increased, likely for the same reasons discussed above: a species that has many protections against herbivory, together with an ecosystem full of nutrients and positively impacted, may increase both herbivory values and variation in herbivory (Spasojevic et al. 2010; Sodhi et al., 2019).

5.3. Community-level weighted means of trait values

As seen in the results, although there is a drop in the intraspecific variability of the CWM, it is not significant and there is little impact of *U. arrecta* on the CWM. This means that other factors influence functional characteristics more than invasive species. This means that *U. arrecta* has little effect on the individual plasticity composition of the functional characteristics of individuals and species and how these characteristic values vary (Leps et al. 2011; Carlucci et al., 2015). Anthropic impacts are known to affect the functional diversity of species. Therefore, it may be that the biggest drops in intraspecific variability in relation to turnover are related to the environmental gradient of the anthropic impacts of eutrophication and pollution than to the invasion of *U. arrecta.*

There was a greater drop in intraspecific variability in the presence of the invasive species in most cases, mainly in the leaf area (so much so that the CWM of the leaf area became more justified by the turnover of species in the presence of alien species; fig 3.), which was also greatly affected in the diversity indexes (Chmara et al., 2019; Sodhi et al., 2019).

Even so, it is necessary to emphasize that this fall must have other causes, which are not the presence of the invasive species. The exception is the width of the stem, in which we observe that the differences between the presence of *U. arrecta* and the residues, in addition to the fact that intraspecific variability has a high contribution in the presence of *U. arrecta*. Therefore, or the introduction of invasive species affects the functional traits of individuals only in the width of the stem, due to the fact that invasive species affect the growth of species (Sodhi et al. 2019) and increases the variability of individuals in herbivory, due to the factors already mentioned in section 5.1., but that in general, these variations in the functional traits are not caused by the presence of *U. arrecta*.

5.4. Future investigation and concluding remarks

The calculation method, although useful, has some limitations, such as the fact that the large abundance proportionally increased the weight of the invasive species in the calculation, which may end up explaining the more significant proportion of the intraspecific diversity in beds with *U. arrecta*, partially contradicting our hypothesis regarding the assignment of the intra-species part of functional diversity (de Belo et al., 2011). There is also the fact that SLA has been advanced in only one period and needs to be tested in more periods to have more robust results (Araujo, 2017).

Most results have the same tendency: the effect of *U. arrecta* in decreasing functional diversity and promoting relatively more importance of intraspecific trait variation compared to interspecific trait variation to functional diversity. Even so, our study highlighted the complexity of patterns, as they depend on the identity of the trait evaluated. Indeed, results, when all traits are considered together, differed from results treating each trait separately.

In our study, we chose to use a method that used Euclidean distance, because only continuous data is needed for measuring intraspecific functional diversity, so it is more suitable for intraspecific functional diversity (de Bello et al. 2011). We advocate that other approaches may complement the diversity patterns in Guaraguaçu River communities, such as phylogenetic diversity (see also Guareschi et al., 2015).

It must also be emphasized that because few relationships are significant, the management of invasive species may not be the best solution for macrophyte beds. It is necessary to better evaluate the relationship of intra and interspecific indices with environmental data, to observe if this change occurs by the gradient of anthropic impacts and even the fact that *U. arrecta* is an ecosystem engineer and may seek other solutions to resolve the impacts on the functional diversity of macrophytes in some other way.

Finally, we also generated evidence that beds with *U. arrecta* have lower functional diversity (total, intra and interspecific), sense the inter most influenced. However,the influence of *U. arrecta* on FD and CWM is small compared to other variables (possibly anthropogenic or linked to the environmental gradient of the river; due to occupation in margins, effluent discharges, channel rectification, see Araújo, 2017). This may have an implication from an aquatic ecosystem management point of view. The reduction of anthropogenic impacts may increase functional diversity due to: the decrease of *U. arrecta*; and mainly by the change in environmental conditions.

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Supplemantary material

Table S1: Average traits in macrophyte beds where the *U. arrecta* is present and where it is absent.

Trait	*U. arrecta* absent	*U. arrecta* present
Root length (cm)	11.82	10.64
Leaf area (cm²)	80.8	80.32
Petiole lenght (cm)	6.54	8.13
Stem width (cm)	0.27	0.39
Herbivory (Braun-Blanquet Degrees)	1.71	1.62
Specific leaf area (cm² g-1)	1055.21	1245.865

Table S2: CWM of traits in macrophyte beds where the *U. arrecta* is present and where it is absent.

Trait	*U. arrecta* absent	*U. arrecta* present
Root length (cm)	10.31	9.35
Leaf area (cm²)	57.57	83.44
Petiole length (cm)	4.73	9.52
Stem width (cm)	0.28	0.41
Herbivory (Braun-Blanquet Degrees)	1.74	1.53
Specific leaf area (cm² g-1)	1199.14	1449.09

Table S3: Lists of aquatic macrophytes and life forms recorded in Guaraguaçu river in beds without *Urochloa arrecta*, Paraná, Brazil. AM = amphibious; EM = emergent; EP = epiphyte; FF = free floating; FS = free submerged; RF = rooted floating; and RS = rooted submerged.

Family	Species	Life form
Amaranthaceae	*Alternanthera philoxeroides* (Mart.) Griseb.	AM
Amaryllidaceae	*Crinum americanum* L.	EM
Araceae	*Lemna sp.*	FF
	Pistia stratiotes L.	FF
	Wolfiella sp.	FF
Araliaceae	*Hydrocotyle leucocephala* Cham. & Schltdl.	FF
Asteraceae	*Sphagneticola trilobata* (L.) Pruski	AM
Commelinaceae	*Murdannia nudiflora* (L.) Brenan	AM
Cyperaceae	*Cyperus blepharoleptos* Steud.	EP
	Eleocharis geniculata (L.) Roem. & Schult.	AM

	Eleocharis interstincta (Vahl) Roem. & Schult.	EM
	Eleocharis minima Kunth	EM
	Rhynchospora corymbosa (L.) Britton	E
	Schoenoplectus californicus (C.A.Mey.) Soják	EM
Haloragaceae	*Myriophyllum aquaticum* (Vell.) Verdc	RS
Hydrocharitaceae	*Egeria densa* Planch.	RS
Lentibulariaceae	*Utricularia gibba* L.	FS
Mayacaceae	*Mayaca sellowiana* Kunth	RS
Nymphaeaceae	*Nymphaea caerulea* Savugny	RF
Onagraceae	*Ludwigia peploides* (Kunth) P.H.Raven	FF
	Ludwigia peruviana (L.) H.Hara	EM
Poaceae	*Hymenachne amplexicaulis* (Rudge) Nees	EM
	Paspalum repens P.J.Bergius	EM
	Unknown species 1	EM
	Unknown species 2	EM
	Unknown species 3	EM
Polygonaceae	*Polygonum hydropiperoides* Michx	EM
	Polygonum stelligerum Cham.	AM
Pontederiaceae	*Pontederia crassipes* (Mart.) Solms	FF
Ricciaceae	*Ricciocarpos natans* (L.) Corda	FF
Salviniaceae	*Azolla caroliniana* Willd	FF
	Salvinia biloba Raddi	FF

Table S4: Lists of aquatic macrophytes and life forms recorded in Guaraguaçu river beds with *Urochloa arrecta*, Paraná, Brazil. AM = amphibious; EM = emergent; EP = epiphyte; FF = free floating; FS = free submerged; RF = rooted floating; and RS = rooted submerged.

Family	Species	Life form
Alismataceae	*Echinodorus grandiflorus* (Cham. & Schltr.) Micheli	EM
Amaranthaceae	*Alternanthera philoxeroides* (Mart.) Griseb.	AM
	Alternanthera sp.	AM
Amaryllidaceae	*Crinum americanum* L.	EM

Araceae	*Lemna sp.*	FF
	Pistia stratiotes L.	FF
	Wolfiella sp.	FF
Araliaceae	*Hydrocotyle leucocephala* Cham. & Schltdl.	FF
Asteraceae	*Sphagneticola trilobata* (L.) Pruski	AM
Charophyceae	*Nitella sp.*	RS
Commelinaceae	*Murdannia nudiflora* (L.) Brenan	AM
Cyperaceae	*Cyperus blepharoleptos* Steud.	EP
	Eleocharis interstincta (Vahl) Roem. & Schult.	EM
	Eleocharis minima Kunth	EM
	Rhynchospora corymbosa (L.) Britton	E
	Schoenoplectus californicus (C.A.Mey.) Soják	EM
Haloragaceae	*Myriophyllum aquaticum* (Vell.) Verdc	RS
Hydrocharitaceae	*Egeria densa* Planch.	RS
Lentibulariaceae	*Utricularia gibba* L.	FS
Mayacaceae	*Mayaca sellowiana* Kunth	RS
Nymphaeaceae	*Nymphaea caerulea* Savugny	RF
Onagraceae	*Ludwigia peploides* (Kunth) P.H.Raven	FF
	Ludwigia peruviana (L.) H.Hara	EM
Orchidaceae	*Habenaria repens* Nutt.	EM
Plantaginaceae	*Bacopa sp.*	AM
Poaceae	*Hymenachne amplexicaulis* (Rudge) Nees	EM
	Panicum aquaticum Poir.	EM
	Paspalum repens P.J.Bergius	EM
	Urochloa arrecta (Hack. ex T.Durand & Schinz) Morrone & Zuloaga	EM
	Unknown species 1	EM
Polygonaceae	*Polygonum hydropiperoides* Michx	EM
	Polygonum stelligerum Cham.	AM
Pontederiaceae	*Pontederia crassipes* (Mart.) Solms	FF
Salviniaceae	*Azolla caroliniana* Willd	FF
	Salvinia biloba Raddi	FF

Table S5: Functional diversity indices (Rao) in each macrophyte bed. (RL=root length (cm); LA=leaf area (cm^2); PL= petiole length (cm); SW=stem width (cm); H=herbivory (Braun-Blanquet); SLA=specific leaf area (cm^2g^{-1}); AST=all standardized traits)

Pontos	Intraspecific	Interespecific	Total
1	RL: 68.921	RL: 75.966	RL: 144.887
	LA: 2399.457	LA: 19386.071	LA: 21785.527
	PL: 945.787	PL: 497.021	PL: 1442.808
	SW: 0.035	SW: 0.066	SW: 0.101
	H: 1.219	H: 0.903	H: 2.122
	SLA: 256671.668	SLA: 11539094.727	SLA: 11795766.395
	AST: 2.711	AST: 3.874	AST: 6.585
2	RL: 166.410	RL: 176.220	RL: 342.630
	LA: 16342.725	LA: 17896.539	LA: 34239.263
	PL: 141.834	PL: 131.803	PL: 273.637
	SW: 0.070	SW: 0.048	SW: 0.118
	H: 0.764	H: 1.348	H: 2.112
	SLA: 17151574.340	SLA: 30288297.761	SLA: 47439872.161
	AST: 2.368	AST: 2.504	AST: 4.872
3	RL: 166.823	RL: 167.861	RL: 334.684
	LA: 5917.523	LA: 9915.795	LA: 15833.318

	PL: 463.332	PL: 439.469	PL: 902.801
	SW: 0.043	SW: 0.046	SW: 0.089
	H: 0.902	H: 0.867	H: 1.769
	SLA: 6123596.436	SLA: 11250743.994	SLA: 17374340.430
	AST: 1.929	AST: 2.105	AST: 4.034
4	RL: 165.282	RL: 129.447	RL: 294.729
	LA: 3902.993	LA: 7425.005	LA: 11327.999
	PL: 338.196	PL: 160.267	PL: 498.463
	SW: 0.038	SW: 0.055	SW: 0.093
	H: 0.716	H: 0.447	H: 1.163
	SLA: 15682.560	SLA: 53720.313	SLA: 69402.873
	AST: 3.210	AST: 2.754	AST: 5.964
5	RL: 113.225	RL: 95.075	RL: 208.230
	LA: 5606.596	LA: 17774.250	LA: 23380.840
	PL: 177.742	PL: 174.930	PL: 352.672
	SW: 0.050	SW: 0.027	SW: 0.077
	H: 0.888	H: 0.620	H: 1.508
	SLA: 120989.131	SLA: 2032238.500	SLA: 2153228.631
	AST: 2.084	AST: 1.980	AST: 4.064
6	RL: 103.240	RL: 101.632	RL: 204.872
	LA: 12636.870	LA: 31039.470	LA: 43676.340
	PL: 159.714	PL: 330.168	PL: 489.882
	SW: 0.059	SW: 0.117	SW: 0.176
	H: 0.822	H: 1.100	H: 1.922
	SLA: 3798673.272	SLA: 10028006.757	SLA: 13826679.029
	AST: 1.770	AST: 2.753	AST: 4.523
7	RL: 77.998	RL: 35.929	RL: 113.927
	LA: 677.189	LA: 59123.945	LA: 59801.134
	PL: 369.362	PL: 154.314	PL: 523.676
	SW: 0.698	SW: 4.452	SW: 5.150
	H: 0.884	H: 0.590	H: 1.474
	SLA: 6449991.202	SLA: 17299670.058	SLA: 23749661.260
	AST: 3.801	AST: 14.237	AST: 18.038
8	RL: 43.068	RL: 42.613	RL: 85.681
	LA: 427.250	LA: 3735.565	LA: 4162.814
	PL: 14.238	PL: 32.361	PL: 46.599
	SW: 0.098	SW: 0.141	SW: 0.239
	H: 0.830	H: 0.793	H: 1.623
	SLA: 267173.394	SLA: 338598.508	SLA: 605771.903
	AST: 1.629	AST: 3.523	AST: 5.152
9	RL: 71.387	RL: 71.945	RL: 143.332
	LA: 5026.800	LA: 10074.900	LA: 15101.700
	PL: 531.893	PL: 893.768	PL: 1425.661
	SW: 0.080	SW: 0.086	SW: 0.166
	H: 0.514	H: 0.817	H: 1.331
	SLA: 11927820.979	SLA: 21961380.927	SLA: 33889202.906
	AST: 2.502	AST: 4.621	AST: 7.123
10	RL: 56.988	RL: 73.352	RL: 130.340
	LA: 453.257	LA: 8335.710	LA: 8763.487
	PL: 171.307	PL: 66.758	PL: 238.065

	SW: 0.041 H: 0.704 SLA: 10426.248 AST: 1.635	SW: 0.101 H: 0.710 SLA: 634040.874 AST: 5.290	SW: 0.142 H: 1.414 SLA: 644467.122 AST: 6.925
11	RL: 33.295 LA: 1923.565 PL: 320.948 SW: 0.047 H: 0.855 SLA: 414533.638 AST: 2.236	RL: 48.043 LA: 44897.682 PL: 903.241 SW: 0.082 H: 0.734 SLA: 20678842.893 AST: 7.420	RL: 81.338 LA: 46821.247 PL: 1224.189 SW: 0.129 H: 1.589 SLA:21093376.531 AST: 9.656
12	RL: 115.639 LA: 52744.315 PL: 518.839 SW: 0.038 H: 0.713 SLA: 89456.338 AST: 1.962	RL: 156.299 LA: 50628.288 PL: 842.983 SW: 0.158 H: 0.842 SLA: 78133.162 AST: 3.174	RL: 271.938 LA: 103372.603 PL: 1361.822 SW: 0.196 H: 1.555 SLA: 167589.500 AST: 5.136
13	RL: 59.542 LA: 9634.611 PL: 277.135 SW: 0.263 H: 0.987 SLA: 305497.178 AST: 1.930	RL: 132.777 LA: 46112.404 PL: 442.386 SW: 0.110 H: 0.692 SLA: 270262.945 AST: 2.664	RL: 192.319 LA: 55747.015 PL: 719.520 SW: 0.373 H: 1.679 SLA: 575760.123 AST: 4.594
14	RL: 524.255 LA: 23164.350 PL: 236.725 SW: 0.097 H: 0.822 SLA: 53264.931 AST: 2.715	RL: 217.136 LA: 59043.960 PL: 368.454 SW: 0.084 H: 1.437 SLA: 60803.818 AST: 3.550	RL: 741.391 LA: 82208.310 PL: 605.179 SW: 0.181 H: 2.259 SLA: 114068.749 AST: 6.265
15	RL: 42.276 LA: 14171.846 PL: 80.596 SW: 0.155 H: 0.937 SLA: 14907.666 AST: 1.868	RL: 130.919 LA: 30688.325 PL: 31.116 SW: 0.036 H: 0.696 SLA: 18123.546 AST: 2.218	RL: 173.195 LA: 44860.171 PL: 111.712 SW: 0.191 H: 1.633 SLA: 33031.212 AST: 4.086
16	RL: 85.907 LA: 4274.522 PL: 54.558 SW: 0.152 H: 0.536 SLA: 149.726 AST: 1.672	RL: 76.727 LA: 10888.201 PL: 64.288 SW: 0.108 H: 1.287 SLA: 0 AST: 2.322	RL: 162.634 LA: 15162.72 PL: 118.846 SW: 0.260 H: 1.823 SLA: 149.726 AST: 3.994

Table S6: ANOVA results (R2, P-values, and F-values) of the relationship between functional diversity indices (intraspecific, interspecific, and total) and months of the year for the evaluation of seasonality.

Traits	R^2	P	F
Root length (cm)	Intra: 0.013 Inter: 0.015 Total: 0.011	Intra: 0.664 Inter: 0.653 Total: 0.703	Intra: 0.197 Inter: 0.211 Total: 0.152
Leaf area (cm^2)	Intra: 0.192 Inter: 0.341 Total: 0.025	Intra: 0.090 Inter: 0.018 Total: 0.563	Intra: 3.315 Inter: 7.252 Total: 0.352
Petiole lenght (cm)	Intra: 0.291 Inter: 0.207 Total: 0.125	Intra: 0.031 Inter: 3.669 Total: 0.180	Intra: 5.749 Inter: 0.076 Total: 1.993
Stem width (cm)	Intra: 0.080 Inter: 0.001 Total: 0.062	Intra: 0.288 Inter: 0.894 Total: 0.354	Intra: 1.219 Inter: 0.018 Total: 0.921

Degree of herbivory (Braun-Blanquet Degrees)	Intra: 0.106 Inter: 0.010 Total: 0.041	Intra: 0.217 Inter: 0.714 Total: 0.450	Intra: 1.671 Inter: 0.140 Total: 0.605
All standardized traits	Intra: 0.012 Inter: 9.228e-04 Total: 0.005	Intra: 0.684 Inter: 0.911 Total: 0.792	Intra: 0.172 Inter: 0.013 Total: 0.072

Table S7: ANOVA results (R2, P-values, and F-values) of the relationship between functional diversity indices (intraspecific, interspecific, and total) of each macrophyte bed and the sites (‘caixetal’, high anthropogenic impacts sites and mangrove.

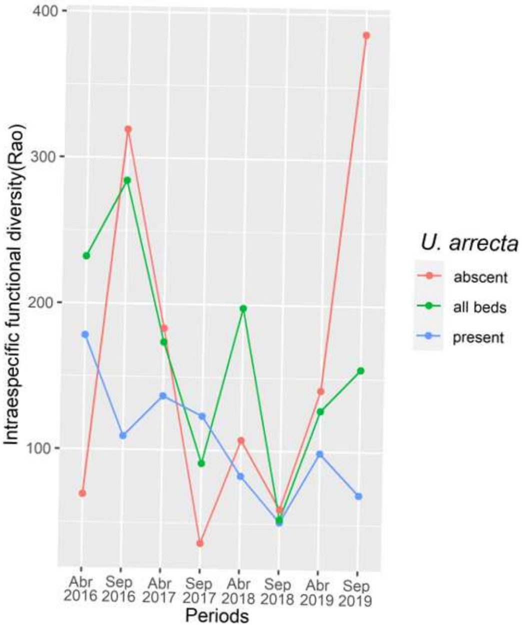
Traits	R^2	P	F
Root length (cm)	Intra: 0.149 Inter: 0.076 Total: 0.113	Intra: 0.349 Inter: 0.600 Total: 0.459	Intra: 1.142 Inter: 0.532 Total: 0.829
Leaf area (cm^2)	Intra: 0.034 Inter: 0.110 Total: 0.182	Intra: 0.798 Inter: 0.469 Total: 0.272	Intra: 0.229 Inter: 0.804 Total: 1.444
Petiole lenght (cm)	Intra: 0.211 Inter: 0.375 Total: 0.184	Intra: 0.215 Inter: 0.012 Total: 0.267	Intra: 1.736 Inter: 8.387 Total: 1.462
Stem width (cm)	Intra: 0.259 Inter: 7.720e-04 Total: 0.258	Intra: 0.142 Inter: 0.919 Total: 0.144	Intra: 2.274 Inter: 0.011 Total: 2.260
Degree of herbivory (Braun-Blanquet Degrees)	Intra: 0.119 Inter: 0.029 Total: 0.020	Intra: 0.440 Inter: 0.821 Total: 0.877	Intra: 0.874 Inter: 0.201 Total: 0.133
Specific leaf area (cm^2g^{-1})	Intra: 0.398 Inter: 0.571 Total: 0.522	Intra: 0.037 Inter: 0.004 Total: 0.008	Intra: 4.294 Inter: 8.677 Total: 7.091
All standardized traits	Intra: 0.246 Inter: 0.249 Total: 0.005	Intra: 0.337 Inter: 0.155 Total: 0.792	Intra: 1.181 Inter: 0.249 Total: 0.072

Fig S1: The alien species *Urochloa arrecta* (Hack. ex T. Durand & Schinz) Morrone & Zuloaga in the Guaraguaçu River, Paraná State, Brazil. Photo: <André A. Padial >

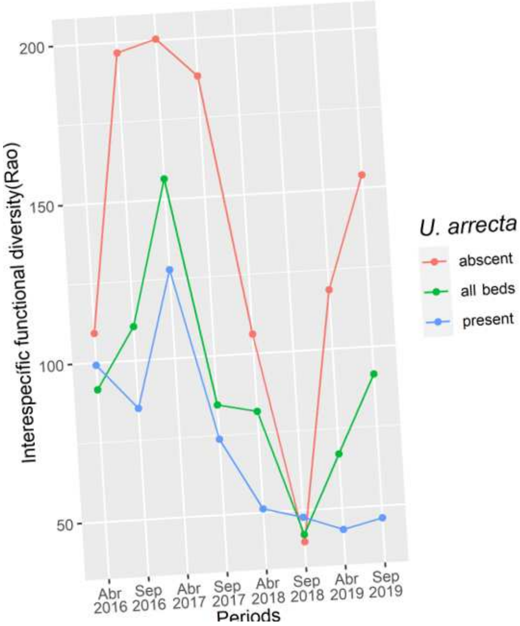
Colors should be used for any figures in print: Black, White, Red, Blue and Green

Fig S2: Functional diversity indices of root length (cm) in beds with (blue) and without *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga (red) and in all beds (green) (A) Intraspecific; (B) Interspecific; (C) Total.

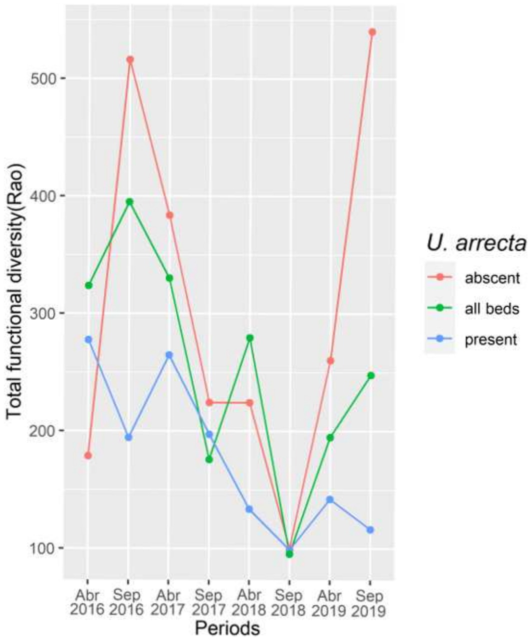
A)



B)

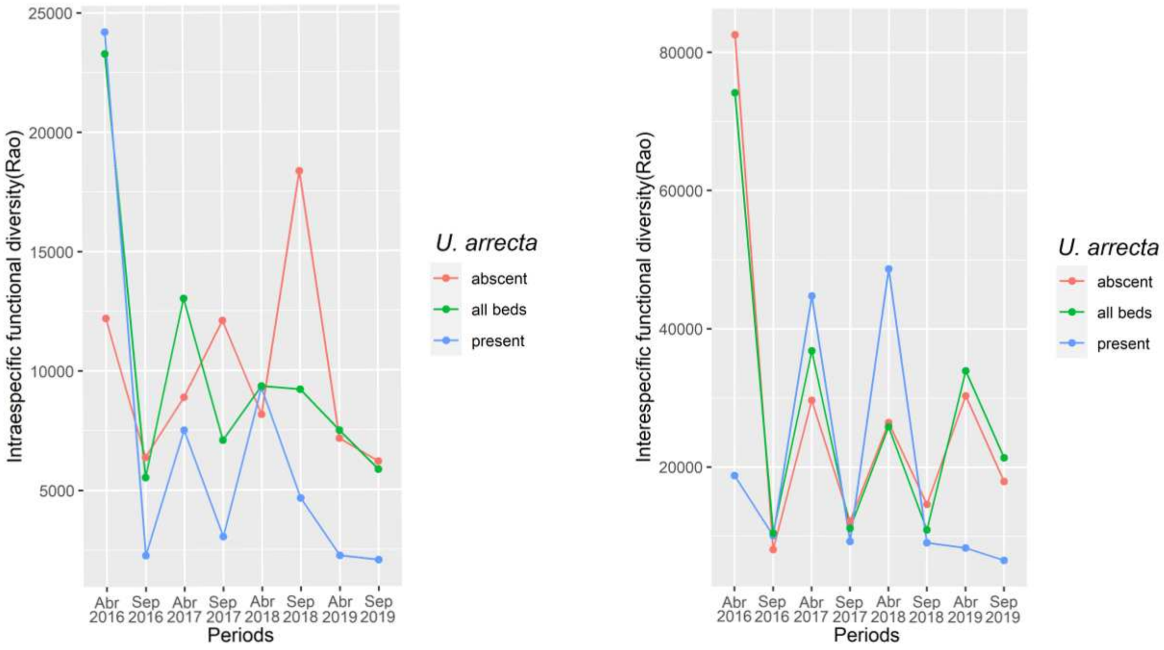


C)



Colors should be used for any figures in print: Black, White, Gray, Light Gray, Red , Light Blue and Green

Fig S3: Functional diversity indices of leaf area (cm²) in beds with (blue) and without *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga (red) and in all beds (green) (A) Intraspecific; (B) Interspecific; (C) Total.


A)

B)

C)

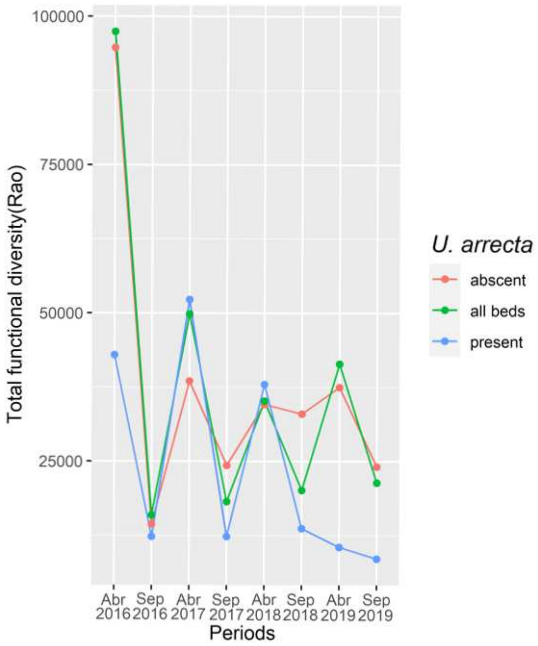


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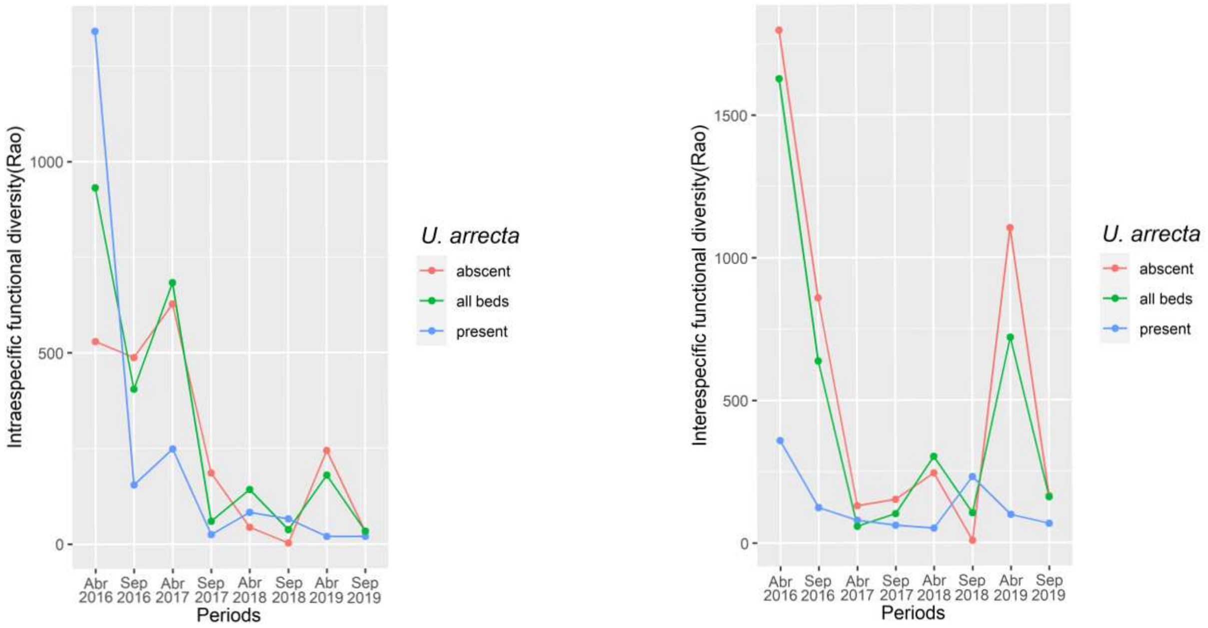
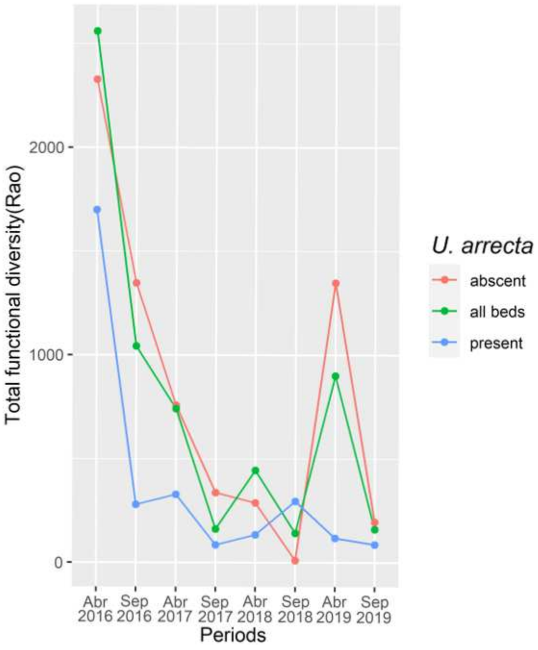
Fig S4: Functional diversity indices of petiole length (cm) in beds with (blue) and without *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga (red) and in all beds (green) (A) Intraspecific; (B) Interspecific; (C) Total.

A) B)

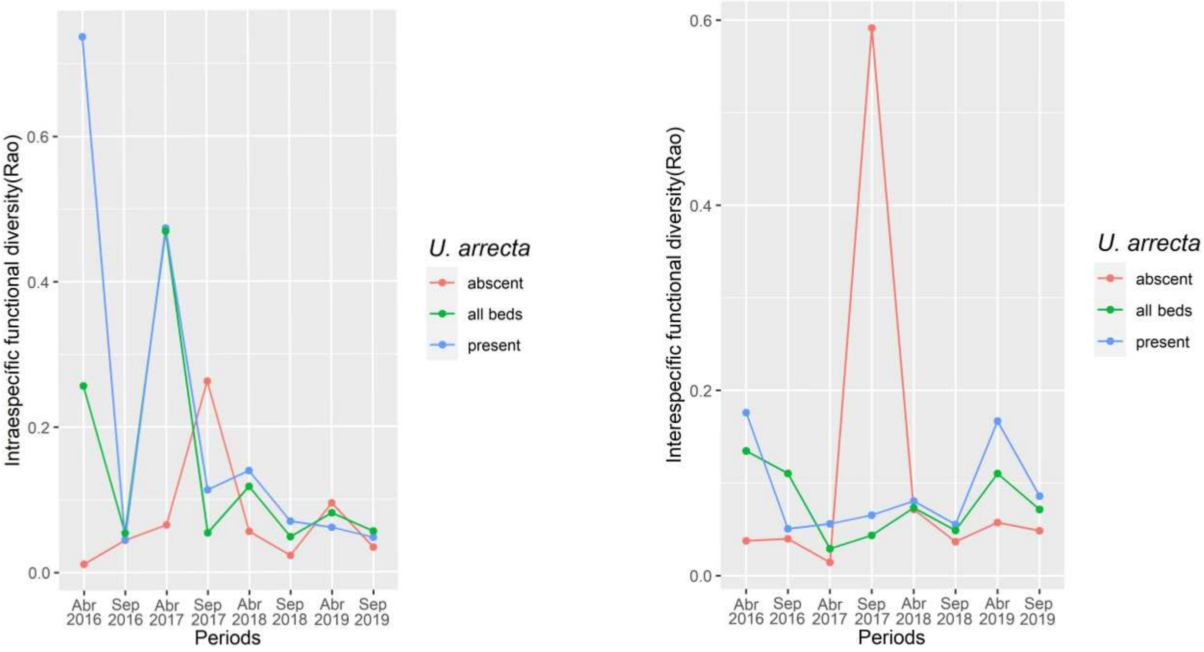


C)



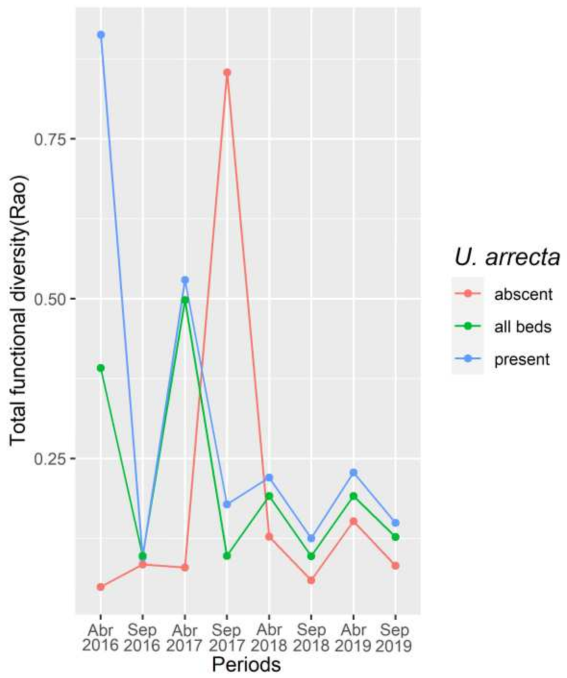
Colors should be used for any figures in print: Black, White, Gray, Light Gray, Red , Light Blue and Green

Fig S5: Functional diversity indices of stem width (cm) in beds with (blue) and without *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga (red) and in all beds (green) (A) Intraspecific; (B) Interspecific; (C) Total.


A)

B)

C)

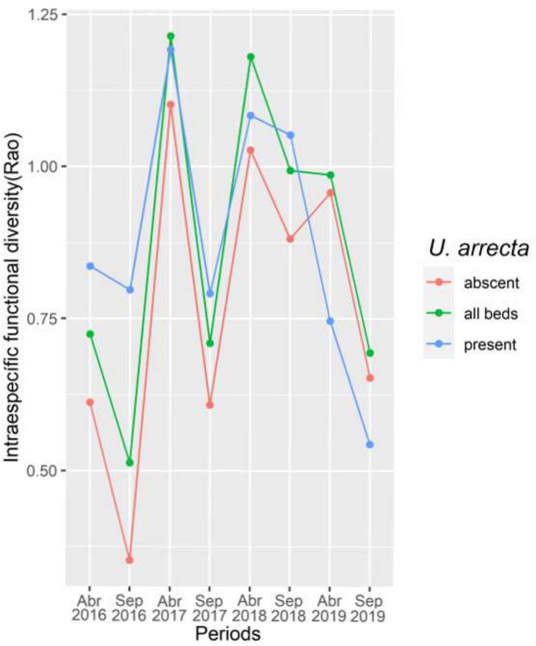


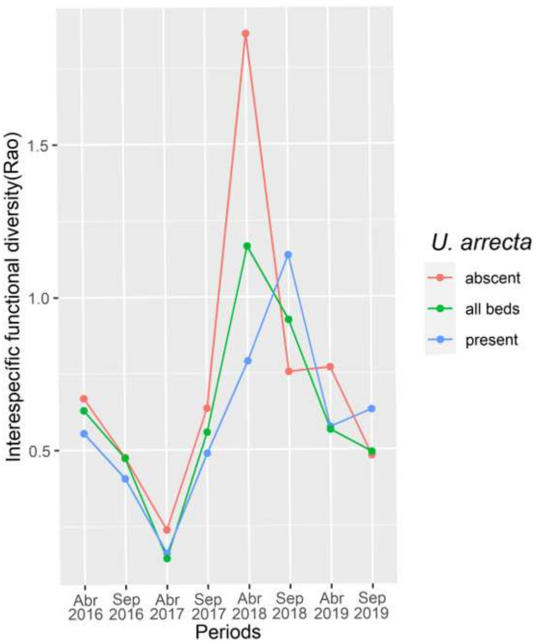
Colors should be used for any figures in print: Black, White, Gray, Light Gray, Red , Light Blue and Green

Fig S6: Functional diversity indices of degree of herbivory (Braun-Blanquet) in beds with (blue) and without *Urochloa arrecta* (Hack. Ex. T. Durand and Schinz) Morrone & Zuloaga (red) and in all beds (green) (A) Intraspecific; (B) Interspecific; (C) Total.

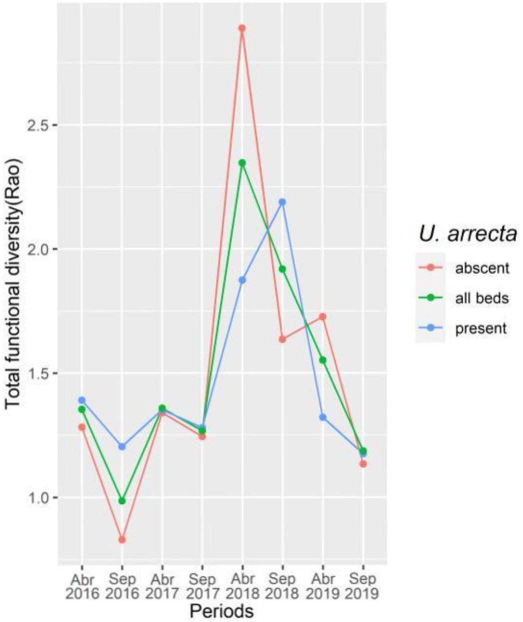
A)

B)


Intraespecific functional diversity(Rao)
1.25
1.00
0.75
0.50
Abr 2016
Sep 2016
Abr 2017
Sep 2017
Abr 2018
Sep 2018
Abr 2019
Sep 2019
Periods
U. arrecta
abscent
all beds
present

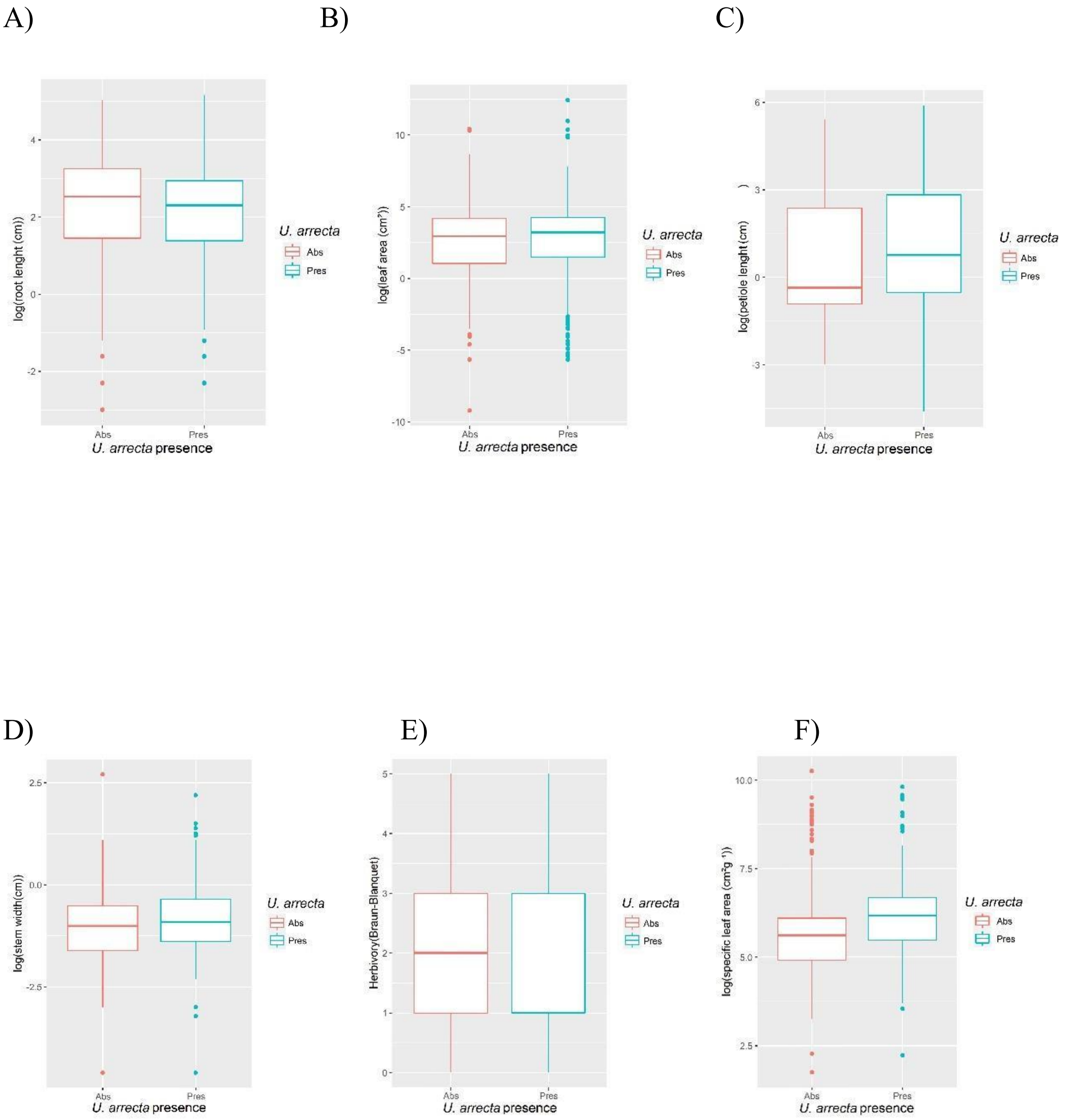

Interespecific functional diversity(Rao)
1.5
1.0
0.5
Abr 2016
Sep 2016
Abr 2017
Sep 2017
Abr 2018
Sep 2018
Abr 2019
Sep 2019
Periods
U. arrecta
abscent
all beds
present

C)


Total functional diversity(Rao)
2.5
2.0
1.5
1.0
Abr 2016
Sep 2016
Abr 2017
Sep 2017
Abr 2018
Sep 2018
Abr 2019
Sep 2019
Periods
U. arrecta
abscent
all beds
present

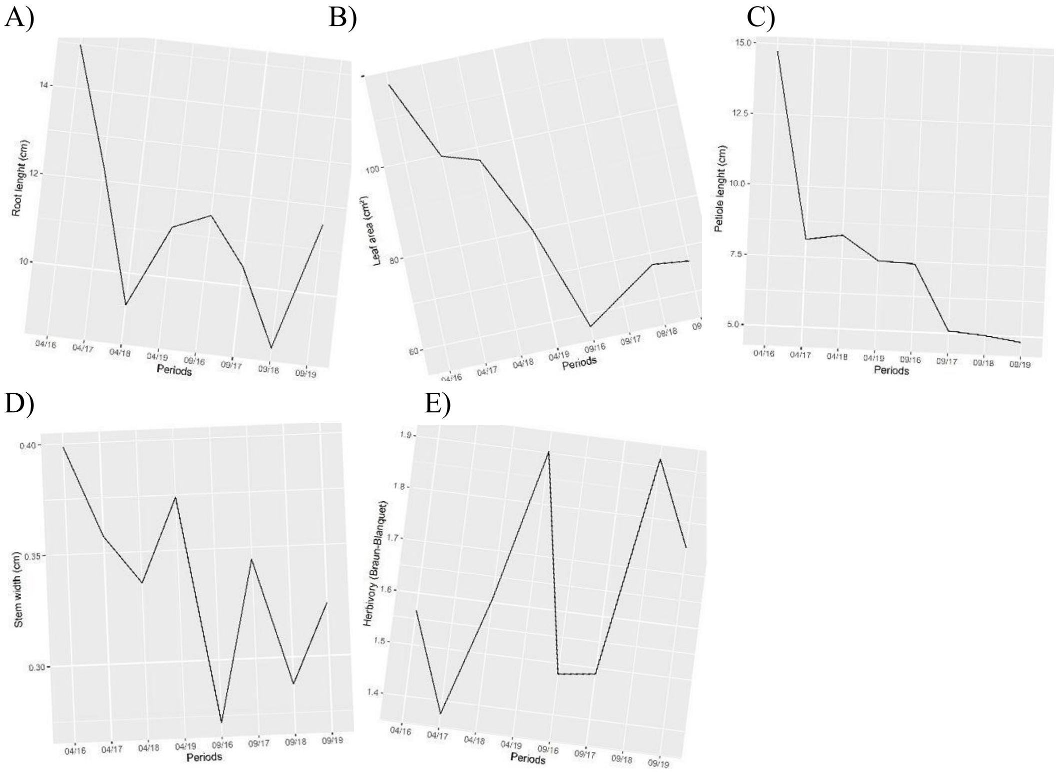
Colors should be used for any figures in print: Black, White, Gray, Light Gray, Red , Light Blue and Green

Fig S2. Boxplots of the different traits values: (A) Root length, (B) Leaf area, (C) Petiole length, (D) Stem width, (E) Degree of herbivory, (F) Specific leaf area.



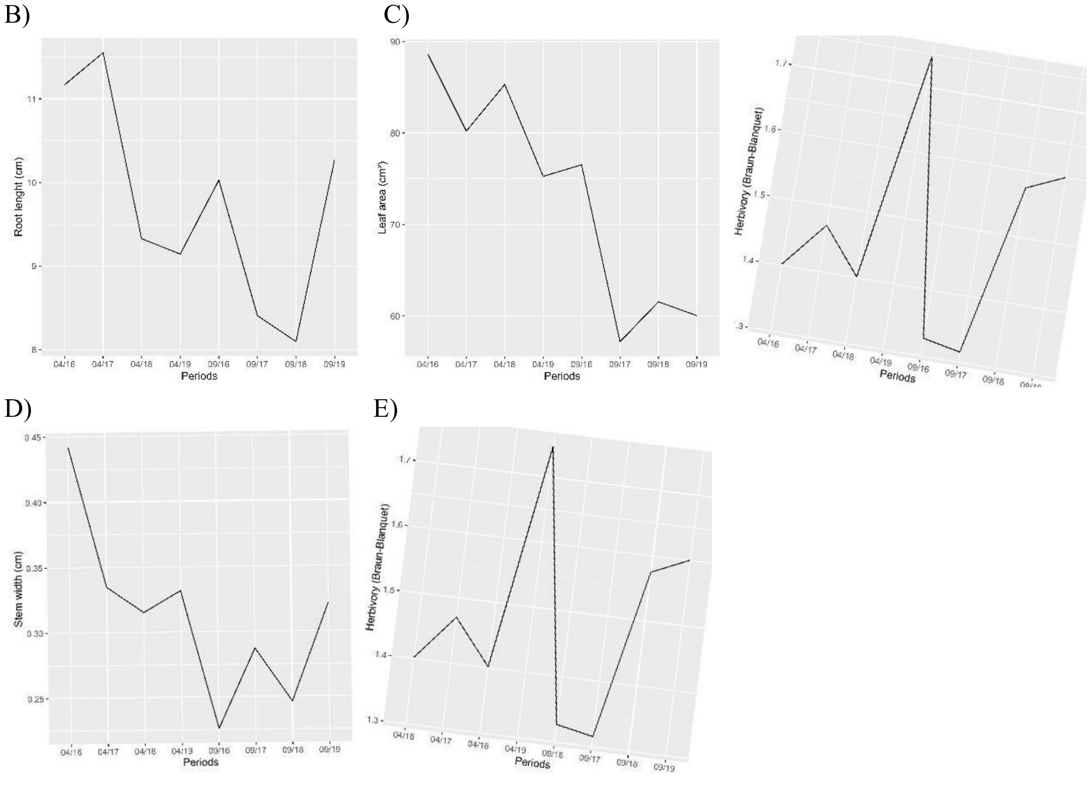
Colors should be used for any figures in print: Black, White, Gray, Light Gray, Red and Light Blue

Fig. S3. Average of the traits of all individuals, by period analyzed. (A) Root length, (B) Leaf area, (C) Petiole length, (D) Stem width, (E) Degree of herbivory.



Colors should be used for any figures in print: Black, White, Gray and Light Gray

Fig. S4. community weighted traits mean, by period analyzed. (A) Root length, (B) Leaf area, (C) Petiole length, (D) Stem width, (E) Degree of herbivory.



Colors should be used for any figures in print: Black, White, Gray and Light Gray