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THIAGO VINÍCIUS TRENTO OCCHI



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THIAGO VINÍCIUS TRENTO OCCHI

BIOLOGICAL INVASIONS AND ITS EFFECTS ON BIODIVERSITY

Tese apresentada ao curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Ecologia e Conservação.

Orientador: Prof. Dr. Jean Ricardo Simões Vitule

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RESUMO

As Invasões biológicas têm sido frequentemente apontadas como uma das principais ameacas à biodiversidade, causando impactos como homogeneização biótica, extinção de espécies e alteração nas funcionalidades dos habitats e ecossistemas. A ictiofauna destaca-se como um dos grupos mais estudados na ecologia de invasões devido às altas taxas de introduções através da aquariofilia, aquicultura e pesca esportiva. Estudos abordando atributos funcionais têm sido de grande utilidade para refinar o conhecimento da dinâmica das comunidades, facilitando a identificação de ligações entre ecossistemas e comunidades. A ecologia da invasão somada à abordagem da diversidade funcional tem sido frequentemente abordada para esclarecer os mecanismos de invasão e interações de espécies não nativas em novos ecossistemas. Nesse sentido, exploramos os tracos morfológicos de espécies nativas e não nativas (i.e. exóticas, translocadas e translocadas de bacias adjacentes), da região Neotropical em relação a ocorrência, distribuição de traços e vetores de introdução. As espécies nativas apresentaram grande diversidade morfológica, sobrepondo às espécies não nativas, enquanto as espécies translocadas e translocadas de bacias adjacentes ocuparam a maior parte do espaço morfológico quando comparada as espécies exóticas. A riqueza funcional de espécies nativas concentrou-se nas principais bacias hidrográficas, por exemplo, Amazônia, Essequibo, Tocantins e Paraná que apresentou alta rigueza funcional de espécies não nativas. O principal vetor de introdução foi a aquariofilia, tanto no número de espécies quanto na ocupação do espaço multidimensional. Posteriormente, no segundo capítulo, testamos os efeitos da macrófita invasora *U. arrecta* nas características funcionais de peixes em um rio Neotropical na Mata Atlântica, o Rio Guaraguaçu. Observamos que a distribuição de densidade dos atributos, ponderado pela métrica CWM (Community Weighted Mean) não varou ao longo do gradiente do rio, mas mostraram padrões conspícuos em diferentes tipos de habitats. Peixes associados as macrófitas nativas ocuparam a maior parte do volume do no espaço multidimensional. Enguanto a rigueza funcional dos peixes associada à macrófita invasora U. arrecta apresentou os menores índices de riqueza funcional.

Palavras-chave: Ecologia de Peixes. Neotropical. Espécies Exóticas. Ecologia Funcional. Alteração de Habitat.

ABSTRACT

Biological invasions had been frequently pointed out as one of the main threats to biodiversity, causing impacts such as, biotic homogenization, species extinction and alteration of the functionalities of habitats and ecosystems. The ichthyofauna stands out as one of the most studied groups in invasion ecology due to high rates of introductions throughout aquaculture, aquarium trade and sport fishing. Studies addressing functional attributes have been of great utility to refine knowledge of communities' dynamics, facilitating the identification of links between ecosystems and communities. The invasion ecology summed up to the functional diversity approach has been frequently tackled to clarify the mechanisms of invasion and interactions non-native species into new ecosystems. In this sense, we explore the morphological traits of native, nonnative species (i.e. exotic, translocated, and translocated neighboring), regarding basins of occurrence, trait distributions, and introduction pathways, in Neotropical region. Native species show great morphological diversity non-native species, while translocated and translocated overlapping neighboring species occupied most morphological space than exotic species. The functional richness of native species is concentrated in the major drainage basins, while the Parana basin shows high functional richness for non-native species. The main introduction pathway was aquarium trade, both in the number of species and occupation of the multidimensional space. Posteriorly, we test the effects of the invasive macrophyte U. arrecta in the functional traits of fishes in a Neotropical river in the Atlantic forest. We founded that CWM trait density distributions do not vary along the river gradient, but show conspicuous patterns in different habitats types. Fishes associated with Native macrophytes occupied the most of the convex hull volume in five-dimensional space. While the functional richness of fishes associated with the invasive macrophyte U. arrecta presents the minor functional richness indices.

Keywords: Fish ecology. Neotropical. Exotic species. Functional Ecology.

Habitat alteration.

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CHAPTER 1

A CLOSE LOOK TO MORPHOLOGICAL TRAITS OF NEOTROPICAL FRESHWATER NON-NATIVE FISHES

A close look to morphological traits of Neotropical freshwater non-native fishes

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Abstract

Aim: To explore the morphological traits of native, non-native species (i.e. exotic, translocated, and translocated neighboring), regarding basins of occurrence, trait distributions, and introduction pathways.

Major taxa studied: Freshwater fish

Location: Neotropical region

Time/period: 1960s-2018s

Methods: We retrieve species occurrence using a global database for freshwater fishes, and complement using the literature, trait information was retrieved from a research paper which compile summarized morphological traits into five principal components from a global pool. We then plot the multidimensional space according to the classification status of each species and introduction pathways. We also describe species richness, and functional index Fric and Feve at drainage basins scale for the Neotropical region.

Results: Native species show great morphological diversity overlapping non-native species, while translocated and translocated neighboring species occupied most morphological space than exotic species. The functional richness of native species is concentrated in the major drainage basins, while the Parana basin shows high functional richness for non-native species. The main introduction pathway was aquarium trade, both in the number of species and occupation of the multidimensional space.

Main conclusion: Translocated and translocated neighboring species shows more representatives in species richness and functional index in comparison with exotic species.

Introduction

Neotropical realm, a megadiverse region, hosts about one-third of the global diversity of freshwater fishes (>5000 species) which reflects in a high taxonomic, phylogenetic and functional diversity of freshwater fishes (Albert et al., 2020; Frehse et al., 2016; Pelicice et al., 2017; Reis et al., 2016; Su et al., 2020; Toussaint et al., 2016; Vitule et al., 2017b). Besides providing valuables ecosystem services (e.g. Nutrient

cycle, climate regulation, and fishery), the neotropics are under constant anthropogenic pressure (Bezerra et al., 2019; Hoeinghaus et al., 2009).

The human-induced alteration has lead to profound modifications in the biota (Sax & Gaines, 2003), such as ecosystem disturbance and introduced of non-native species and biological invasions (Lövei, 1997; McKnight et al., 2017). Biological invasions had been frequently pointed as the main threat to local (Ferreira et al., 2015) and global biodiversity (Clavero & García-Berthou, 2005; Lövei, 1997; Ricciardi et al., 2017; Simberloff & Vitule, 2014). Causing several ecological impacts, such as species loss and local extinction, changes in the trophic level (McKnight et al., 2017; Pinto-Coelho et al., 2008), biotic homogenization (Olden & Rooney, 2006; Rahel, 2000), reduction of genetic diversity, and ecosystems alteration (Hulme, 2007). Also, biological invasions have been generated economic loss (Pimentel et al., 2001, 2005), which consequently draws political attention (CBD, 2020). Unraveling patterns of distribution of non-native species, as well as its likely negative impacts, is paramount to decision-makers and ecosystem management (Leprieur et al., 2008; Pyšek & Richardson, 2006). Furthermore, explore the distribution of functional traits across scales is key to understand the gradients of ecosystem services in macro-scales (Violle et al., 2014).

Functional diversity approaches had been broadly used in aquatic ecology, focusing on species fitness in a given community and/or spatial gradient (Adam et al., 2015; Su et al., 2020; Toussaint et al., 2016; Villéger et al., 2014). In this context, fishes standouts as one of the main studied groups in invasion ecology. Mainly due to the high rates of species introductions, social-economic importance as a food source (Aquaculture and fisheries harvest) and cultural activities, such as sport fishing and aquarium trade (Casal, 2006; Leprieur et al., 2008; Jean Ricardo Simões Vitule et al., 2009, 2019), and the constant threats by anthropogenic impacts (Bezerra et al., 2019). Most approaches on fish biodiversity patterns in global scale had focused in the taxonomic components (Casal, 2006; Leprieur et al., 2008, 2011; Tedesco et al., 2017; Jean Ricardo Simões Vitule et al., 2019), nonetheless, functional diversity efforts in large scales has been constantly increasing, exploring trait distribution (Su et al., 2019), effects of climate changes (Buisson et al., 2013), species vulnerability (Mouillot et al., 2014; Toussaint et al., 2016; Vitule et al., 2017b) and also, biological invasions (Su et al., 2020).

Macro-ecological approaches had contributed broadly to the development of the invasion ecology. However, the nuances of biogeographical limits of species, and granulometric scale should be considered with caution, mainly for fishes (Vitule et al., 2019). Geopolitical scales (i.e. Countries, states, provinces) may be useful for correlating non-native species with anthropogenic drivers (Dawson et al., 2017). Nonetheless for ecological approaches, geopolitical boundaries could lead to misunderstanding conclusions (Vitule et al., 2019). This is outstanding in invasion ecology due to the complexity to define species status. In general, a species can be considered non-native when occurs beyond their natural range by human assistance (Blackburn et al., 2011a; Guo & Ricklefs, 2010). The definition seems to be clear and simple, however, applying this for aquatic species, such as freshwater fish in a perspective of a megadiverse region (e.g. Neotropical realm) can be tricky. Usually, rivers are the boundaries of geopolitical divisions (e.g. the border between states/provinces or countries), which may underestimate or overestimate the species records (Occhi et al., 2017). For example, species records from a river which is a geopolitical border (i.e. country or state/province) may be accounted for one side of the border (underestimating the records) or both sides of the border (overestimating the record). To avoid this problem a better choice is to use biogeographic boundaries e.g. Drainage Basins or ecoregions (see Abell et al., 2008). Yet, some problems regarding granulometric scale may persist. For example, translocated species or intra-country introductions, i.e. species that can be considered non-native outside (or even inside) the basins which they are native, but in the same biogeographical realm, biome, or geopolitical territory (Occhi et al., 2017; Vitule et al., 2019). This is a massive problem in countries with continental dimensions, for example, is largely observed for major, large size and aggressive predators such as Arapaima gigas in Amazon Basin (Miranda-Chumacero et al., 2012), Salminus brasilienses in Parana Basin (E. A. Gubiani et al., 2010; Vitule et al., 2014), and also other examples pointed by Vitule et al., 2019.

Several characteristics can affect the capability of a non-native species to spread into new environments, such as its origins (Paolucci et al., 2013), vectors of introduction (Gubiani et al., 2018) and functional characteristics (Su et al., 2020). In this sense, linking the pathways of introductions (i.e. vectors) its origins (exotic, or translocated) and the functional traits of the species may help to understand the drivers and mechanisms of the invasion process (Azzurro et al., 2014; Blackburn et al., 2011b).

In this sense, here we explore the morphological traits of native and non-native species of the major basins of the neotropical realm, according to their occurrence status, such as native, exotic (i.e. native range outside Neotropical realm), translocated (native range into the neotropical realm) and translocated neighboring (i.e. native from an adjacent drainage basin) (Figure 1), the morphological space according to the occurrence status and introduction pathways.

Material and Methods

Datasets

Fishes occurrences were compiled for 301 major basins of the neotropical realm (data from Tedesco et al., 2017) and complemented using the data published by Gubiani et al., (2018), and by Inter-American Biodiversity Information Network - IABIN (i.e. I3N database available at http://bd.institutohorus.org.br/www/). The 21.968 occurrences records of the 5.804 species were classified as to the species occurrence status (i.e. native, exotic, translocated, and translocated neighboring at the granulometric level of the freshwater ecoregion of the world - FEOW (see Abell et al., 2008). Despite the species occurrence status has been classified at the ecoregion level, the majority of the native species had information only at the drainage basins level, so major basins were kept as the spatial unit in the analyses.



FIGURA 1 Major basins and freshwater ecoregions of the world -FEOW at the Neotropical realm. Fishes with different colors represent the occurrence status according to the species origin, and arrows indicate the donor and recipient region.

Morphological traits were compiled from the dataset published by Su et al., The dataset covers 9.150 species from all of the world, describing 10 (2019).morphological traits related to locomotion and food acquisition (Table S2 in Su et al., 2020). We then combine the five principal components (PC), obtained by Su et al., (2019) which summarizes the 10 morphological traits, and explained 78.6% of the total variance (See Su et al., 2019, 2020 for further methodological details), with the occurrences of neotropical fishes. Information regarding the main pathways of introductions (i.e. vectors) was compiled from FishBase (www.fishbase.org), using the rFishBase package in R software (v. 4.0.2). Once species could be related to more than one introduction pathway, we opted to multiple counts the species registers i.e. if a given species is related to aquaculture and game fish it was account for both vectors. Also, it is important to highlight that we considered vectors according to FishBase, which excluded pathways like the removal of a biogeographic barrier (e.g. the flood of the "sete quedas" falls by the construction of Itaipu dam). The resulting dataset contains information on occurrence status, morphological traits, and introduction pathways of 3.591 of complete information (i.e. traits and vectors) of species of neotropical fishes (Table S1).

Statistical analyses

Once the morphological trait data was provided by Su et al., (2019). All statistical procedures regard to data manipulation (e.g. missing data, standardize), and the principal component analyses, which summarized the morphological traits, were already performed, further details can be found in Su et al., (2019, 2020).

Using the five PC's axes (explained 78.6% of the total variance), we compute two functional diversity indices (Villéger et al., 2008): Functional Richness (FRic), and evenness (Feve), for total, native, exotic, translocates and translocated neighboring species, into each Drainage basins of the Neotropical realm. The convex hull was also calculated for each group of occurrence status, IUCN status, and pathways of introductions. We then illustrate the trait distributions of the four occurrence status groups for five main drainage basins of the Neotropical realm (Amazon, Essequibo, Orinoco, Parana, and Tocantins).

All statistical analyzes were performed in R software version 4.0.2., we used the 'dbFD' function of the FD R package to calculated the functional diversity indices (Laliberté et al., 2014; Laliberte & Legendre, 2010). The convex hull was calculated using the function 'convulln' of the geometry R package (Barber et al., 1996), and the trait distributions were performed using the transformed rain cloud plots (Allen et al., 2018).

Results

A total of 6.014 species from 304 drainage basins were compiled for the Neotropical region: 5.979 natives, 83 exotics, 76 translocated, and 71 translocated neighboring. Among these species 3.591 (59.7%) of the total had information of morphological traits, and for each classification status the proportions of species with trait information were 3.558 (59.5%) of native species, and 77 (92.7%), 66 (86.8%), 60 (84.5%) of exotics, translocated and translocated neighboring, respectively. Native species occupying the majority of the convex hull volume (95.98%), non-native species occupies 4.02% of the hull volume, divided into exotic (1.74%), translocated (0.67%) and translocated neighboring (1.59%) (Figure 2).



FIGURE 2 Five dimensional morphological space for the total, native, exotic, translocated and translocated neighboring species for the Neotropical region. The five principal components (hereafter PC), explain 78.6% of the global total variance of fish traits (Su et al., 2020). PC1 are represented by oral gape position, pectoral fin vertical position, and relative maxillary length, while PC2 represents body elongation and Eye position, PC3 showed higher contribution to body elongation and pectoral fin size, PC4 also showed contribution related to body elongation, relative eye size, and maximum body length, and PC5 presented a contribution to caudal peduncle throttling.

In general, the total species richness was concentrated in a few and larger drainage basins of the neotropical region (i.e. Amazon, Parana, Orinoco, Tocantins, and Essequibo), and the same pattern can be seen for native species. However exotic, translocated, and translocated neighboring species were highly concentrated at the Parana Basin (Figure 3). Amazon basin showed the greatest functional richness for native species (Fric: 54,45), Parana basin presented the higher functional richness for exotic, translocated and translocated neighboring species (Fric: 10,13; 11,32 and 16,65 respectively). To show if native, exotic, translocated, and translocated neighboring species may be functionally similar inside each drainage basins, we perform functional richness presented the highest functional evenness with values near to 1 (e.g. Yelcho, Sarandi, Piraque, Courland, and Copiapo). Basins with high species and functional richness also show high values of functional evenness for native species (e.g. Corantjin, Feve: 0,75), São Matheus (Feve: 0,79) for exotic species, Uruguay (Feve: 0,90) for translocated species, and finally for translocated neighboring species Amazon basin (Feve: 0,90).



FIGURE 3 Richness, functional richness (Fric), and functional evenness (Feve), for total, native, translocate, and translocated neighboring species of the Neotropical region.

For the five most richness basins we show the distribution of the five PC for the native, exotic, and translocated species (Figure 4). In the majority of the basins, native species were widely distributed along the PC axes. All the basins excepted the Tocantins had registered of exotic species. Amazon and Parana basins had the presence of all types of non-native species (i.e. exotic, translocated, and translocated neighboring). The trait distribution at the Parana basin shows highly overlap among the occurrence status of species, however at PC4, which is related mainly to body length the distribution of exotic species is slightly separated from the others. Interestingly, translocated and translocated neighboring species formed a peak in the trait distribution of PC1 (related to oral gape position), with very low variation. Still for the Amazon basin, the PC4 distribution (related to maximum length) shows a separate peak for translocated neighboring species.



FIGURE 4 Density trait distribution for the five most species richness basins of the Neotropical region, and the first five principal components (PC).

The pathways of introduction (i.e. Vectors) for exotic, translocated and translocated neighboring species, show that non-native species are more related to the aquarium trade, independently of the species status (Table 1).

TABLE 1 Number of species for each introduction pathways for exotic, translocated, and translocated neighboring species, once species may show more than one pathway, we adopted multiple counts. Only species that have trait information were considered, yet not all species had information on introduction pathways.

Status	Aquarium	Aquaculture	Game Fish	Bait
Exotic	40	36	29	5
Translocated	29	7	6	2
Translocated neighboring	16	6	4	0
Total	85	49	39	7

To show the functional space occupied by the species according to the pathways of introduction we perform the five dimension space for each vector. Species related to aquarium trade occupy the hull volume (78%), while aquaculture, game fish, and bait occupy 15%, 6%, and 0,02%, respectively.



FIGURE 5 Five dimensional morphological space for species related to the aquarium trade, aquaculture, game fish and bait in the Neotropical region. The five principal components, explain 78.6% of the global total variance of fish traits (Su et al., 2020). PC1 are represented by oral gape position, pectoral fin vertical position, and relative maxillary length, while PC2 represents body elongation and Eye position, PC3 showed higher contribution to body elongation and pectoral fin size, PC4 also showed contribution related to body elongation, relative eye size, and maximum body length, and PC5 presented a contribution to caudal peduncle throttling.

Discussion

To dismember the classification of non-native species in exotic, translocated, and translocated neighboring species, highlighted that species from adjacent basins, play an important role to understand dynamics of fish invasion. Interestingly, translocated and translocated neighboring species occupied the majority part of the convex hull, almost two times the space occupied by exotic species (Figure 2). Considering biogeographic scales appropriately to define the origin of non-native species, is critical for more accurate results and conclusions. For example, if we had considered exotic species using geopolitical boundaries rather than ecoregions scale, certainly exotic species would have presented a higher occupation of the convex hull volume. In all realms of the world translocated species (see Su et al., 2020), reinforcing the importance of fish invasions from adjacent basins (e.g. translocated and translocated neighboring species may be as dangerous as exotic species (Occhi et al., 2017; Vitule et al., 2019). Besides, translocated and neighboring species occupied a higher space in convex hull than the translocated species, which indicate that species from neighboring basins should be

even more important than the translocated species. The Neotropical realm had emblematic examples of species introduction from neighboring basins, such as the flood of the "sete quedas" fall, which introduced approximately 50 species from lower Parana to upper Paraná ecoregions (see Lima Junior et al., 2015; Skóra et al., 2015). Other examples are the introduction of large and voracious predator *Salminus brasiliensis* from Paraná river to Iguaçu ecoregion (Gubiani et al., 2010; Vitule et al., 2014), and also the invasion of *Arapaima gigas* in the Madeira river in Amazon (Doria et al., 2019; Miranda-Chumacero et al., 2012). These examples are masked in studies using geopolitical boundaries (Vitule et al., 2019), however, we understand that geopolitical scale may be useful for politicians and decision-makers since environmental legislation and management and conservation policies are limited to this scale. But the fact is that it is easier and more practical to apply and transform data in refined scales to geopolitical scales since the opposite cannot be done accurately.

The total species and functional richness (i.e. including all the classification status) show that Neotropical realms concentrate species richness and functional richness in major basins, such as Amazon, Parana, Orinoco and Tocantins, and same is seeing for native species. However, exotic, translocated and translocated neighboring species show contrasting patterns in these basins (Figure 3). Furthermore, theses basins, in general, have registered in majority exotic species, in comparison with translocated and translocated neighboring species. The high and emblematic fish diversity of the Neotropical region is also reflected in the morphological functional richness (Su et al., 2020; Toussaint et al., 2016; Vitule et al., 2017b). The high concentration of species in the major basins of Neotropical realms may be related to high habitat heterogeneity, once habitat complexity may be driven the ecological interaction (MacArthur & MacArthur, 1961). However, multiple hypotheses may explain fish distributions patterns in the Neotropical region, such as water-energy, productivity, and temporal heterogeneity (Vieira et al., 2018), and this is also observed for fish occurrence patterns globally (Guégan et al., 1998). The Neotropical region holds the majority of functional diversity of the world (Su et al., 2020; Toussaint et al., 2016), and not surprisingly functional richness of total and native species are higher in Amazon basin and adjacent regions (Figure 3), however, these basins showed a relatively high functional evenness. That is, even with a higher functional richness, possibly driven by species which diverge of the majority (i.e. expanding the functional space), most species show low trait diversification (see Toussaint et al., 2016). These implications based on morphological traits maybe help to understand general patterns of functional diversity in the Neotropical region. However, it is essential to look into these data with caution, once the relationship between species traits and

ecosystems function it is complex and high functional richness and evenness, may mask unique and vital functions performed by rare species (Violle et al., 2017; Vitule et al., 2017b)

While native fish species patterns may be evaluated by natural processes, occurrences of non-native species are driven by human-mediated actions (Blackburn et al., 2011a; Frehse et al., 2016; Gubiani et al., 2018; Leprieur et al., 2008), which are critically increasing with globalization (Dawson et al., 2017; Hulme, 2009). Especially in Neotropical region, quantify non-native species occurrences, may be highly biased by the concentration of research centers (i.e. regions with a high concentration of universities or specialists on invasion ecology), for example, the southeast and south Brazil shows the most number of publications regarding invasion ecology (Frehse et al., 2016), and a similar pattern is seeing for Neotropical fishes at ecoregions scale (Gubiani et al., 2018). This is critical, once macroecological approaches depend on data availability and quality. For instance, the Parana River is exhaustively studied by researchers of the Research Center in Limnology, Ichthyology, and Aquaculture In counterpoint, northeast of Brazil, a region with strong aquaculture productions, based mainly on exotic species i.e. constant propagule and colonization pressure (Lima Junior et al., 2018), have lower registers of non-native species comparison with south and southeast (Frehse et al., 2016; Vitule et al., 2019).

In general, functional index (i.e. Fric and Feve) showed complex patterns for nonnative species (Figure 3), with great variation among basins, which should not be interpreted in general terms, but according to the particularities of each basin. For example, the Parana basin showed the higher functional richness of non-native species independently of the classification status, while functional evenness varies according to the classification status, showing higher functional evenness for translocated neighboring species. These results observed for the Parana basins are possibly associated with the major introduction event caused by the flood of the "sete quedas" falls, which introduced approximately ~50 species from lower Parana basin i.e. Translocated neighboring species (Skóra et al., 2015). These species are likely to share similar morphological traits, both among themselves (i.e. successful colonizers) and with the native fauna of the upper Paraná, once they have similar evolutionary conditions along the time (Abell et al., 2008; Skóra et al., 2015; Vitule et al., 2012), which may deviate toward a more equitable fauna after the introduction. Another conspicuous example is the Amazon basin, which showed higher functional richness for exotic and translocated species, but lower for translocated neighboring species. This may be due to the low number of translocated neighboring species, which provided a low functional richness and high functional evenness. While for translocated species the opposite was observed,

probably because translocated species registered in Amazon had distant origins high trait dissimilarity, which may inflate Fric (even showing few species), but low functional evenness.

The distribution of the principal components shows a high overlap among the classification status of the species with few exceptions. For example, for PC4 the outlier distribution for translocated neighboring species in Amazon and translocated species in the Essequibo basin is related to the A. gigas occurrences in these basins. Although this species is native from the major Amazon basin (i.e. Amazon low lands ecoregion), occurs as non-native species in the Madeira Brazilian shield ecoregion (Doria et al., 2019; Miranda-Chumacero et al., 2012). Arapaima gigas is a clear example of the dangerous of translocated and translocated neighboring species, once is a large and voracious predator, which is already spreading in Bolivia and Peru (Doria et al., 2019; Miranda-Chumacero et al., 2012). The overlap among the classifications status of species is probably related to the wide distribution of traits of native species, once the Neotropical region holds the majority functional diversity worldwide (Su et al., 2020; Toussaint et al., 2016). Hardly non-native species do not overlap in trait distribution. However, some peaks can be observed in non-native species, which probably may be indicated the hypothesis of species attributes that may facilitate the establishment of non-native species (Duncan et al., 2003). Yet, we strongly believe that this type of hypothesis should be carefully analyses considering the context of each recipient local community. Also, these peaks observed for some basins may be related to the artificial selection of non-native species by human-mediated introduction i.e. pathways of invasion (García-Berthou et al., 2005; O'Malia et al., 2018; Smith et al., 2020).

Fishes are used for a myriad of human activities (Olden et al., 2020), and frequently these activities result in fishes introductions (Britton & Orsi, 2012; Magalhães & Jacobi, 2013; García-Berthou et al., 2005; Hulme, 2009; Magalhães et al., 2020; Vitule et al., 2009). For the Neotropical regions, aquarium trade was the main pathway of non-native fishes introductions, followed by aquaculture, game fish, and a few species used as bait for fishermen (Table 1). Exotic species had more information regarding the introduction pathways comparing with translocated and neighboring species. This is expected once exotic species are widely more explored as for your vectors than the translocated and translocated neighboring. Besides, translocated and translocated neighboring species are highly related to impoundment, which frequently eliminates biogeographical barriers allowed new introductions from adjacent basins (Bezerra et al., 2019; Gubiani et al., 2018; Miranda-Chumacero et al., 2012; Skóra et al., 2015; Vitule et al., 2012).

The five-dimensional space for each introductions pathways shows interesting patterns, as expected aquarium trade occupied most of the convex hull, followed by aquaculture, game fish, and bait (Figure 5). Aquarium trade offers a high risk of species introductions into Neotropics due to the high variety of species of different forms (i.e. morphological traits). Most than 330 non-native species are marketed in at least southern Brazil, and 151 of these species are from Neotropics i.e. Translocated species (Magalhães & Jacobi, 2013; Magalhães et al., 2020). Indeed, not all these species will reach natural ecosystems, however, this type of introduction pathway offers a dangerous propagule and colonization pressure, and high risk of impact to the Neotropical biota.

It is possible to see some species overlapping on the five-dimensional space of vectors, this is because some species are related to more than one vector, more interesting, game fish and aquaculture species show some points outside the functional space occupied by the aquarium trade, represented by extreme species such A. gigas and Acipenser transmontanus, which are related to the aquaculture, and game fish. Besides aquaculture and game fish species do not represent the majority of introduction pathways in the Neotropical region, these vectors may be as dangerous as aquarium trade. Aquaculture represents a strong sector in the economy, due to that it is frequently that political actions influence the activity (Britton & Orsi, 2012; Lima Junior et al., 2018; Pelicice et al., 2014). Also, non-native species used in aquaculture are usually highly invasive, fed on low trophic levels, and may pose irreversible impacts on ecosystems (Britton & Orsi, 2012). On the other side, game fishes usually occupying higher trophic levels, that is large and voracious predators, generating powerful and exciting fighting for anglers, which motivated them to introduced these fishes, but unfortunately offering high risks to native biota (Britton & Orsi, 2012; Espínola et al., 2010; Vitule et al., 2014). Neotropical is an outstanding region in terms of fish biodiversity, thus increasing the potential of the introduction of translocated and translocated neighboring species inside the Realm. Also, the Neotropical region had major potential to act as a donor of non-native species to other realms worldwide (Bezerra et al., 2019; Vitule et al., 2019). Importantly, is key to consider non-native fishes in approaches related to biodiversity patterns and conservation status (Vitule et al., 2017a). More importantly, the focus on functional diversity approaches is needed on a local scale, to fill the lack and quality of functional attributes data in large databases, in this way macroecology studies can be more accurate and forceful.

Conclusion

In conclusion, the classification status of non-native fish species showed that translocated and translocated neighboring species should be considered in macroecological approaches focused on invasion ecology. Once they were highly representative in comparison with exotic species, regarding five-dimensional space, and maybe more likely to be introduced because of the short distance to a non-native range (i.e. the adjacent basin). Still, species that were exposed to similar evolutionary conditions with the recipient community may be established easily.

Also, the disproportionated functional diversity patterns should be analyzed based on the context of each basin, and it is needed more research efforts in small basins, mainly considering accurate occurrences records, thus enabling to properly classify the status and origin of species, as well as, functional traits measures. Due to that, we should look carefully to the basins with lower occurrences of non-native species, once these species may be already spread and simply are not sampled, or registered in public databases.

Besides, it is crucial to better understand introductions pathways of non-native fishes, mainly from a functional point of view, to guide public policies which may prevent new nonnative species introduction.

Finally, incorporated functional diversity patterns to invasion ecology is paramount to better understand non-native species occurrences, and it is needed to try to add more and precise attributes in local scale to expanding to macroscale analyzes.

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CHAPTER 2

EFFECTS OF THE INVASIVE MACROPHYTE Urochloa arrecta IN THE FISH COMMUNITY OF A NEOTROPICAL RIVER

Effects of the invasive macrophyte *Urochloa arrecta* in the fish community of a Neotropical river

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Abstract

1. Biological invasions had been frequently pointed out as one of the main threats to biodiversity, causing impacts such as biotic homogenization, species extinction, and alteration of the functionalities of habitats and ecosystems. Studies addressing functional attributes have been of great utility to refine knowledge of communities' dynamics, facilitating the identification of links between ecosystems and communities. The invasion ecology summed up to the functional diversity approach has been frequently tackled to clarify the mechanisms of invasion and interactions non-native species into new ecosystems. In this sense, we test the effects of the invasive macrophyte *U. arrecta* in the functional traits of fishes in a Neotropical river in the Atlantic forest.

2. We collected fish community semiannually 2016 to 2018 cover all extension of the river, with an effort of 10 gillnets of 20 meters (2, 4, 6 and 8 mm) and 10 traps (22x22x50 and 3 mm mesh). The traps and gillnets of the same mesh size were settled in the *U. arrecta* and paired with native macrophytes banks and structured habitats. We analyzed 10 functional traits of the fishes, plot the Community Weighted mean traits (CWM traits) density distributions, as well as, five-dimensional spaces of the traits, and calculated functional indices.

3. We founded that CWM trait density distributions do not vary along the river gradient, but show conspicuous patterns in different habitats types. Fishes associated with Native macrophytes occupied the most of the convex hull volume in five-dimensional space. While the functional richness of fishes associated with the invasive macrophyte *U. arrecta* presents the minor functional richness indices.

4. We concluded that besides no statistical differences, *U. arrecta* may affect fish functional trait distributions, species richness, and fish occurrences. Also, monitoring programs and management of the invasive macrophytes are needed to conserve and avoid future negative impacts on fish biodiversity.

Introduction

It is not new that biological invasions might cause massive negative effects in natural ecosystems (Elton, 1958; Mack et al., 2005; Novoa et al., 2020; Palmer, 1896; Vitule et al., 2009). Freshwater ecosystems are particularly vulnerable to invasions (Moorhouse &

Macdonald, 2015), which may be worst due to synergic impacts promote by human alteration of habitats.

Invasive macrophytes may cause dangerous impacts in freshwater communities, reducing biodiversity, and altering habitat complexity (Amorim et al., 2015; Thomaz & Cunha, 2010). The invasive Poaceae *Urochloa arrecta* (Hack. ex T.Durand & Schinz) Morrone & Zuloaga is a widespread invasive aquatic species native from Africa (Amorim et al., 2015), which generate several impacts in the aquatic environment (See Thomaz et al., 2009). This highly invasive macrophyte shows fast growth, and it is rooted on the banks of the rivers, but its stems reach limnetic regions (Michelan et al., 2018; Michelan et al., 2010), which could cover entire small channels surfaces.

Modifications in the habitat structure such as the dominance of an invasive macrophyte can modify the fish assemblage (Carniatto et al., 2013; Ferreira & Casatti, 2006). Fish pose as an important group, once they are used as a food source and for a myriad of other human-related activities (Olden et al., 2020). Grass dominates sites, may decrease habitat heterogeneity and complexity (Casatti et al., 2009), which may influence the movement of small fishes i.e. prey of large piscivorous fishes (Gilliam & Fraser, 2001), and consequently change the performance of predators (Finstad et al., 2007). The invasive macrophyte *Urochloa arrecta* is characterized by an ecosystem engineers species that can modify the landscape (i.e. dominate the water blade of entire small rivers), habitat structure by direct compete with native plants, fish communities, and may also alter ecosystem functioning (Carniatto et al., 2013; Michelan et al., 2010).

Besides changes in the species composition is an important metric to measure communities' responses to habitat alteration, functional traits approaches may reveal patterns beyond species richness alone (Villéger et al., 2008), mainly in cases of events of biological invasions (See Toussaint et al., 2018).

Aquatic ecosystems had been broadly studied regarding functional traits, evaluating species performance in communities or spatial gradients (Adam et al., 2015; Su et al., 2020; Aurelé Toussaint et al., 2016; Villéger et al., 2014). Most studies regarding functional traits and invasions focus on the same group of species (e.g. Skóra et al., 2015; Su et al., 2020; Toussaint et al., 2018). However, once invasions by other groups may affect fish fauna, for example, the invasive macrophyte *U. arrecta* (see examples above), it is key to understand if fish functional traits are affected by the invasion of plants such as of *U.arrecta*.

The Guaraguaçu river (Figure 1) provides a good scenario to test the effects of ecosystem engineers such as *U. arrecta* on the fish fauna, once the river had the presence of

huge banks of this invasive macrophyte, and also locals without the presence of *U. arrecta*, with the predominance of native macrophyte and natural structure provides by the roots of the trees in the shores. In this sense, we intend to test the effects of the ecosystem engineer *U. arrecta* on fish functional traits, in comparison with native habitats, such as native macrophytes and structured habitats of the Guaraguaçú river.

Material and Methods

Study area

Located in the Atlantic rain forest, one of the global hotspots for conservation priorities (Myers et al., 2000), the Guaraguaçu (25°42'S and 48°31'W) is the largest river in Parana coastal basin, southern Brazil. The region has a humid subtropical climate, and present cfa type according to köppen' climates classification (Alvares et al., 2013). The river rises in the "Serra da Prata" mountains and disembogues in the estuarine complex of Paranagua bay. The sixty kilometers of extension provides an area of drainage of approximately 400 km², which generates a range of different types of habitats. From shallow lagoons dominated by *Tabebuia cassinoides* (Lam.) DC. trees in upstream regions, a region highly influenced by mountain streams in "Serra da Prata" at 720 meters of altitude, flowing into shallow lagoons of the Guaraguaçu river that are practically at sea level. The regions downstream are influenced by the tide and characterized as a channel river, the occurrence of the invasive macrophyte U. arrecta is notable, closing entire channels of small affluent and forming huge banks in the river margins, this dominance by U. arrecta is only stopped by the ecotone formed in mangrove areas at the mouth of the river.

Sampling

The samples were performed among the 2016 and 2018, totalizing four field campaigns. The sample design was draft to cover all the courses of the Guaraguaçu river, in this sense, the river was subdivided into four sectors according to the longitudinal gradient (Figure 1). The field campaigns were performed semiannually (i.e. March and October) with an effort of 10 gillnets of 20 meters (2, 4, 6 and 8 mm) and 10 traps (22x22x50 and 3 mm mesh) in each sector. Within sectors, the traps and gillnets of the same size were settle paired in the *U. arrecta* banks and the closer native microhabitat (i.e. native macrophytes banks or structures provide by the Roots of the traps and gillnets were paired in native macrophytes banks and the closer structured microhabitat. The fishes were fixed in formalin 10%, posteriorly

passed to alcohol 70%, and then identified with the assistance of the team of the Natural history Museum of Capão da Imbuia, Curitiba-PR.



FIGURE 1 Panorama of the location of the Guaraguaçu river in Brazil. The state Parana state is highlighted in black, and the upstream to the downstream extension of the Guaraguaçu river, black circles indicate the four sectors sampled, black lines indicate roads and streets of the cities adjacent to the river.

Functional traits

Thirteen fish measures were compiled using ImageJ software (version 1.52a) and then used to calculate 9 morphological traits related to food acquirement, locomotion and habitat position (Su et al., 2020; Aurelé Toussaint et al., 2016; Villéger et al., 2017), and also a categorical trait (i.e. habitat position) was extracted from FishBase (www.fishbase.org), totalizing a trait dataset with 10 functional traits (Table s2). Only adult individuals were considered, and individuals with damaged body parts, which prevented the appropriated measures, were excluded from the analyses. A few individuals that had trait missing values were submitted to the 'missForest' algorithm to fill the data (miss forest R package) with 999 repetitions.

Statiscal analyzes

All traits were standardized using community weight means - CWM (Naniar R package), and to illustrate the traits distributions, we plot density distributions of the traits (CowPlot R package), according to the sectors and microhabitats (i.e. *U. arrecta*, native macrophytes, and structures). To show the functional space we submitted the trait data to a distance matrix using Gower distance (FD R package) and posterior to done a Principal Coordinates Analyses – PCoA (Vegan R package), and plot the first five axes, and calculated the convex hull (Geometry R package) for microhabitat of the Guaraguaçu river. We also calculated the functional richness (Fric), functional evenness (Feve), and functional dispersion (Fdis) for each microhabitat of the Guaraguaçu river (FD R package). We also performed a betadisper and permutest to compare the CWM traits among the microhabitats of the Guaraguaçu river (Vegan R package).

Results

A total of 21 species from 5 orders and 14 families had the traits information compiled for each sector and microhabitat of the Guaraguaçu river. The three most abundant families were Characidae (n:563) represented mainly by *Deuterodon langei* (n:444), followed by the family Erythrinidae (n:133), represented only by the species *Hoplias malabaricus*, and the family Crenuchidae (n:129) represented by the species *Characidium lanei*. The number of species richness and abundance for each sector are shown in Table 1. Sector 1 which is dominated by native macrophytes banks, had the predominance of *Deuterodon langei* (n:346), while sector 2, where the first banks of *U. arrecta* show up, had also the predominance of *D. langei* (69), followed by *Geophagus brasiliensis* (n:50). In sector 3 *G. brasiliensis* was the most abundant species (n:35) followed by *D. langei* (n:29), in this sector *U. arrecta* occurs with high predominance and huge banks. The margins of sector 4 are mainly dominated by mangroves, which configures a predominance of structured habitats, in this sector the most abundant species where *Genidens genidens* (n:77) and *Bardiella ronchus* (n:18).

TABLE 1 Species richness and abundance for each sector and habitat of the Guaraguaçu river.

	Sector	U. arrecta	Native macrophyte	Structure	Total
	1	-	12	3	12
Species richness	2	6	8	5	9
	3	6	4	3	7
	4	-	2	10	11

	1	-	691	12	703
Species	2	37	132	25	194
abundance	3	53	42	16	111
	4	-	11	113	124

The CWM traits distribution for each sector and microhabitat are shown in figure 2, in general sectors and habitats show a high overlap of the CWM traits, with a few exceptions. In Sector 1 fishes associated with streams habitats e.g. *Phallocerus pellus* appears as outliers in the distribution, while in sector 3 and 4 the outlier distribution are represented by the species *Eugerres brasilianus*, which is characteristic to use this habitat seasonally.





The first five PCoA axis explained 99% of the total variance for all sectors and microhabitats of the Guaraguaçu river (Figure 3). The first axis was correlated to the total length of fish species (0,77), while the second axis was more correlated to lateral shape and habitat position, which are also most correlated in the axis 3 followed by eye position. Axis 4 and 5 were more correlated to maxillary length and habitat position, respectively. In the five-dimensional space, native macrophytes occupied the majority of the hull volume (81%) followed by African grass (18%), and habitat structured occupied only 1% of the convex hull volume.



FIGURE 3 Five dimensional morphological space for fish species of the Guaraguaçu river. We gather all the sectors and considered only the habitat variation. Green lines refer to native macrophytes, red lines to *U. arrecta*, and blue to structured habitats.

The native macrophytes presented the highest functional richness and evenness among the microhabitats (Table 2), while African grass shows the highest functional dispersion.

TABLE 2 Functional richness (Fric), functional evenness (Feve) and functional dispersion (Fdis), for each sector of the Guaraguaçu river.

Fric	Feve	Fdis
0,000114758	0.6866783	5,52513
0,002045496	0,759141	2,605371
0,000753707	0,74513	2,57243
	Fric 0,000114758 0,002045496 0,000753707	FricFeve0,0001147580.68667830,0020454960,7591410,0007537070,74513

The betadisper and permutest show no significant differences in the CWM traits among the habitats of the Guaraguaçu river.

Discussion

Guaraguaçu River is a rare and complex ecosystem, and also an important system to understand the dynamics of heterogeneous environmental systems struggling with the invasive and ecosystem engineer macrophyte. In general, all sectors of the river showed overlap density distribution of CWM traits, suggesting niche overlap of fish species of the Guaraguaçu river, independently of the habitat. Which may be explained by environmental filtering, already observed to estuarine communities (Mouchet et al., 2013; Mouillot et al., 2007). However, it is impressive that this pattern was observed practically along the entire river, despite invasions that can be limit functional diversity in aquatic environments (Milardi et al., 2019). This also can be related to physicochemical and hydrological parameters, which may influence species occurrence, and consequently functional diversity, and could help to explain the CWM trait distributions in the Guaraguaçu river (see Pool et al., 2010).

Besides the native macrophytes occupied the majority part of the convex hull volume in the Guaraguaçu river. The five-dimensional space according to habitat type showed that besides some overlap, fishes that use *U. arrecta* and structured habitat, tend to be bigger, with large mouths and eyes in the upper portion of the head. Which clearly described the predators of the Guaraguaçu river, such as *Centropomus paralelus*, *Hoplias malabaricus*, and also the omnivorous and estuarine species *Eugerres brasilianus*. While native macrophytes, hold small body fishes, with big eyes and greater relative maxillary length. Functional diversity may vary according to time, space, and habitat complexity (Lechêne et al., 2018). Macrophytes with high underwater density and biomass (e.g. *U. arrecta*) hinder fish movement, and consequently the availability of refuge, turning small-bodied fish susceptible to predators (Agostinho et al., 2007; Carniatto et al., 2013; Dibble et al., 1996; Harrel & Dibble, 2001). Also in banks of *U. arrecta* in Guaraguaçu river, there is a huge predominance of shrimps of the Palemonidae family (personal observation T.V.T.O; J.R.S.V), turning the habitat attractive for predators, which use shrimps as prey (see (Vitule et al., 2013), selecting specific species and traits through resource opportunism (Stefani et al., 2020).

Functional diversity indices corroborated the results founded in CWM trait distribution and the five-dimensional functional space. Indicating that native macrophytes, hold the majority of fish functional diversity, while structured and *U. arrecta* habitats concentrated similar traits. For instance, in stretches of the river dominated by *U. arrecta*, species richness showed a slight decrease, and wider CWM density distributions were observed in this habitat. This may be a small but a real effect of *U. arrecta* on fish diversity, and it is a crucial take into account that negative impacts of *U. arrecta* may vary according to density and biomass (Carniatto et al., 2013), which drastically change along the gradient of Guaraguaçu river since there are sectors dominated by *U. arrecta* (e.g. sectors 2 and 3), and sectors where *U. arrecta* does not occur (e.g. sector 1 and 4).

We found the lower values of Functional richness and evenness but high functional dispersal in *U. arrecta* banks, which corroborate with the idea that predators and omnivorous

species, used this habitat for resource opportunism (Stefani et al., 2020). Functional diversity metrics (e.g. Fric, Feve, Fdis) in structured habitats indicated low functional richness and dispersion, and relatively high functional evenness. While native macrophytes showed the high functional richness and evenness, but low functional dispersion (Table 3). Statistical tests indicated no differences in CWM traits among the habitats of the Guaraguaçu river. This may be related to the wide distribution of the same species along the gradient of the Guaraguaçu river, resulting in similar traits along with the river and habitats. For example, only five species used exclusively structured habitats (e.g. *Bardiella ronchus, Cathorops spixii, Cysnoscium guatupuca, Oligoplites saurus*, and *Stellifer brasiliensis*) and all these species were exclusive from sector 4. In the same way, only four species used exclusively native macrophytes habitats (e.g. *Hyphessobricom griemi, Mimagoniates microlepsis,* and *Phallocerus pellus*), all exclusive from sector 1. So it is comprehensive that there are no differences among habitats in the Guaraguaçu river (see Villéger et al., 2010).

Particularities are observed in each sector of the river, for instance, sector 1, is a monotonic system dominated by *Tabebuia cassinoides* (commonly know as caixeta) and shallow lagoons highly influenced by mountain streams from "*Serra da Prata*" (see Vitule et al., 2008). This sector shows a predominance of small-body fishes in terms of the number of individuals and species, and wide density distribution of CWM traits in native macrophyte habitat. This environment is notable by the great shelter availability provided by the predominance of the native macrophytes, which is key for survivors of small fishes (Winemiller & Jepsen, 1998), explain the predominance of small fishes. Moreover, it is an area of difficult access, with lower tide influence, which may prevent *U. arrecta* propagules from downstream regions.

Down the river, the first occurrences of the invasive macrophyte *U. arrecta* are observed (i.e. sector 2 and 3), consequently making the system more homogeneous in areas dominated by *U. arrecta*. For the Guaraguaçu river, it is clear that disturbances caused by the invasion of *U. arrecta* affected fish functional diversity CWM trait density distributions in sectors 2 and 3. It is important to highlight again, that sector 3 is influenced by the brackish water from the estuarine regions downstream (Pupo & Disaró, 2006). Physicochemical parameters (e.g. salinity) may act as an environmental filter, and thus limiting fish occurrence and by consequence drive functional diversity patterns (Mouillot et al., 2007). Suggesting that salinity influence may be limiting fish occurrences in sector 3, selecting specific traits, explaining the restricted CWM trait distribution in native macrophytes, and structured habitats.

The amplitude of CWM trait density distribution and species richness of fishes associated with native macrophytes and structured habitats reduces in this sector, while in U. arrecta banks, trait density distribution tends to be more homogenous (i.e. greater occurrence of similar traits). In sector 3 CWM density trait distributions of fishes associated with native macrophytes decrease even more. However, fishes in U. arrecta banks showed a wider distribution of the CWM trait in comparison with native macrophytes and structured habitats. As native macrophytes and U. arrecta are scarce in sector 4, given so no comparisons between habitats can be made. However, comparing sectors 4 and 3 we can observe similar CWM traits density distribution in structured habitat between these sectors. Sector 4 is dominated by mangroves, with a predominance of brackish water, in this way, featuring not only an extremely different region of the river but also an important ecotone (Contente et al., 2011, 2012; Contente et al., 2009, 2011). It was expected different species occurrences in sector 4 e.g. typical estuary species (Mourão et al., 2014), but not similar CWM trait distributions. For instance, this sector shares only four species with other sectors of the river. So, it is curious that even with different species between these sectors the CWM trait distributions were similar. However, Villéger et al., (2010) founded that changes in functional diversity patterns may be weaker related to species turnover, and more affected by the abundance of dominant species, i.e. dominant species with similar traits.

The conspicuous changes along with the Guaraguaçu river do not were reflected in the fish diversity patterns, but certainly, the invasion of the *U. arrecta* should look with caution. Once, *U. arrecta* is a dangerous invasive macrophyte, capable to change the habitat and the landscape, for instance, closing whole small channels. Fundamentally, long-term monitoring programs, associated with proper management must be carried out on the Guaraguaçu river, to avoid more impacts caused by *U. arrecta*.

Conclusion

Guaraguaçu river besides its extension proved to be a very complex and heterogenous river, but with similar patterns of species richness and functional diversity, provided by the poor species richness, and wide distribution of these species, provides similar functional traits distribution, along with the extension of the river. In general, there were no statistical differences in functional traits among sectors and habitats of the Guaraguaçu river, but the occurrence of the invasive macrophyte *U. arrecta* in the Guaraguaçu river, tend to change the fish trait distribution among the habitats.

Also, functional space shows that native macrophytes are key for fish functional diversity and species richness, while structured habitats and *U. arrecta* banks selecting

specific traits in majority related to predators and omnivorous fishes seeking for the abundant shrimps of the Palemonidae family. Besides, areas dominated by *U. arrecta* limits the occurrences of small body fishes, through the exclusion of native macrophytes which provided shelter to several species these species.

The relation among habitats and fish functional diversity in the Guaraguaçu river is not trivial, but we may confidently affirm, that the *U. arrecta* may undermine the fish community of Guaraguaçu river, if not properly managed and extinguished.

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