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Patterns of functional diversity of native and non-native fish species in a neotropical floodplain

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Abstract

1. Human activities affecting freshwater ecosystems, such as regulation of rivers by dams and introduction of non-native species, are recognised as major threats to freshwater biodiversity, with fish communities strongly impacted.
2. We evaluated patterns of functional diversity of native and non-native species in local fish assemblages in the upper Paraná River floodplain over a 33-year period (1986–2019) in three rivers with different degrees of alteration by dams (highly altered, moderately altered, and little altered). We also examined the effect of non-native species on functional diversity of native species and investigated the responses of functional traits of native and non-native fishes in regions with different histories of flow alteration.
3. We measured 13 functional traits associated with five niche dimensions: feeding, habitat use, metabolism, life history, and defence. Functional diversity was evaluated from functional richness, functional redundancy, and Rao's quadratic entropy. The effect of non-native species on functional diversity indices of native species was evaluated using a simple linear regression between each index and the level of dominance by non-native species. To evaluate changes in functional traits of native and non-native species over time and among rivers, we performed an RLQ analysis.
4. Functional richness and Rao's quadratic entropy of native species decreased over time, while functional redundance increased especially in the most altered river. The level of dominance by non-native species was negatively associated with functional richness and Rao's quadratic entropy of native species. Native species that are migratory with high fecundity, single spawning events and large body size were most common during the first 2 decades and within the least altered river. Non-native species with parental care, multiple spawning, relatively large eggs, and brood defence tended to have greater prevalence during the last 2 decades and within the moderately altered region.
5. Comparison of temporal trends in the functional diversity and characteristics of native and non-native fishes within regions of the upper Paraná River floodplain having different levels of environmental alteration suggests that non-native species and alteration by dams interact to adversely impact the functional diversity

of native fishes, with especially strong effects on migratory fishes with a periodic life history strategy.

KEYWORDS
dams, freshwater fishes, nonindigenous fishes, Paraná River, Rao's quadratic entropy

1 | INTRODUCTION

Biological diversity influences ecological processes, including nutrient cycling, primary and secondary production, trophic interactions, and community assembly (Gamfeldt et al., 2008; Hillebrand & Matthiessen, 2009; Lanari & Coutinho, 2010; Moi, Romero, et al., 2021). Because ecological processes provide ecosystem services that benefit human society (Gamfeldt et al., 2008; Polania et al., 2011), the loss of biological diversity is a serious concern (Cao et al., 2018; Colin et al., 2018). Freshwater ecosystems are biologically diverse (Balian et al., 2008) and provide essential ecological services, such as drinking water and food (Lévêque et al., 2008), and yet they are considered to be one of the most degraded ecosystems on Earth (Dudgeon et al., 2006; Michelan et al., 2010). Human activities, such as regulation of river hydrology by dams and introduction of non-native species, are recognised as major threats to freshwater biodiversity (Gois et al., 2015; Johnson et al., 2008; Rahel, 2007; Shuai et al., 2018), with fishes often being strongly affected (Moi, Alves, et al., 2021; Olden et al., 2006; Villéger et al., 2017).

In addition to altering the fluvial connectivity and limnological characteristics of rivers (Pereira et al., 2021; Pompeu et al., 2012), dams affect the composition of fish communities, including facilitation of invasion and establishment of non-native species (Oliveira et al., 2018; Pelicice et al., 2014). Once established in a new environment, non-native species can affect native fauna through predation (Bampfylde & Lewis, 2007; Yonekura et al., 2007), competition (Blanchet et al., 2007), habitat alteration (McDowall, 2006), disease transmission (Gozlan et al., 2006), or hybridisation (D'Amato et al., 2007). These affects can not only reduce the abundance and distribution of native species, but also alter their functional roles in local community (Carey & Wahl, 2010; Shuai et al., 2018), with repercussions for ecological processes (Moi, Alves, et al., 2021; Mori et al., 2013; Mouillot et al., 2013; Polania et al., 2011). Biological diversity has been estimated using various metrics that may involve taxonomic, phylogenetic, and functional dimensions (Kuczynski et al., 2018; Zhao et al., 2019). Whereas taxonomic diversity normally evaluates the number of species in an assemblage, phylogenetic diversity measures their evolutionary breadth, and functional diversity estimates behavioural, physiological, morphological, and ecological characteristics, especially those that can influence community processes (Cianciaruso et al., 2009; Kuczynski et al., 2018). Community functional diversity can be divided into components (e.g., functional richness, functional redundancy, and Rao's quadratic entropy) (Córdova-Tapia & Zambrano, 2015; Mason et al., 2005; Villéger et al., 2008). Functional richness represents the diversity of species trait combinations within a community, and is estimated as the trait space occupied by species (Mouillot et al., 2013; Villéger et al., 2008). Functional redundancy measures the degree that species share similar trait combinations (Ricotta et al., 2016). Rao's quadratic entropy reflects the relationship between the relative abundances and paired distances of species based on functional trait similarity (Mouillot et al., 2013).

A functional approach provides more information about community responses to disturbances (Mouillot et al., 2013; Suding et al., 2005), such damming of rivers (Lin et al., 2021; Oliveira et al., 2018; Pereira et al., 2021; Zhang et al., 2020), and invasion by non-native species (Shuai et al., 2018). For example, Oliveira et al. (2018) found a reduction in functional richness and Rao's quadratic entropy in the fish community of the upper Paraná River (Brazil) after the construction of the Porto Primavera dam. Similarly, Zhang et al., 2020 found decreasing trends in functional richness and Rao's quadratic entropy in the Yangtze River fish community after the construction of the Three Gorges Dam (China). Another study by Lin et al. (2021) also found a significant reduction in the functional richness of fish species from the Min River (China) after 36 years of environmental changes and species invasion. Conversely, a study by Pereira et al. (2021) found that although taxonomic composition and beta temporal diversity of fish assemblages in the Tocantins River (Brazil) changed after the construction of the Cana Brava dam, there was no significant change in functional richness. Furthermore, Zhao et al. (2019) found that functional richness of fish increased significantly with the level of dominance by non-native species in eighteen artificial lakes located in the river Garonne floodplain (France). In general, although the number of studies using measures of functional diversity has grown in recent years (Colin et al., 2018; Hillebrand & Matthiessen, 2009; Zhao et al., 2019), this approach still needs to be explored, especially over longer time intervals.

The Paraná River basin is one of the largest in South America, and its upper stretch contains more than 130 hydroelectric dams that make it one of the most regulated rivers on the continent (Agostinho et al., 2008). The upper Paraná River floodplain currently has nearly 60 introduced fish species that represent more than 30% of the regional ichthyofauna (Ota et al., 2018). Many nonindigenous fishes gained entry to the upper basin with the submersion of Salto de Sete Quedas, a natural barrier (cataracts) to upstream fish dispersal, when the Itaipu reservoir was created in 1982 (Júlio et al., 2009). In addition, construction of a fish passage around the Itaipu Dam allows fishes to ascend to the upper basin (Agostinho et al., 1994; Vitule et al., 2012). Fish invasions also occurred via escapes from fish farms (Casimiro et al., 2018; Ortega et al., 2015) and releases by sport fishermen (live baits, stocks) and aquarists (Langeani et al., 2007; Ortega et al., 2015). Dispersal of introduced fish species has been facilitated by the large number of reservoirs constructed throughout this basin (Gois et al., 2015; Johnson et al., 2008).

This study compares functional diversity patterns of native and non-native fishes within floodplain habitats of three rivers of the upper Paraná Basin that experienced different degrees of alteration by dams (including limnological conditions and flow regulation) over a period of 33 years (1986–2019). Specifically, we: (1) assessed temporal and spatial variation in species abundance and assemblage functional diversity indices (functional richness, functional redundancy, and Rao's quadratic entropy) of native and non-native fishes; (2) evaluated the relationship of non-native species with functional diversity indices of native species; and (3) investigated functional traits of native and non-native fishes to rivers in relation to alteration history. We predicted that: (1) functional richness and Rao's quadratic entropy (relationship between the relative abundances and paired distances of species based on functional trait similarity) of native fishes decreased over time, especially in the river with greatest alteration; (2) dominance by non-native species is associated with a decline in functional richness and an increase in the functional redundancy of native species; and (3) functional traits of native species respond differently to those of non-native species over time and in rivers with different degrees of alteration by dams. The present study expands the scope of earlier research carried out by Oliveira et al. (2018) that was based on a portion of the same survey dataset, but here we used a longer-term and more extensive dataset to compare functional traits and diversity of native and non-native species.

2 | METHODS

2.1 | Study area

This study was carried out in the upper Paraná River floodplain (22°40′–22°50′S and 53°15′–53°40′W), which is currently the only major stretch of the mainstem river without dams. The upper Paraná River floodplain has high fish species diversity and contains an environmental protection area and two parks (Ilha Grande National Park and the Ivinhema River State Park; Agostinho et al., 2000). The Paraná, Baía, and Ivinhema rivers join together in this floodplain which contains an anastomosed system of secondary channels with lotic (rivers), semi-lotic (channels), and lentic (connected and disconnected lagoons) habitats (Figure 1).

The upper Paraná River floodplain has been influenced by several hydroelectric dams upstream of the Paraná River (Oliveira et al., 2018). For instance, the Porto Primavera Dam is the first of dozens of dams built upstream of the upper Paraná basin (Agostinho et al., 2008) and caused significant limnological and flow alteration in the floodplain (Oliveira et al., 2018). Before the completion of the Porto Primavera Dam in 1998, the floodplain measured 480 km. Subsequently, the floodplain was reduced to a 230-km stretch between the Porto Primavera Dam and Itaipu Reservoir (built in 1982). The Paraná River is the most regulated by dams and besides flow regulation, sediment, and nutrient retention have resulted in lower concentrations of phosphorus and high values of water transparency and pH in downstream reaches (Figure S1). The Baía River runs parallel to the Paraná River and flows in its upper reaches are also influenced by dams (Granzotti et al., 2018). Compared with the Paraná River, the Baía River has high values of phosphorus concentration and dissolved oxygen and relatively low values of conductivity, transparency, and pH (Figure S1). The lower Ivinhema River lies within the Ivinhema State Park, and there are no dams on its course (Granzotti et al., 2018). However, the Ivinhema River had intermediate limnological characteristics when compared to the Baía and Paraná rivers (Figure S1). Thus, based on the degree of alteration by dams (including limnological conditions and flow regulation), these rivers can be classified as highly altered (HA: Paraná), moderately altered (MA: Baía), and little altered (LA: Ivinhema).

2.2 | Data collection

During the course of multiple long-term projects, fish surveys were conducted at 23 locations in the upper Paraná River floodplain, including lotic (rivers), semi-lotic (channels), and lentic (connected and disconnected lagoons) habitats belonging to the Paraná, Baía, and Ivinhema rivers (Figure 1). Sampling effort varied throughout the study period. From 1986 to 1988 and from 1992 to 1995, monthly surveys were performed, and surveys were done quarterly from 2000 to 2019. Fishes were collected with gill nets (10 and 20 m in length) of different mesh sizes (24, 30, 40, 50, 60, 70, 80, 100, 120, 140, and 160 mm between opposite knots) deployed for 24 hr during each survey at each location.

Upon capture, fish were anaesthetised using 5% benzocaine and then euthanised by benzocaine overdose following guidelines of the Ethics Committee on the Use of Animals (Comissão de Ética no Uso de Animais – CEUA; N° 1420221018; ID 001974) and transported to the Base Avançada do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia) of the Universidade Estadual de Maringá (UEM). In the laboratory, fishes were identified, weighed, measured (total and standard length) and dissected to remove the gut. Data were recorded as: location and date of capture (in field), species name, total and standard length, and total weight (in the laboratory). Native and non-native species from the upper Paraná River floodplain were determined based on relevant literature (Júlio et al., 2009; Langeani et al., 2007; Ortega et al., 2015; Ota et al., 2018).

2.3 | Functional traits

We estimated 13 functional traits for native and non-native fishes from floodplain of the upper Paraná River Basin (Table 1). These traits were selected considering five dimensions of the ecological

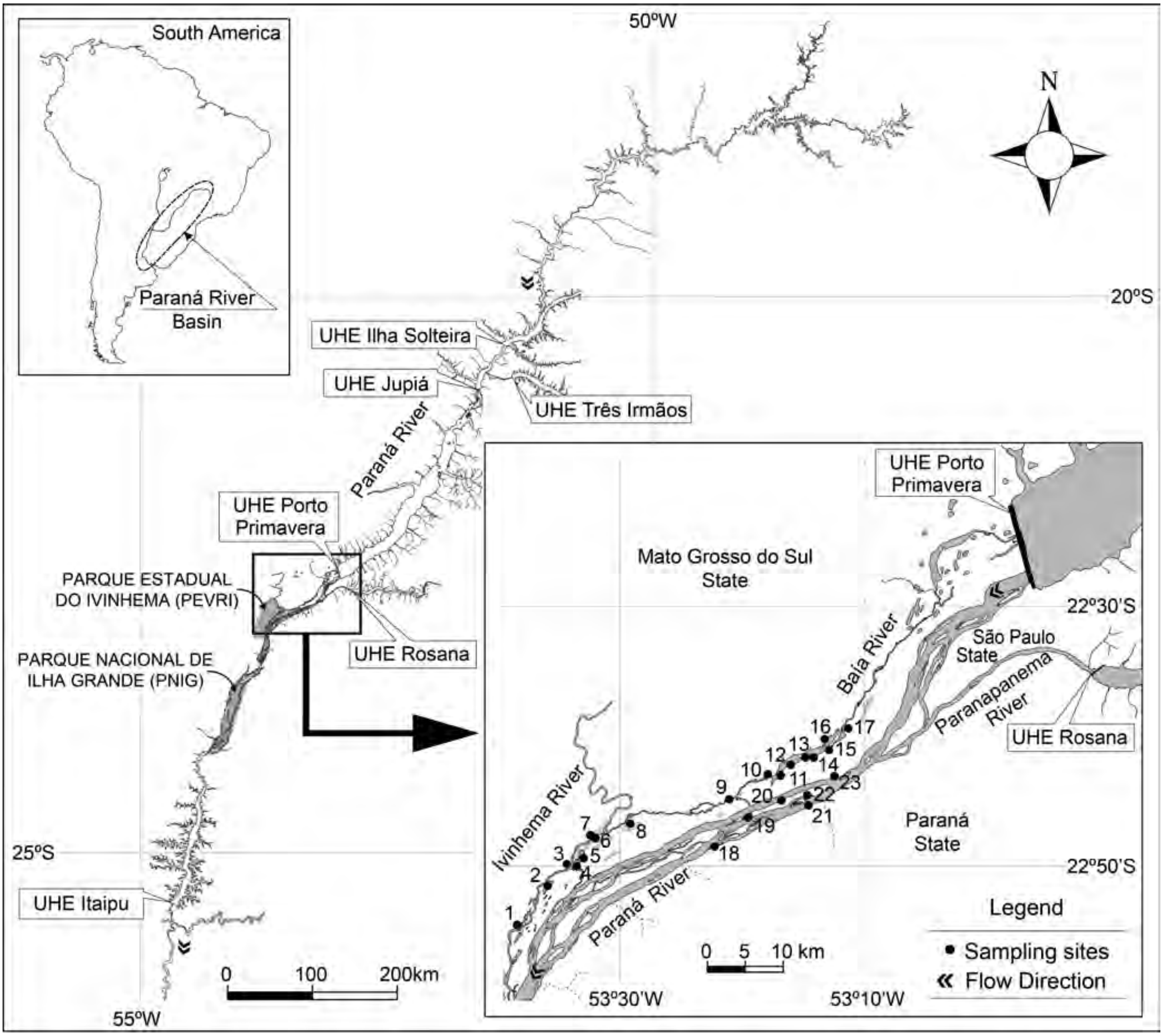

FIGURE 1 Map of the study region located in the upper Paraná River floodplain (Paraná, Baía and Ivinhema rivers) showing sampling locations, dams closest to the floodplain, and environmental protection areas. 1 = Peroba Lagoon; 2 = Ventura Lagoon; 3 = Zé do Paco Lagoon; 4 = Ipoitã Channel; 5 = Patos Lagoon; 6 = Ivinhema River; 7 = Finado Raimundo Lagoon; 8 = Sumida Lagoon; 9 = Curutuba Channel; 10 = Guaraná Lagoon; 11 = Baía River; 12 = Fechada Lagoon; 13 = Pousada das Garças Lagoon; 14 = Porcos Lagoon; 15 = Baía Channel; 16 = Gavião Lagoon; 17 = Onça Lagoon; 18 = Cortado Channel; 19 = Osmar Lagoon; 20 = Bilé Lagoon; 21 = Paraná; 22 = Pau Véio Lagoon; 23 = Garças Lagoon

niche: feeding, habitat use, metabolism, life history, and defence capabilities. Also, we included the native and non-native status as an additional trait (Table 1). Functional traits data were measured and obtained for each species from literature sources and FishBase (Froese & Pauly, 2020; Table S2).

2.4 | Data analysis

A total of 103 fish species (61 native and 42 non-native) was analysed. The abundance of native and non-native species was indexed by the catch per unit effort (CPUE = number of individuals/1,000 m^2 gill-nets during 24 hr). CPUE values were grouped by river (Paraná—HA; Baía—MA; Ivinhema—LA) and decade (1980–1989; 1990–1999; 2000–2009; 2010–2019). To evaluate differences in CPUE between rivers and decades and their interaction (river*decade), two-way ANOVA was used. This analysis provided estimates of linear coefficients for interpretation (Table S3).

Functional diversity was evaluated from three indices: functional richness (FRic), functional redundancy (FRed) and Rao's quadratic entropy (Rao). These indices were calculated for each sample (location/month/year) and each group of species (native and non-native).

TABLE 1 Dimensions of ecological niches and functional traits selected for the native and non-native species in the upper Paraná River floodplain

Dimensions of the ecological niche	Functional traits	Codes	Descriptions
Feeding	Position of the mouth,	M.T M.ST M.L M.U	Terminal Sub-terminal Lower Upper
	Trophic guild	Det Ins Inv Her Omn Pis	Detritivore Insectivore Invertivore Herbivore, Omnivore Piscivore
Habitat use	Position in the water column	P.B P.D P.P	Benthic Demersal Pelagic
	Migration	Migr	Long distance migrations over 100 km
	Maximum standard length.	SL	Standard length in mm
Metabolism	The Fulton condition factor	K	K = (total weight/(standard length))^3
Life history	Size at maturation	L50	Size at first maturity (L50, mm)
	Batch fecundity	Fec	Number of mature oocytes in ripe ovaries
	Egg size	EgS	Diameter of the oocytes in mm
	Spawning frequency (reproductive events per year)	Spw.S Spw.M	Single Multiple
	Internal fertilisation	F. Int	
	Parental care	PC	Represented as the total energetic contribution of parents to their offspring and estimated as the sum of (i) special placement of zygotes (0,1); (ii) live bearing (0,1); (iii) guarding (0,1); (iv) mouthbrooding (0,1); (v) stage of offspring when parental care is ended (eggs = 1; larvae = 2; young = 3); (vi) contribution of parents (monoparental = 1; biparental = 2; monoparental or biparental = 1.5); and (vii) prolonged gestation = 8 (only for *Potamotrygon* species) (Winemiller, 1989; Olden et al., 2006; Peláez & Pavanelli, 2018).
Defence against predators	Defence	Def.	Indicated by: (i) presence of spines (0 = absence; 1 = only one spine at the anterior edge of the pectoral or dorsal fin; 2 = a spine in both the pectoral and dorsal fin; 3 = multiple spines); (ii) presence of venom in spines = 1; (iii) armour (0 = absence of bone structures covering the body; 1 = covering only the anterior region of the body; 2 = covering more than half of the body)
Native and non-native status of fish species.		N NN	Native Non-Native

The dbFD function of the *FD* package (Laliberté et al., 2014) in R (R Core Team, 2020) was used to calculate functional diversity indices; the exception being use of the Uniqueness function of the *Adiv* package (Pavoine, 2020) for the redundancy index. Differences in functional diversity indices between rivers, decades, and their interaction (river*decade) were evaluated by two-way ANOVA (Table S3).

The relationship of non-native species with the functional diversity indices (FRic, FRed and Rao) of native species was evaluated using a simple linear regression between each index and the level of dominance by non-native species (LDNN), treating each sample as an independent estimate. LDNN is defined as the relative biomass of non-native species (non-native species biomass/total biomass) in the local fish community (Zhao et al., 2019). The biomass of all fish species was calculated considering the sampling effort (biomass/1,000 m^2 gillnets during 24 hr).

RLQ analysis was performed (Dray et al., 2014; Legendre & Dray, 2008) to evaluate the responses of functional diversity patterns of native and non-native species in relation to time (decades) and the degree of river alteration (HA, MA, and LA). RLQ provides ordination scores to summarise the joint structure among species abundances in samples (L), associated environmental variables (R), and species traits (Q). The fourth-corner method tests for individual trait-environment relationships (one trait and one environmental variable at a time). Here we used temporal (decades) and spatial (rivers) variables to represent the environmental variables. Since RLQ is an extension of co-inertia analysis, an ordination is required for each matrix prior to computation. For the L matrix, correspondence analysis was used because it performs well when there are some zero values (McCune & Grace, 2002). Because they had mixed data (binary and continuous), the R and Q matrices were submitted to a Hill–Smith ordination (Hill & Smith, 1976). These analyses were performed in R using the rlq and randtest functions of the *ade4* package (Dray & Dufour, 2007).

3 | RESULTS

3.1 | Variation in abundance and functional diversity indices

In all three rivers, the mean abundance of native species increased during the first 2 decades of the study (1980–1999), then declined during the third decade (2000–2009), and increased again during the fourth decade (Figure 2a). During all 4 decades, the lowest abundance was recorded in the highly altered river (HA). Highest abundance of native fishes was obtained in the Ivinhema River (LA) during the last decade (2010–2019). Significant differences were found between decades ($F = 18.75$; $p < 0.0001$) and the river–decade interaction ($F = 2.27$ $p = 0.0349$). The abundance of non-native species increased gradually in the three rivers over time (Figure 2b). Non-native species attained greatest abundance in samples from the Baía River (MA) during the two most recent decades (Figure 2b). Significant differences were found between decades ($F = 230.41$; $p < 0.0001$) and the interaction river–decade ($F = 4.89$; $p = 0.0001$).

Among native species, FRic tended to be higher in the LA river and lower in the HA river. Although there were no statistically significant interactions between rivers and decades, FRic tended to be lower during the last 2 decades in the LA river. In the other two rivers, there was no apparent trend (Figure 3a; Table 2). Among non-native species, FRic increased over time in all three rivers, and was highest in the MA river. In the HA river, FRic was highest during the second decade (Figure 3b). The functional redundancy index (FRed) of native species increased over time and in all three rivers, and this increase was highest for HA (Figure 3c). FRed revealed significant between-river ($F = 34$; $p < 0.0001$) and inter-decadal ($F = 9.7$; $p < 0.0001$) differences (Table 2). Among non-native species, FRed increased for the HA and MA rivers and was highest for the HA river. However, FRed decreased for the LA river during the second decade (Figure 3d). FRed revealed significant inter-river ($F = 36.1$; $p < 0.0001$) and inter-decadal ($F = 10.6$; $p < 0.0001$) differences (Table 2). Rao's quadratic entropy of native species declined over time in all three rivers. Significant differences were found between decades ($F = 7.21$; $p = 0.0001$) and rivers ($F = 25.17$ $p < 0.0001$; Figure 3e). This decline was greatest for the MA river. Among non-native species, Rao's quadratic entropy declined in the HA river and increased in the MA and LA rivers (Figure 3f). Significant differences were found between rivers ($F = 24.66$ $p < 0.0001$) and decades ($F = 71.07$; $p < 0.0001$; Table 2).

3.2 | Relationships between non-native species and functional diversity indices of native species

Functional richness ($r^2 = 0.0852$; $p < 0.001$) and Rao's quadratic entropy ($r^2 = 0.0095$; $p = 0.001$) of native species decreased significantly with increasing level of dominance by non-native species (LDNN), while functional redundancy did not show significant changes ($r^2 = 0.0004$; $p = 0.453$; Figure 4).

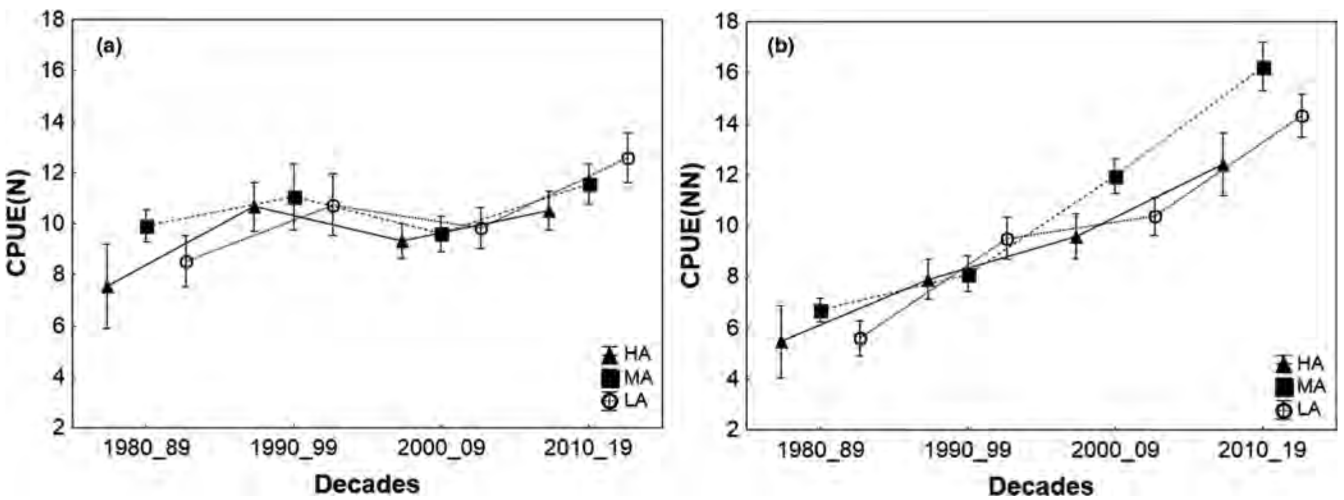

FIGURE 2 Average values of abundance (catch per unit effort, CPUE) for native (N: a) and non-native (NN: b) fishes over time (decades) and in the three rivers (HA, MA, LA) in the upper Paraná River floodplain. The bars represent the standard error. N = native species; NN = non-native species; HA = highly altered; MA = moderately altered; LA = little altered

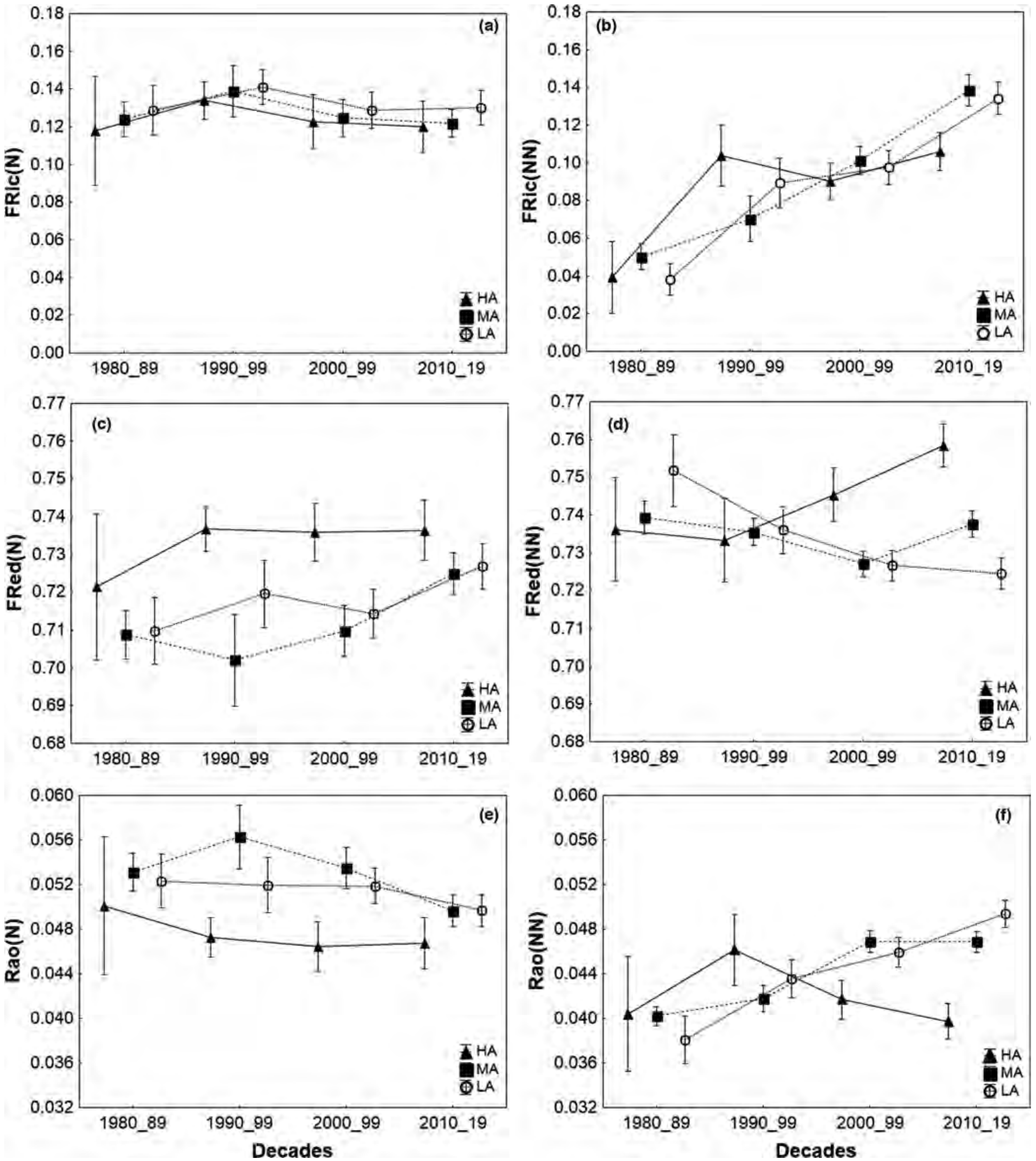

FIGURE 3 Average values of the functional diversity index for native (N: a, c, e) and non-native (NN: b, d, f) fishes over time (decades) and in three rivers (HA, MA, LA) in the upper Paraná River floodplain. The bars represent standard errors. FRic = functional richness; FRed = functional redundance; Rao = Rao's quadratic entropy; N = native species; NN = non-native species; HA = highly altered; MA = moderately altered; LA = little altered

3.3 | Response of functional traits of native and non-native species

The first two axes of the RLQ analysis accounted 77.4% of the variation among temporal and spatial variables as they related to functional traits of fish assemblages (Table 3). The first axis of RLQ was negatively related to the two first decades (1980–1989 and 1990–1999) and the river LA, and it also positively related to the two last decades (2000–2009 and 2010–2019), the HA and MA rivers. The second RLQ axis was negatively related to HA river

TABLE 2 Results of two-way ANOVA for abundance and functional diversity indices in relation to floodplain river, decade, and their interaction (river*decade)

	Native Species				Non-native Species			
	CPUE	FRic	FRed	Rao	CPUE	FRic	FRed	Rao
River	$F = 1.72$ $p = 0.1788$	$F = 2.66$ $p = 0.0705$	$F = 34$ $p < 0.0001$	$F = 25.17$ $p < 0.0001$	$F = 2.45$ $p = 0.087$	$F = 0.44$ $p = 0.646$	$F = 36.1$ $p < 0.0001$	$F = 24.66$ $p < 0.0001$
Decade	$F = 18.75$ $p < 0.0001$	$F = 4.34$ $p = 0.0047$	$F = 9.7$ $p < 0.0001$	$F = 7.21$ $p < 0.0001$	$F = 230.41$ $p < 0.0001$	$F = 188.4$ $p < 0.0001$	$F = 10.6$ $p < 0.0001$	$F = 71.07$ $p < 0.0001$
River*Decade	$F = 2.27$ $p = 0.0349$	$F = 0.08$ $p = 0.9977$	$F = 1.70$ $p = 0.1142$	$F = 1.71$ $p = 0.1159$	$F = 4.89$ $p = 0.0001$	$F = 5.86$ $p < 0.0001$	$F = 8.9$ $p < 0.0001$	$F = 10.25$ $p < 0.0001$

Abbreviations: CPUE, abundance; FRed, functional redundancy; FRic, functional richness; Rao, Rao's quadratic entropy.

(Figure 5a). The correlations between species traits and RLQ axis 1 indicated that native species were more associated with the two first decades and the LA river, especially native fishes that perform migrations (Migr), have high fecundity (Fec), single spawning (Spw.S), great length (SL), and larger size of first maturation (L50), such as *Prochilodus lineatus* (47), *Pseudoplatystoma corruscans* (48), and *Hemisorubim platyrhynchos* (19), and native fishes with upper position of mouth (M.U) such as *Rhaphiodon vulpinus* (50; Figure 5b,c). Likewise, the correlations between species traits and RLQ axis 2 indicated that non-native species were more abundant in the last 2 decades and the MA river, especially non-native fishes with parental care (PC), multiple spawning (Spw.M), big eggs (EgS), high defence capacity (Def), and inferior position of mouth such as *Loricariichthys platymetopon* (82), *Loricariichthys rostratus* (83), *Hypostomus commersoni* (80), *Potamotrygon amandae* (90), and *Potamotrygon* cf. *falkneri* (91; Figure 5b,c).

4 | DISCUSSION

After the construction of the Itaipu Dam in 1982, the abundance of non-native fish greatly increased, while the abundance of most native fish increased slightly in the three rivers with different degrees of alteration by dams. However, functional diversity patterns differed between native and non-native species and between fish assemblages in rivers with different degrees of alteration. As expected, functional richness and Rao's quadratic entropy of native species decreased over time, while functional redundance increased especially in the most altered river. For non-native species, functional richness and Rao's quadratic entropy increased over time, except in the most altered river where functional redundance also increased. The level of dominance by non-native species had significant relationships with functional richness and Rao's quadratic entropy of native species, but functional redundancy was not strongly associated. Native species that perform migration, have high fecundity, a single seasonal spawning event, and large size at maturation were common during the first 2 decades and within the least altered river. Non-native species with parental care, multiple spawning events per year, large eggs and well-developed defence capabilities were more common during the last 2 decades and within the moderately altered river.

4.1 | Variation in abundance and functional diversity indices

The present study revealed a decline in the abundance of native fishes during the third decade, with lowest abundance in the highly altered river (Paraná River floodplain). This decline in the Paraná River coincides with the limnological and flow alterations caused by operation of the Porto Primavera Dam (Abujanra et al., 2009; Oliveira et al., 2018). The increase in abundance of non-native fishes in all three rivers could have been associated with environmental

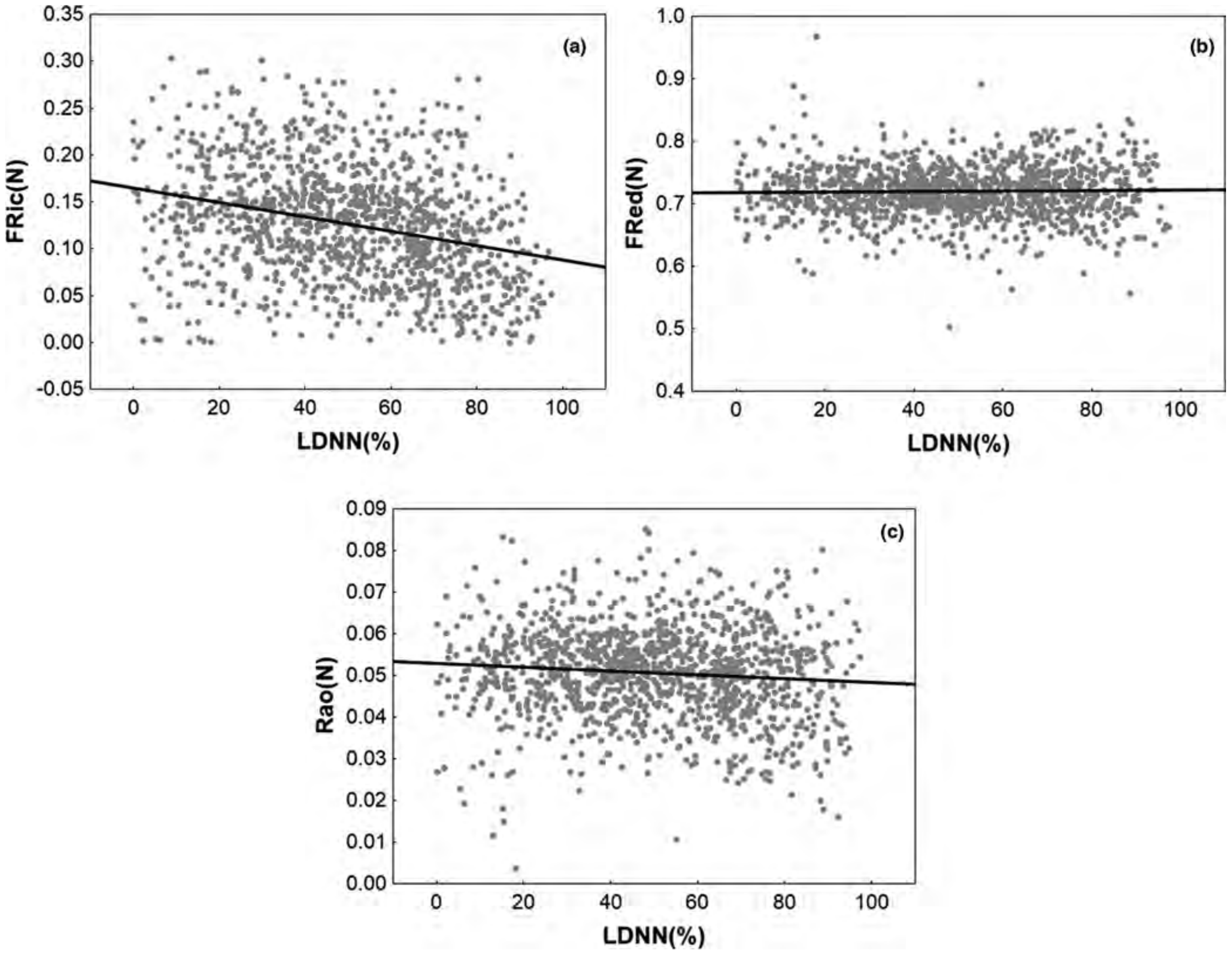

FIGURE 4 Relationships between functional diversity indices of native species (N) and the level of dominance by non-native species (LDNN). (a) FRic = functional richness (r^2 = 0.0852; p < 0.0001); (b) FRed = functional redundancy (r^2 = 0.0004; p = 0.453); (c) Rao = Rao's quadratic entropy (r^2 = 0.0095; p = 0.001)

TABLE 3 Percentage of inertia for axes and eigenvalues from RLQ analysis for native and non-native species

Variables	axis 1	axis 2
Projected inertia (%)	65.059	12.386
Cumulative projected inertia (%)	65.06	77.45
Eigenvalues	0.1075	0.0204
Total inertia	0.1653	

changes, an increase in propagule pressure (the number of individuals introduced and the frequency in which they arrive in the new environment), or both. According to Ahlroth et al. (2003), propagule pressure not only increases the chance of non-native species establishment, but also may increase the likelihood of successful adaptation to a the novel environment once established. The propagules pressure of non-native species in the upper Paraná River Basin has increased over time due to various human actions, such as installment of a fish passage around Itaipu Dam in 2002 (Vitule et al., 2012) and releases of aquarium and bait fish (Agostinho et al., 2005; Clavero et al., 2013; Ortega et al., 2015; Pelicice et al., 2017).

Functional richness of native species decreased over time in all three floodplain regions, and this pattern of decline was strongest in the moderately altered river during the most recent decade. Generated from the analysis of a longer time series, these results corroborate and extend inferences from an earlier study conducted by Oliveira et al. (2018) that surveyed fishes of the upper Paraná River floodplain immediately before and after construction of the Porto Primavera Dam, revealing a decline in functional richness in the Baía and Paraná Rivers and a slight increase in the Ivinhema River. In contrast, functional richness of non-native species increased over time in all three rivers, with the greatest change occurring in the moderately altered river. This implies that replacement of native species by non-native species was mediated by the manner in which species functional traits created fitness advantages depending on changing abiotic and biotic environmental conditions (Shuai et al., 2018). Although functional richness generally increased for non-native

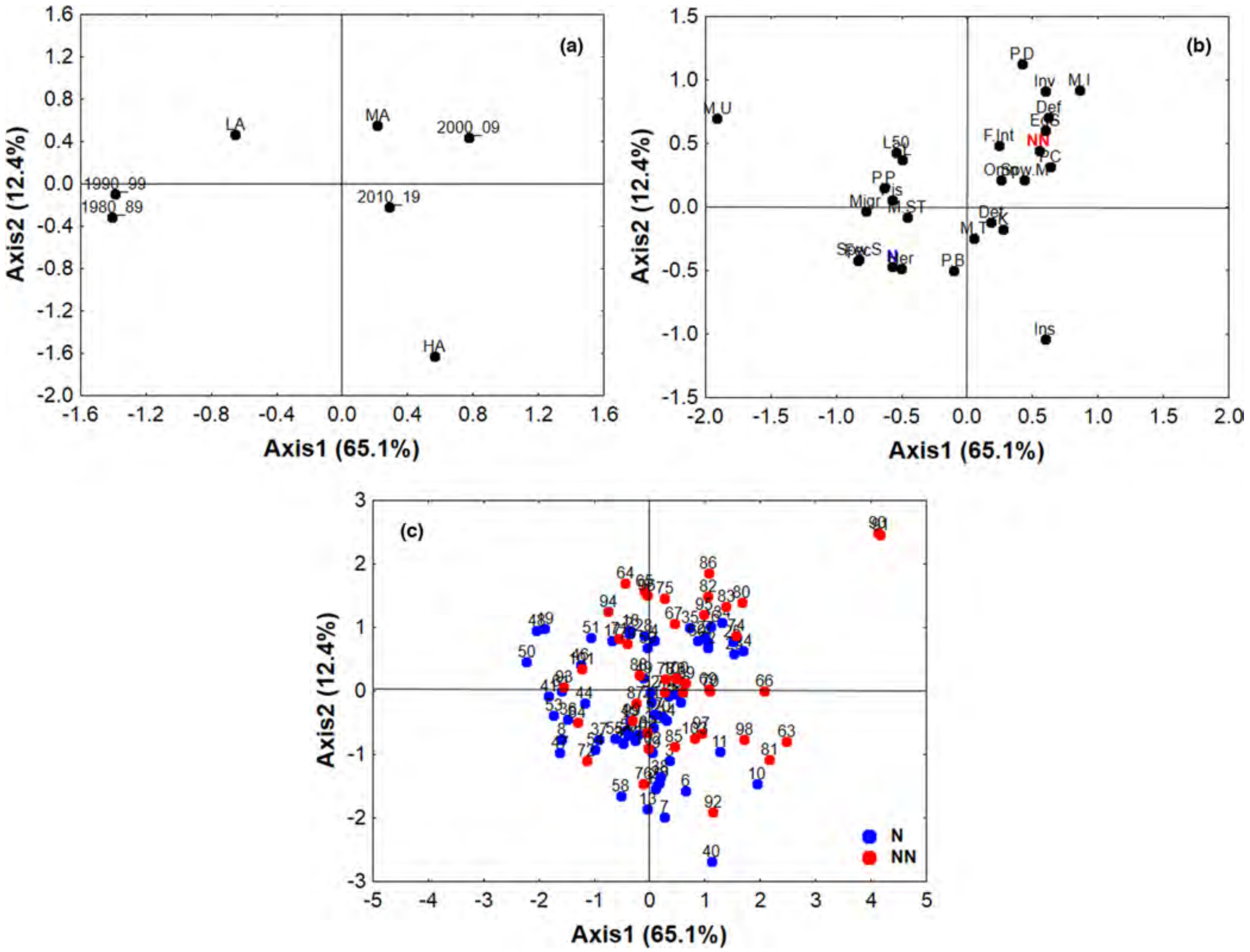

FIGURE 5 Plots from of RLQ analysis showing axis loadings of temporal (decades) and spatial (HA = highly altered; MA = moderately altered; LA = little altered rivers) variables (a), axis loadings of functional traits (b), and ordination of native (N, blue dots) and non-native (NN, red dots) fish species (c). See Table 1 for the codes of functional traits. N = native species; NN = non-native species; HA = highly altered; MA = moderately altered; LA = little altered. **Native species:** 1 = *Acestrorhynchus lacustris*; 2 = *Ageneiosus militaris*; 3 = *Apareiodon affinis*; 4 = *Apteronotus ellisi*; 5 = *Astyanax* aff. *fasciatus*; 6 = *Astyanax lacustris*; 7 = *Astyanax schubarti*; 8 = *Brycon orbignyanus*; 9 = *Callichthys callichthys*; 10 = *Cichlasoma paranaense*; 11 = *Crenicichla britskii*; 12 = *Cyphocharax modestus*; 13 = *Cyphocharax nagelii*; 14 = *Eigenmannia trilineata*; 15 = *Eigenmannia virescens*; 16 = *Galeocharax gulo*; 17 = *Gymnotus inaequilabiatus*; 18 = *Gymnotus sylvius*; 19 = *Hemisorubim platyrhynchos*; 20 = *Hoplias argentinensis*; 21 = *Hoplias* sp.2; 22 = *Hoplosternum littorale*; 23 = *Hypostomus ancistroides*; 24 = *Hypostomus hermanni*; 25 = *Hypostomus iheringii*; 26 = *Hypostomus regani*; 27 = *Hypostomus strigaticeps*; 28 = *Iheringichthys labrosus*; 29 = *Leporellus vittatus*; 30 = *Leporinus friderici*; 31 = *Leporinus lacustris*; 32 = *Leporinus octofasciatus*; 33 = *Leporinus striatus*; 34 = *Loricaria prolixa*; 35 = *Megalancistrus paranaus*; 36 = *Megaleporinus obtusidens*; 37 = *Megaleporinus piavussu*; 38 = *Moenkhausia* aff. *intermedia*; 39 = *Myloplus tiete*; 40 = *Piabarchus stramineus*; 41 = *Piaractus mesopotamicus*; 42 = *Pimelodella avanhandavae*; 43 = *Pimelodella gracilis*; 44 = *Pimelodus maculatus*; 45 = *Pimelodus mysteriosus*; 46 = *Pinirampus pirinampu*; 47 = *Prochilodus lineatus*; 48 = *Pseudoplatystoma corruscans*; 49 = *Rhamdia quelen*; 50 = *Rhaphiodon vulpinus*; 51 = *Rhinelepis aspera*; 52 = *Rhinodoras dorbignyi*; 53 = *Salminus brasiliensis*; 54 = *Salminus hilarii*; 55 = *Schizodon altoparanae*; 56 = *Schizodon nasutus*; 57 = *Serrasalmus maculatus*; 58 = *Steindachnerina insculpta*; 59 = *Sternopygus macrurus*; 60 = *Synbranchus marmoratus*; 61 = *Zungaro jahu*. **Non-native species:** 62 = *Acestrorhynchus pantaneiro*; 63 = *Aequidens plagiozonatus*; 64 = *Ageneiosus inermis*; 65 = *Ageneiosus ucayalensis*; 66 = *Astronotus crassipinnis*; 67 = *Auchenipterus osteomystax*; 68 = *Catathyridium jenynsii*; 69 = *Cichla kelberi*; 70 = *Cichla piquiti*; 71 = *Clarias gariepinus*; 72 = *Colossoma macropomum*; 73 = *Erytrhinus erythrinus*; 74 = *Geophagus sveni*; 75 = *Gymnotus pantanal*; 76 = *Hemiodus orthonops*; 77 = *Hoplerythrinus unitaeniatus*; 78 = *Hoplias mbigua*; 79 = *Hypophthalmus oreomaculatus*; 80 = *Hypostomus commersoni*; 81 = *Laetacara araguaiae*; 82 = *Loricariichthys platymetopon*; 83 = *Loricariichthys rostratus*; 84 = *Megaleporinus macrocephalus*; 85 = *Metynnis lippincottianus*; 86 = *Parauchenipterus galeatus*; 87 = *Pimelodus ornatus*; 88 = *Plagioscion squamosissimus*; 89 = *Platydoras armatulus*; 90 = *Potamotrygon amandae*; 91 = *Potamotrygon* cf. *falkneri*; 92 = *Psellogramus kennedyi*; 93 = *Pseudoplatystoma reticulatum*; 94 = *Pterodoras granulosus*; 95 = *Pterygoplichthys ambrosettii*; 96 = *Rhamphichthys hahni*; 97 = *Roeboides descalvadensis*; 98 = *Satanoperca* sp.; 99 = *Schizodon borelli*; 100 = *Serrasalmus marginatus*; 101 = *Sorubim lima*; 102 = *Steindachnerina brevipinna*; 103 = *Trachydoras paraguayensis*

species over time, this index was lower for the highly altered river during the two most recent decades. This finding is consistent with the idea that functional richness declines with increasing levels of ecosystem disturbance (Cornwell et al., 2006; Flynn et al., 2009; Mouillot et al., 2013).

Rao's quadratic entropy declined for native species over the four decades in all three rivers, whereas for non-native species it increased for assemblages in the moderately and little-altered rivers, and declined in the highly altered river. Since high values for Rao's quadratic entropy indicate high dissimilarity between species, this implies that non-native species had greater functional differentiation in assemblages of the two least altered rivers, whereas native fish species were fairly similar in all three rivers. Rao's quadratic entropy tends to be inversely proportional to the intensity of the disturbance (Botta-Dukát, 2005; Mouillot et al., 2013; Rao, 1982; Ricotta et al., 2016; Villéger et al., 2010), and in the present study, this index usually was lowest in the highly altered river. In a previous study conducted in the upper Paraná River (Oliveira et al., 2018), the magnitude of anthropogenic alteration of the hydrological regime was negatively associated with Rao's entropy of floodplain fish assemblages.

In the current long-term study, functional redundancy of non-native fishes increased over time within the highly and the moderately altered rivers, but decreased in the least altered river. For both native and non-native fishes, functional redundancy was greatest in the highly altered river. According to Mouillot et al., 2007, functional redundancy should occur when the effect of environmental filtering of assemblage trait distributions is stronger than the effect of limiting similarity. This suggests that anthropogenic environment impacts constituted an environmental filter that increased functional redundancy, and non-native fishes in the least-altered river may also have responded to biotic factors that limit similarity.

4.2 | Relationships between non-native species and functional diversity indices of native species

As expected, the level of dominance by non-native species (relative biomass of non-native species) had a negative relationship with functional richness of native species, possibly indicating that non-native species supplant niche space occupied by native species. This same trend also was observed among non-native and native fishes in the Pearl River in southern China (Shuai et al., 2018). Rao's quadratic entropy for native fishes of the upper Paraná River floodplain also was negatively associated with the level of dominance of non-native species. Considering that Rao's quadratic entropy reflects the relationship between relative abundances and distances between pairs of species based on similarity of functional characteristics (Mouillot et al., 2013), we infer that populations of non-native species caused, either directly or indirectly, declines in the abundance of native species, including local extirpation of some. Conversely, the dominance of non-native species did not appear to affect the functional redundancy of native species. Functional redundancy often is associated with species loss (Matsuzaki et al., 2013, 2016). It is important to note that the number and types of traits considered can influence estimates of functional redundancy (Petchey & Gaston, 2006).

4.3 | Response of functional traits of native and non-native species

Native and non-native fish assemblages tended to have different dominant functional traits throughout the 33-year study period. During the first 2 decades, more native fishes in the least-altered river tended were large and migratory with high fecundity and single bouts of seasonal spawning. These traits were negatively associated with the 2 most recent decades in the highly altered river. This finding also coincides with the operation of the Porto Primavera Dam, which obstructed fish migratory routes (Abujanra et al., 2009; Agostinho et al., 2008). In addition, large migratory fishes, such as *Prochilodus lineatus*, *Pseudoplatystoma corruscans*, *Hemisorubim platyrhynchos*, and *Rhaphiodon vulpinus*, are intensely fished due to their high commercial value (Agostinho et al., 2004; Lopes et al., 2020; Oliveira et al., 2014), and reduction of these migratory species represents an economic impact for regional communities.

Non-native fishes that increased in abundance within the moderately altered river during the two most recent decades tended to have multiple spawning bouts per year, large egg size, and well-developed parental care. These equilibrium-type life history strategies seem to be associated with invasion success in fishes (Agostinho et al., 2015; Moyle, 2006; Winemiller et al., 2015) and hydrologic alteration by dams (Mims & Olden, 2013). *Loricariichthys platymetopon*, *Serrasalmus marginatus*, and *Hoplias mbigua* are non-native fishes with these traits that are now common in the Paraná River floodplains (Agostinho et al., 2007; Pereira et al., 2017; Rodrigues et al., 2018). Non-native fishes that invaded the moderately altered river also had well-developed defence capabilities. Fish defence strategies are sometimes associated with physicochemical characteristics of water (Pinto et al., 2012). For example, defensive strategies involving reflective, cryptic, or mimicry coloration patterns can be effective defences against visually orienting predators when water transparency is high (Johnsson, 2009; Pinto et al., 2012). In the upper Paraná, non-native species with other types of defences, such as spines, venom, or armour, were more common in the moderately altered river that had lower transparency.

The analysis of functional diversity can facilitate inferences about the mechanisms by which non-native species and habitat alterations affect biodiversity and native ecosystems. In the present study, the comparison of temporal trends in the functional diversity and characteristics of native and non-native fishes in rivers with different levels of environmental alteration by dams revealed functional trait changes within both groups. This suggests that both non-native species and habitat alterations played significant roles in the decline of some native species, especially migratory fishes with a periodic life history strategy. It remains to be determined how changing patterns of fish functional diversity will affect ecosystem processes and associated services in the upper Paraná River floodplain.

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CONFLICT OF INTEREST

All authors agree with the submission of the manuscript, and declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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