

# Drastic reduction of the functional diversity of native ichthyofauna in a Neotropical lake following invasion by piscivorous fishes



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Biological invasions are leading several species to extinction and are projected as a main driver of biodiversity changes in lakes for this century. However, the knowledge of their impacts on the Neotropical ichthyofauna over time remains largely incipient, especially when considering the functional diversity of native communities. Here we aim to identify the effects of non-native species, especially the non-native piscivorous *Cichla kelberi* and *Pygocentrus nattereri*, on the functional diversity of the native ichthyofauna of the Carioca Lake, Middle Rio Doce basin, state of Minas Gerais. Using fish occurrence data for eight years from 1983 to 2010 combined with an ecomorphological-trait analysis, we found that while the native species richness dropped to 56%, the functional richness is only 27% of that found before introductions. In other words, more than species, the ichthyofauna suffered an impressive decline in the range of functional traits, which can further have severe impacts on ecological processes within that system. When considering all the components of the current ichthyofauna (native and non-native species), neither taxonomic nor functional richness have changed over time. However, even keeping biodiversity levels, non-native species are not able to fully compensate for the extinct native ones in terms of functions.

**Keywords:** Biodiversity erosion, Biological invasions, Functional traits, Non-native fish, Rio Doce basin.

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Invasões biológicas vêm levando várias espécies à extinção, sendo projetado como o principal causador de mudanças na biodiversidade em lagos neste século. Entretanto, o conhecimento dos impactos sobre a ictiofauna Neotropical ao longo do tempo permanece bastante incipiente, especialmente quando se considera a diversidade funcional de comunidades nativas. Neste estudo, nós procuramos identificar os efeitos das espécies não nativas, especialmente os piscívoros não nativos *Cichla kelberi* and *Pygocentrus nattereri*, sobre a diversidade funcional da ictiofauna da Lagoa Carioca, bacia do médio rio Doce, Minas Gerais. Utilizando dados de ocorrência de oito anos entre 1983 e 2010, combinados a uma análise de atributos ecomorfológicos, observamos que a riqueza de espécies decaiu a 56%, enquanto a riqueza funcional é de apenas 27% da encontrada antes das introduções. Ou seja, mais do que espécies, a ictiofauna sofreu um declínio significativo na amplitude de atributos funcionais, o que pode levar a impactos severos em processos ecológicos neste sistema. Ao considerar todos os componentes da ictiofauna atual (espécies nativas e não nativas), as métricas de riqueza não sofreram alterações ao longo do tempo. Entretanto, mesmo mantendo os níveis de biodiversidade, espécies não nativas não são capazes de compensar totalmente as espécies nativas extintas em termos funcionais.

**Palavras-chave:** Atributos funcionais, Bacia do rio Doce, Erosão da biodiversidade, Invasões biológicas, Peixes não nativos.

## INTRODUCTION

Biological invasions cause strong changes in ecosystems resulting in devastating ecological consequences. Together with resource overexploitation, landscape alterations (e.g., deforestation), pollution and climatic changes, species invasion is considered one of the most important causal factors of biodiversity erosion on Earth (Vitule *et al.*, 2009). Particularly to freshwater systems, invasions have already led several species to extinction (Clavero, García-Berthou, 2005), and are projected as the main driver of biodiversity changes in lakes for this century (Sala *et al.*, 2000). As a result of globalization, the introduction of aquatic species out of their original area of distribution became more frequent and intense, with main vectors related to water released from ships' ballast, biological control agents, aquarium trade, sport fishing, and food allowance (Millennium Ecosystem Assessment, 2005). After introduced, non-native species can settle down in a native community and extirpate native organisms by a variety of mechanisms frequently related to ecological interactions, such as predation (Kaufman, 1992; Pereira *et al.*, 2015) and competition (Bøhn *et al.*, 2008; Pelicice *et al.*, 2017). Nevertheless, the sequence of events involved behind these general mechanisms is largely unknown and highly unpredictable, hampering effective actions to detect, control and restore natural conditions (Blackburn *et al.*, 2011; Lockwood *et al.*, 2013).

Systematic studies on the impact of invasive species in tropical aquatic ecosystems are still incipient. One of the biggest challenges for understanding the consequences of biological invasions is the lack of long-term historical series that evidence the temporal

alterations on the structure of native biological communities (e.g., Olden, 2006; Magalhães *et al.*, 2020). Additionally, despite of the recent conceptual and methodological advances to describe alterations on the structure of communities induced by anthropogenic disturbances, the taxonomic approach remains the rule. This traditional view to quantify biodiversity (*i.e.*, based purely on species richness and/or diversity indices) has been constantly shown as scarcely predictive, given that it neglects the species functional traits and how they mediate ecological interactions (Villéger *et al.*, 2008). Therefore, these community descriptors are frequently considered as a limited quantitative tool in monitoring environmental impacts. Different processes may affect species from different ways, potentially providing delayed or even mistaken signs of perturbation (Mouillot *et al.*, 2013). Therefore, approaches such as the functional diversity of communities in the context of anthropogenic disturbances have been growing in several fields of ecology and for different biological groups (Biswas, Mallik, 2010; Dolbeth *et al.*, 2016; Arnan *et al.*, 2018; Teresa *et al.*, 2021).

The functional diversity of a community can be described as the range of the species ecological traits (Mouillot *et al.*, 2013). Such an approach allows the characterization of species by their functional relations with the environment and with other species, regardless of their taxonomic identities (Cianciaruso *et al.*, 2009). For freshwater fishes, traits related to ecomorphology and life's history have shown to be particularly good predictors of habitat degradation and biological invasions (Olden, 2006; Leitão *et al.*, 2018). As so, it is possible to better evaluate the causes of species extinctions, and the consequences on the sustainability of ecological processes (Leitão *et al.*, 2016). The functional approach is thus gaining importance, once that it provides a more mechanistic way to assess the human-induced impacts on biodiversity (Magurran, 2004; Ernst *et al.*, 2006; Petchey, Gaston, 2006). Therefore, using this approach in the context of biological invasions seems to be a promising strategy to increase our capacity to detect and predict their impacts on Neotropical aquatic communities.

One of the most emblematic cases of biological invasion in Brazilian freshwater ecosystems has been occurring in the Middle Rio Doce basin. This region holds one of the largest lacustrine systems in South America (Maia-Barbosa *et al.*, 2010), and harbor about a third of all fish species of the basin (Godinho, Vieira, 1998). The introduction of fishes since the 1970's culminated with the local extinction of several native species, such as the small characin *Moenkhausia vittata* (Castelnau, 1855) and the carnivore *Oligosarcus solitarius* Menezes, 1987, currently not found in many lakes (Sunaga, Verani, 1991; Latini *et al.*, 2004; Latini, Petrere, 2004; Oporto, 2013; Fragoso-Moura *et al.*, 2016). The history of introduction and dispersion of fish species across the Rio Doce basin is related mostly to aquaculture and sport fishing (Godinho *et al.*, 1994; Latini *et al.*, 2004; Magalhães *et al.*, 2021). The latter is likely the reason for the establishment of the peacock bass *Cichla kelberi* Kullander & Ferreira, 2006, native to the Tocantins-Araguaia basin, and the red piranha *Pygocentrus nattereri* Kner, 1858, native to the Amazon, Paraguay-Paraná, northeastern Brazilian coastal rivers and Essequibo basins (Fricke *et al.*, 2021), impacting the local ichthyofauna given their piscivorous habits and high voracity (Sazima, Machado, 1990; Chellappa *et al.*, 2003).

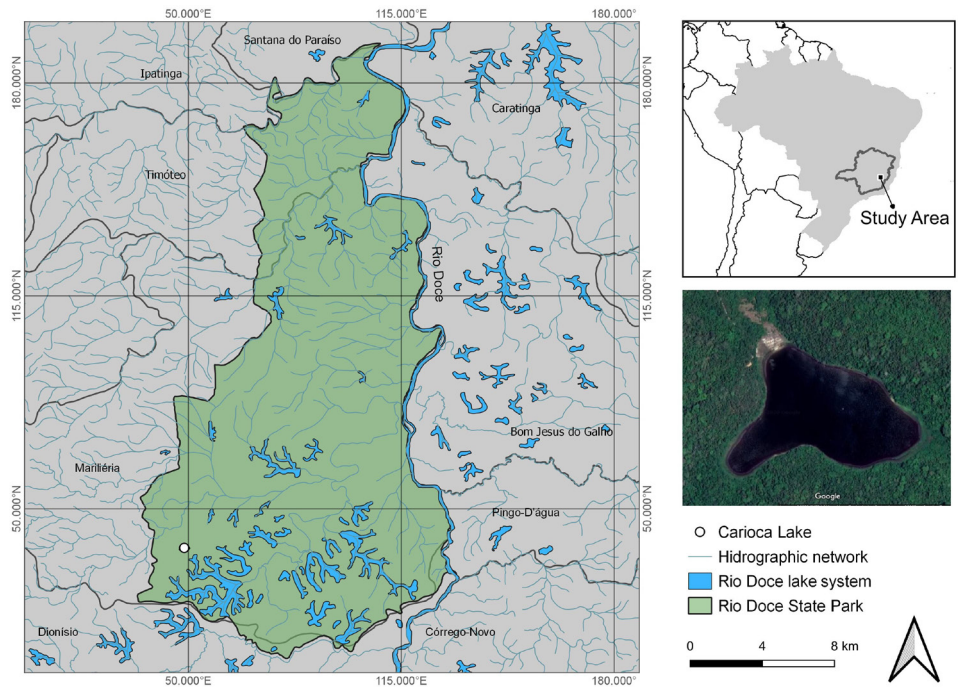
Recently, Fragoso-Moura *et al.* (2016) conducted a thorough compilation of a rare historical data of the ichthyofauna from Carioca Lake, a well-studied system located at the Rio Doce State Park (PERD acronym in Portuguese, hereafter) and detected a broad

dominance of *C. kelberi* and *P. nattereri*, besides the presence of other introduced fishes in the community, e.g., the oscar *Astronotus cf. crassipinnis* (Heckel, 1840), the cascarudo *Hoplosternum littorale* (Hancock, 1828), and the African catfish *Clarias gariepinus* (Burchell, 1822). The authors detected an impressive decline in the number of native species during the last four decades. Still unknown, however, is how this community has been changed in its functional structure. We intend here to fill such a gap from this alternative perspective and point out some mechanistic ways to explain this biodiversity erosion. For this, we compared the levels of fish taxonomic and functional diversity over time, from 1983 to 2010, in Carioca Lake. Given that the functional approach is supposedly more sensible to anthropogenic disturbances (Mouillot *et al.*, 2013), we hypothesize that the decline in functional richness is more pronounced than that of species richness after the introduction of non-native fish species, especially *C. kelberi* and *P. nattereri*. We expect to get a better comprehension of the processes behind biological invasions and thus helping to implement conservation and management actions for the ichthyofauna in the region.

## MATERIAL AND METHODS

**Study area.** The Middle Rio Doce basin, state of Minas Gerais, comprises one of the largest lacustrine systems of the Brazilian territory (Tundisi, de Meis, 1985), with more than 250 natural lakes of different sizes, dynamics, biodiversity, and levels of ecological integrity (Maillard *et al.*, 2012). Studies have shown that this system originated around ten thousand years ago as a result of blockages of the mouth of ancient Rio Doce tributaries, creating natural dams (Godinho, 1996). Their ichthyofaunas can thus be treated as closed communities and dispersion rates of species between them can be considered very low over time (Latini *et al.*, 2004). The relief of the region is sinuous with elevation varying from 195 to 525 m and depressions occupied by water bodies (Gilhuis, 1986). The weather is hot and wet, with annual rainfall between 1000 and 1250 mm and defined dry (April to September) and rainy (October to March) seasons. The region comprises the Rio Doce State Park (PERD; Fig. 1), which represents the biggest remnant portion of the Atlantic Forest in Minas Gerais (~36,000 ha), surrounded by *Eucalyptus* plantations, pasture and diverse agriculture (Barbosa, Moreno, 2002). In 1998, PERD was included in the Long-Term Ecological Research Programme (PELD Rio Doce – Site MLRD), and in 2009 the region was recognized internationally as a major area for conservation of biodiversity (*i.e.*, Ramsar site), as well as for ecological, economic, cultural, scientific, and recreational services (Mikhailova, Barbosa, 2002).

More than 40 lakes are found within the limits of PERD which are well preserved, at least in terms of adjacent forest and water quality (Maillard *et al.*, 2012). Amongst them, Carioca Lake was chosen in this study because its fish community has been repeatedly sampled over the last decades and the introduction history of the non-native predators *Cichla kelberi* and *Pygocentrus nattereri* is known. Located at the southern portion of PERD, Carioca Lake has 0.12 km<sup>2</sup>, is considered mesotrophic, with water temperature varying between 24.3 °C to 33.4 °C, maximum depth of 11.8 m, and surrounded by dense vegetation (Bezerra-Neto *et al.*, 2010).



**FIGURE 1 |** The lacustrine system of the Middle Rio Doce basin, state of Minas Gerais, Brazil. The green polygon delimits the area of the Rio Doce State Park (PERD) and the white circle indicates the location of Carioca Lake.

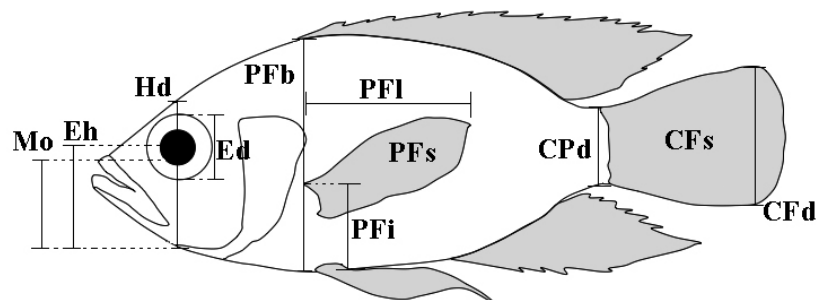
**Database.** We used occurrence data of native fishes from Carioca Lake obtained from the literature that spans nearly three decades (from 1983 to 2010) (Sunaga, Verani, 1991; Godinho *et al.*, 1994; Latini *et al.*, 2004; Vasconcellos *et al.*, 2005; Pinto-Coelho *et al.*, 2008; Fragoso-Moura *et al.*, 2016), already compiled in Fragoso-Moura *et al.* (2016). Fish samples were conducted with gillnets of different mesh sizes, seine, dragging and casting nets (specific details given in each published study). Sampling effort was different among studies, with new records of some native species occurring only in the most recent ones. However, given that Carioca Lake is a closed system and the last studies applied greater sampling effort, we assumed that native species listed only in recent records were already present in the fish assemblage since the earliest event of the temporal series. We also limited the analysis to presence-absence, rather than abundance data, to minimize the different sampling effort between years. Finally, we excluded species identified only at the family level in Fragoso-Moura *et al.* (2016). When needed, we updated the nomenclature of species, based on Fricke *et al.* (2021).

**Functional diversity.** We first conducted an ecomorphological analysis to functionally characterize all species. Eleven morphometric measures (Fig. 2) were taken from a digital picture (obtained from the authors' image banks or from the original description of the species) of one adult individual from each species, and processed in ImageJ software (Abràmoff *et al.*, 2004). These measures were then combined in eight ecomorphological traits representing three key functions: foraging, locomotion, and preferential habitat use (Tab. 1; values for each species in Tab. S1). All traits were



standardized (mean zero and one standard deviation) to make it possible to compare different measurement units and to avoid trivial correlation with body size (Villéger *et al.*, 2010). We used ecomorphological traits first because they represent an important dimension of the species niche (Winemiller *et al.*, 2015), and are the only set of characteristics available for all species recorded in Carioca Lake over the time series; *i.e.*, the lack of information on fish diet, life history and other biological traits are still a recurrent limitation for functional studies of the Neotropical freshwater ichthyofauna (Leitão *et al.*, 2016; Teresa *et al.*, 2021). Additionally, although some categorical traits could have been used based on literature (*e.g.*, feeding guild), many species characteristics may change over time, even as a result of non-native introductions. For example, there is evidence that after the arrival of *P. nattereri* (introduced) in PERD lakes, the native *Hoplias malabaricus* (Bloch, 1794) has changed from a piscivorous to an invertivorous diet (Pompeu, Godinho, 2001). Using such categorical trait would thus weakly express the functional roles of some species and could represent circularity on the relations investigated here.

**Data analysis.** We conducted all analytical procedures considering two different scenarios: “all species”, which included both native and non-native species; and “only native species”. From the eight ecomorphological traits, we built a Euclidean distance matrix considering the entire time series (1983–2010) and then performed a Principal Component Analysis (PCA) to represent the multidimensional functional space for each scenario. After accounting for the balance between the number of dimensions and the quality of the functional space (according to Maire *et al.*, 2015), we kept the first three PCA axes to synthesize the eight ecomorphological traits. From this three-dimensional functional space, we quantified Functional Richness (FRic); *i.e.*, the volume of the convex hull polygon occupied by the species found in each sampled year (1983, 1985, 1987, 1992, 2003, 2005, 2008, and 2010). FRic quantitatively describes the range of trait combinations by the focal set of species (Villéger *et al.*, 2008).



**FIGURE 2 |** Morphometric measures taken from digital pictures: CPd – caudal-peduncle minimal depth, CFd – caudal-fin maximum depth, CFs – caudal-fin surface, PFi – distance from pectoral-fin insertion to the bottom of the body, PFb – body depth at the level of the pectoral-fin insertion, PFI – pectoral-fin length, PFs – pectoral-fin surface, Hd – head depth along the vertical axis of the eye, Ed – eye diameter, Eh – distance from the center of the eye to the bottom of the head, Mo – distance from the tip of the upper jaw to the bottom of the head along the head depth axis. Adapted from Leitão *et al.* (2016).

**TABLE 1** | List of the eight ecomorphological traits used to functionally characterize fish species from the Carioca Lake, Middle Rio Doce basin, state of Minas Gerais, southeastern Brazil.

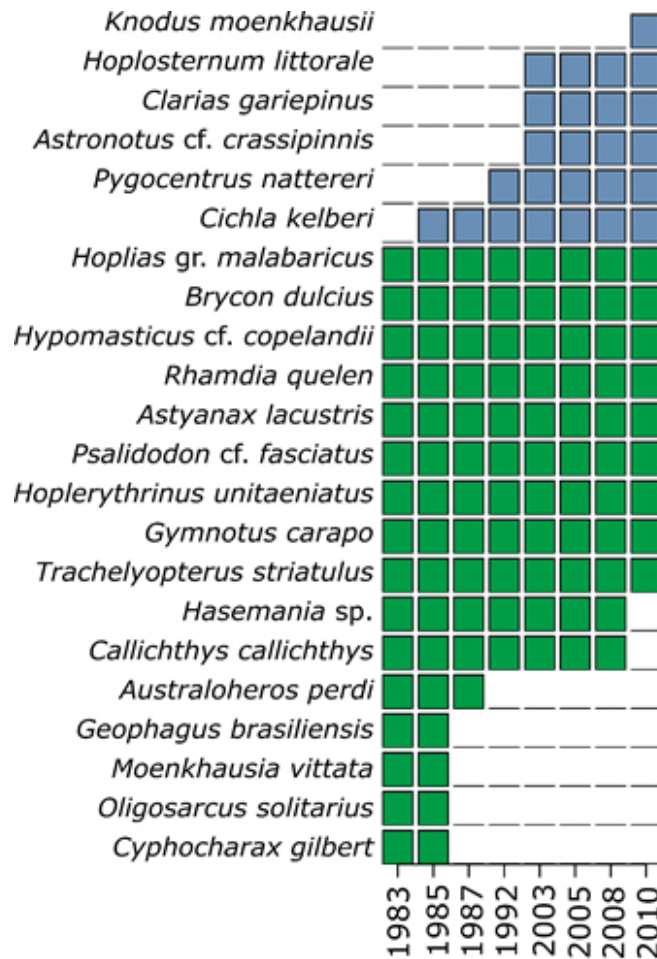
Morphological trait	Calculation	Ecological meaning	References
Oral-gape position (Ops)	Mo/Hd	Feeding method in the water column	Adapted from Sibbing, Nagelkerke (2000)
Eye size (Edst)	Ed/Hd	Prey detection	Adapted from Boyle, Horn (2006)
Eye position (Eps)	Eh/Hd	Vertical position in the water column	Gatz (1979)
Pectoral-fin position (PFps)	PFi/PFb	Use of pectoral fin for maneuverability	Dumay <i>et al.</i> (2004)
Pectoral-fin aspect ratio (PFar)	PFI <sup>2</sup> /PFs	Use of pectoral fin for propulsion	Adapted from Fulton <i>et al.</i> (2001)
Caudal-peduncle throttling (CPt)	CFd/CPd	Use of caudal fin for propulsion and/or direction	Webb (1984)
Caudal-fin aspect ratio (CFar)	CFd <sup>2</sup> /CFs	Caudal fin use for propulsion and/or direction	Webb (1984)
Fins surface ratio (Frt)	2 x PFs/CFs	Main type of propulsion between caudal and pectoral fins	Villéger <i>et al.</i> (2010)

To investigate the changes in fish diversity over the years for each scenario, we conducted an analysis of covariance (ANCOVA), which considers the differences between taxonomic and functional approaches, as well as the interaction between both factors (year × diversity approach). All analyses were carried out in the software R (R version 4.0.0; R Core Team, 2020). FRic was computed using the *multidimFD* (<http://villegger.sebastien.free.fr/Rscripts.html>), and ANCOVA was conducted using the *lm* (base package) and the *Anova* function (type III test; *car* package).

## RESULTS

Fish species composition of Carioca Lake changed over the sampling years, with the replacement of seven native (the saguiru *Cyphocharax gilbert* (Quoy & Gaimard, 1824), the lambari-bocarra *Oligosarcus solitarius*, the lambari-chatinha *Moenkhausia vittata*, the cará *Geophagus brasiliensis* (Quoy & Gaimard, 1824), the cará-verde *Australoheros perdi* Ottoni, Lezama, Triques, Fragoso–Moura, Lucas & Barbosa, 2011, the tamboatá *Callichthys callichthys* (Linnaeus, 1758) and the lambari *Hasemania* sp.) by six non-native species (*Cichla kelberi*, *Pygocentrus nattereri*, *Astronotus* cf. *crassipinnis*, *Clarias gariepinus*, *Hoplosternum littorale*, and *Knodus moenkhausii* (Eigenmann & Kennedy, 1903)) between 1983 and 2010 (Fig. 3). An updated list of the 22 species registered in Fragoso–Moura *et al.* (2016) is available in Tab. S2.

We did not detect changes in taxonomic or functional richness (FRic) over time when considering all species, native and non-native, of the fish assemblage (years:  $F_{1,12} = 2.13$ ,  $p = 0.17$ ; diversity approach:  $F_{1,12} = 0.06$ ,  $p = 0.81$ ; interaction:  $F_{1,12} = 1.33$ ,  $p = 0.27$ ; Fig. 4). On the other hand, when considering only the native ichthyofauna, both diversity indicators decreased (years:  $F_{1,12} = 20.12$ ,  $p < 0.001$ ; diversity approach:  $F_{1,12} = 0.72$ ,  $p = 0.41$ ; interaction:  $F_{1,12} = 4.49$ ,  $p = 0.06$ ; Fig. 4), firstly after the introduction of

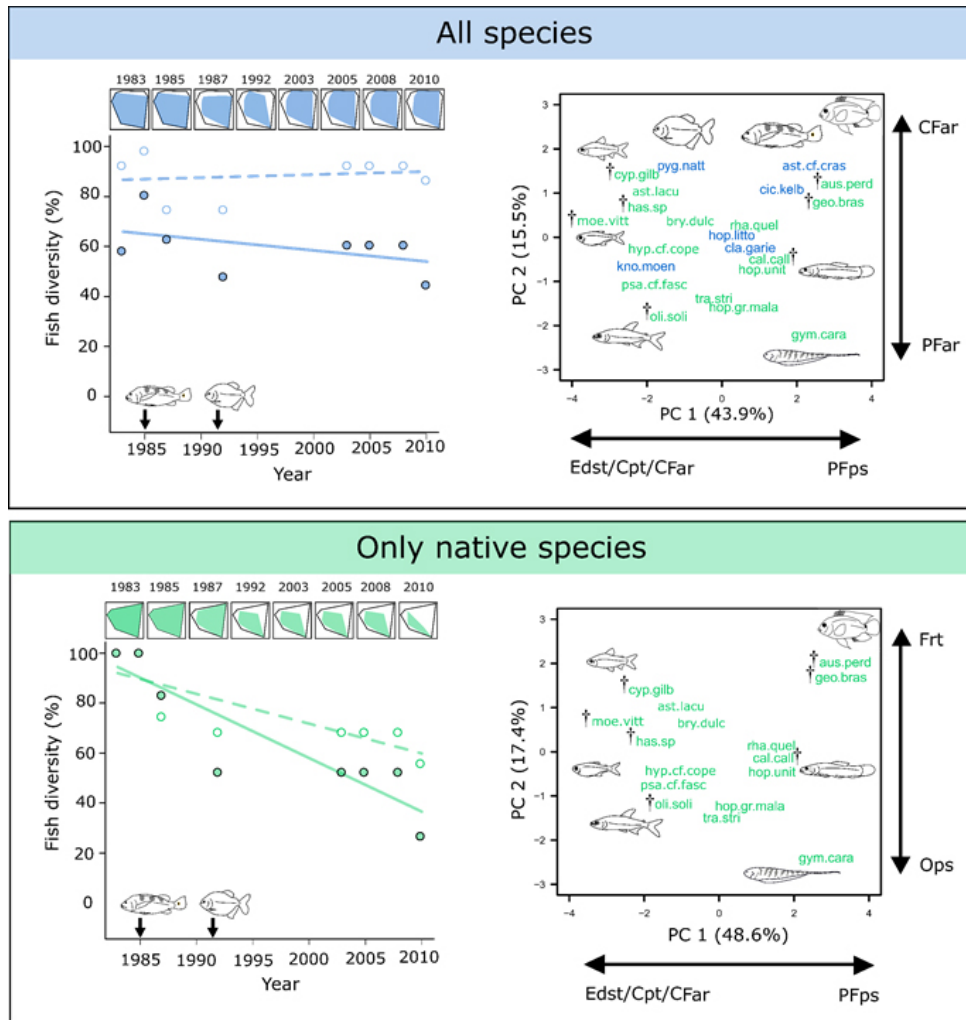


**FIGURE 3** | Compositional change of the ichthyofauna from Carioca Lake, Middle Rio Doce basin state of Minas Gerais, southeastern Brazil. Green and blue squares indicate, respectively, the presence of native and introduced species in each year.

*C. kelberi* (decay of 16.5% in FRic) and especially with the introduction of *P. nattereri*, in 1992 (decay of 47.3% in FRic). Overall, while the number of native species decreased to 56.3% (9 species in 2010 out of 16 species in 1983), FRic dropped down to 27.2% in relation to the pre-introductions condition (Fig. 4).

The morphological traits more negatively associated with PC1 were eye size (Edst), caudal-peduncle throating (Cpt) and caudal-fin aspect ratio (CFar) (Fig. 4; Tab. 2). Species with high values for these traits are visually oriented and predominantly use the water column due to their swimming capacity (Tab. 1). The loss of the species with these characteristics was the main responsible for the first FRic decay in 1987 (Fig. 4). Pectoral-fin position (PFps) was positively correlated with PC1, while fins surface ratio (Frt) and oral-gape position (Ops) were, respectively, the most positively and negatively correlated morphological traits with PC2 (Fig. 4; Tab. 2). These characteristics are found in species with good maneuverability in complex habitats and association with the bottom for feeding (Tab. 1), whose loss in the assemblage were responsible for the great FRic decay in 1992 (Fig. 4).





**FIGURE 4** | Temporal changes in species richness (dashed lines) and functional richness (FRic; continuous lines) of the ichthyofauna from Carioca Lake, Middle Rio Doce basin, state of Minas Gerais, considering two scenarios: “all species”, including native and non-native; and “only native species” (left figures). Plotted values expressed as a proportion to the maximum richness. The arrows represent the first records of the introduced piscivorous *Cichla kelberi* (in 1985) and *Pygocentrus nattereri* (in 1992) in the system. The upper plots represent the functional space (only two dimensions for simplify visualization), with polygons indicating the proportion filled by the set of species (FRic) in each year. Right figures illustrate the functional space showing the position of each species. Green and blue colors indicate, respectively, the native and introduced species, and crosses indicate native species extirpated from the lake. Codes at the ends of the arrows are the most important ecomorphological traits for each axis of the PCA (for functional trait and species codes, see Tab. 1 and Tab. S2).

**TABLE 2** | Correlation matrix between ecomorphological traits and each of the three axes of the PCAs representing the functional space of the two scenarios (“all species” and “only native”) of the fish assemblage from Carioca Lake, Middle Rio Doce basin. The most significant traits for each dimension are represented in bold.

Morphological traits	“All species”			“Only native”		
	PC1	PC2	PC3	PC1	PC2	PC3
Oral-gape position (Ops)	-0.38	-0.33	<b>0.73</b>	-0.57	<b>-0.54</b>	<b>0.50</b>
Eye size (Edst)	<b>-0.80</b>	0.01	0.17	<b>-0.87</b>	0.07	-0.28
Eye position (Eps)	0.50	0.07	0.42	0.34	-0.49	<b>-0.71</b>
Pectoral-fin position (PFps)	<b>0.83</b>	0.26	0.28	<b>0.84</b>	0.08	-0.20
Pectoral-fin aspect ratio (PFar)	-0.50	<b>-0.46</b>	<b>-0.49</b>	-0.42	-0.29	-0.31
Caudal-peduncle throttling (CPt)	<b>-0.77</b>	0.54	0.07	<b>-0.86</b>	0.31	-0.20
Caudal-fin aspect ratio (CFar)	<b>-0.78</b>	<b>0.60</b>	0.04	<b>-0.84</b>	0.40	-0.19
Fins surface ratio (Frt)	0.60	0.46	-0.32	0.58	<b>0.71</b>	0.01
<b>Variance explained (%)</b>	43.9	15.5	14.6	48.6	17.4	13.4

## DISCUSSION

Fish species introductions in the Middle Rio Doce basin have led to one of the most emblematic cases of biological invasion in Brazilian freshwater ecosystems, imperiling the aquatic biota even in protected areas. After compiling published studies and building a precious temporal dataset of the ichthyofauna from Carioca Lake, Fragoso-Moura *et al.* (2016) registered a significant decay in the number of native species. Over the last decades, many native fishes, including the endemic (and with the type locality inside PERD) *Australoheros perdi* and *Oligosarcus solitarius*, were no more captured soon after the detection of the non-native piscivorous *C. kelberi* and *P. nattereri*, which indicates that they became rare or extinct in the lake. By considering the functional diversity of this fish assemblage, we have now shown that the impacts of the biological invasion were even more severe than the loss of species itself. Relative to the condition found before the introductions, the current functional richness of the native ichthyofauna is more than 70% lower, a loss two times higher than its taxonomic counterpart. In other words, more than species, there is a drastic reduction in the range of functional traits related to forms of locomotion and use of habitat and food resources.

The erosion of functional richness of the native ichthyofauna occurred in sequential steps, a first one soon after the introduction of *C. kelberi* in 1985, with a decrease of ~16% in FRic, and a second just with the first record of *P. nattereri* in 1992, with an additional fall of 30%. This degradation profile is related to the position of the species in the ecomorphological space. Of the seven native species not registered in the system after the introductions, four are located at the edge of the space, which means the extirpation of highly specialized functions. Particularly the strongest second fall

can be explained by the sequential loss of the cichlids *Geophagus brasiliensis* and *A. perdi*, which hold unique sets of ecomorphological traits within the local assemblages. In the following years after that, new introductions were recorded and, after relative stability in FRic levels, the native species *Hasemanina* sp. and *C. callichthys* were not recorded in the last sampling event (2010). Particularly, the absence of *C. callichthys*, also a morphologically specialized species, caused a significant final decay in FRic of the native ichthyofauna. Among several factors, the impact of invasive species in natural environments is dependent upon local biotic characteristics, and systems with few native species tend to present higher vulnerability to invasion (Moyle, Light, 1996). The strong domination of the two predators at initial phases of invasion may have created a destabilized environment more conducive to the establishment of other introduced species. This can be seen as an empirical example of the invasive meltdown hypothesis, a process by which non-native species facilitate the invasion of each other through positive interspecific interactions (Simberloff, 2006).

The set of lost morphological traits is likely sensitive to predation. The first species lost have large eyes and high values of caudal-peduncle throttling and caudal-fin aspect ratio, characteristics of diurnal species (Boyle, Horn, 2006) and good swimming ability in open waters (Webb, 1984), feeding along the vertical column (e.g., *O. solitarius* and *M. vittata*) or closer to the lake bottom (e.g., *C. gilbert*). Although not positioned close to these species in the ecomorphological space, *Cichla kelberi* also has a diurnal habit and preys both in open waters or close to shelters (Chellappa *et al.*, 2003; Pelicice *et al.*, 2015). Species with more developed and upper-inserted pectoral fins (*G. brasiliensis* and later *A. perdi*) were also lost. These characteristics favor maneuverability (Villéger *et al.*, 2010) and allows the occupation of structured habitats, such as areas dominated by aquatic macrophytes and wood debris. This habitat type is frequently occupied by *P. nattereri*, which uses it as spawning sites, development of juveniles (Pauly, 1994), and as suitable shelters to ambush their preys (Sazima, Machado, 1990). Therefore, the sequence of species extirpation in Carioca Lake seems to follow a predictable relation between prey characteristics associated with the use of habitats and the different predation strategies applied by the two introduced piscivores.

Besides predation, the native ichthyofauna of Carioca Lake has probably been also affected by competitive interactions with introduced species. Studying the diet of *Hoplias* gr. *malabaricus*, Pompeu, Godinho (2001) observed a clear difference when comparing lakes (including Carioca Lake) with and without *C. kelberi* and *P. nattereri*, with high proportion of shrimps rather than fish in the diet when occurring in sympatry with the introduced piscivores. The authors suggested that this feeding plasticity may be allowing the maintenance of *Hoplias* gr. *malabaricus* in the system. On the other hand, *O. solitarius*, a species endemic of Rio Doce's lakes, disappeared from Carioca Lake just after the introduction of *C. kelberi*. It is one of the smallest piscivores of the region (Godinho, 1996), and perhaps it was disfavored by a combination of predation and competition with the invasive peacock bass. Finally, given their similar ecological demands, it is plausible that *Hasemanina* sp. and *C. callichthys* have been negatively affected by competition with, respectively, the small characin *Knodus moenkhausii* and the catfish *Hoplosternum littorale*, more recently introduced in the system. Although feasible, these are yet tentative interpretations to explain the absence of such native

species in Carioca Lake, given that testing competitive hypotheses in the field is operationally difficult (Jackson *et al.*, 2001). However, we believe this represents a vast avenue for further investigation on the role of interspecific interactions in the context of freshwater biological invasions.

Some native species still resist in this competitive and high predation-pressure environment. Taking a deeper look at the ecomorphological space, we can argue that this resistance can be in part associated with characteristics related to the use of habitats not dominated by the introduced piscivores. For instance, a great part of the ecomorphological space not suppressed over time is composed of species with small eyes positioned in the upper portion of the head and subterminal mouth. These traits generally favor benthic habits (Gatz, 1979), which make more difficult the predation by both *C. kelberi* and *P. nattereri*. Other traits not directly evaluated here may also be important in the context of antipredatory mechanisms. This is the case of rigid fin spines (*e.g.*, found in *Trachelyopterus striatulus* (Steindachner, 1877)), large body sizes (*e.g.*, *Hoplias gr. malabaricus*, *Hypomasticus cf. copelandii* (Steindachner, 1875), *Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829), *Rhamdia quelen* (Quoy & Gaimard, 1824), and *Brycon dulcis* Lima & Vieira, 2017), or cryptic coloration (*e.g.*, *Gymnotus carapo* Linnaeus, 1758) that helps in the camouflage of visually oriented predators (Keenleyside, 1979). Another set of traits that may also explain the maintenance of some native species is related to behavioral and life-history aspects, such as nocturnal habits (*e.g.*, *R. quelen*, *T. striatulus*, *G. carapo*), which minimize the chance of being captured by *C. kelberi* and *P. nattereri* (Nico, 1990; Sazima, Machado, 1990; Santos *et al.*, 2011), and parental care (*e.g.*, *H. gr. malabaricus* and *H. unitaeniatus*), which aids preventing predation of eggs, larvae and juveniles (Ota *et al.*, 2018).

Taking into account the whole ichthyofauna, considering both native and non-native species, there was no significant changes in functional richness over time. However, this does not mean that the new elements of the ichthyofauna fully compensate for the loss of the native ones. By visualizing the functional space (Fig. 4), we can note that the positions of some non-native fish, particularly *P. nattereri*, *C. kelberi* and *Astronotus cf. crassipinnis*, are at the extreme portions, contributing to the assemblage FRic. However, these areas were not all previously filled by native fishes. Therefore, the maintenance of FRic levels over time, even with the native species losses, indicates more a change in the functional structure than a maintenance of functions; *i.e.*, the functional roles promoted by the non-native are somewhat different from the ones promoted by the extirpated natives. Such a change can lead to significant impacts to community or even to ecosystem properties. For instance, although positioned relatively close to *C. kelberi* and *A. cf. crassipinnis* in the morpho-functional space, the natives *G. brasiliensis* and *A. perdi* are omnivorous-benthophagous feeders, having thus quite different roles to the trophic structure of the ichthyofauna compared to these non-native piscivores. The extirpated native detritivore *C. gilbert* stirs the sediment when feeding at the lake bottom (see Sazima, Caramaschi, 1989) for a detailed description of this behavior in related curimatids). Studies on sediment-feeding behavior have already revealed significant effects of fish on ecosystem functioning by modulating carbon flux, primary production and respiration in aquatic ecosystems (*e.g.*, Flecker, 1996; Taylor *et al.*, 2006). Another example of potential loss of a unique and specialized functional role is the extirpation of *O. solitarius*. Although also being a piscivore, *O. solitarius* is morphologically very

different from *C. kelberi* and *P. nattereri* (opposing extremes in the functional space, Fig. 4), possessing higher caudal peduncle throattling, bigger eyes and longer pectoral fins positioned at the lower portion of body. These characteristics favor a high visual accuracy to detect preys in the water column and a long-distance swimming ability (Gatz, 1979; Winemiller, 1991), likely enabling the consumption of different resources and transportation of matter and energy across broader areas in the lake.

This study provided empirical evidence that the functional richness was more sensitive than species richness in response to non-native fish invasions in Carioca Lake. However, we are aware that there are still important gaps to be filled. Firstly, we used only ecomorphological traits that, although widely used and recognized as a suitable proxy to infer some functional aspects, do not inform about several other niche dimensions (Teresa *et al.*, 2021). For example, life-history aspects, such as fecundity and spawning site, may clarify issues related to the resilience of native populations against the pressures promoted by introduced species. Accurate diet information would contribute to our interpretations about the degree in which non-native species compensate the absence of extirpated native for the structure and dynamics of local food webs. Another important limitation is the differences in sampling efforts among the studies used in the temporal series, which led us i) to assume that native species recorded only in the last studies were already present before, and ii) to disregard species abundance data. Precisely knowing the occurrence and abundance for each species in each sampling event would allow a more realistic picture of the biodiversity changes following introductions. This clearly illustrates the need for long-term ecological research programs (LTERs), which unfortunately is receiving much less attention and financial support in recent times in Brazil. Despite the limitations, we consider that this research represents an important first step for understanding the changes in Carioca Lake's ichthyofauna functional structure.

With the purpose of local and regional biodiversity conservation it is expected that management actions, for instance, population reduction by allowing sport fishing with selective removal of non-native fish (Britton *et al.*, 2011; Coggins *et al.*, 2011), will be taken in PERD and its surroundings for an urgent control against new introductions, considering the impacts that have occurred and those predicted in the medium and long term. Studies on behavior, feeding ecology, reproduction, as well as the impacts of other non-native species in the region are essential to create subsidies that enable the conservation of fish species that still resist. Since most of the introductions were intentional, environmental education activities that raise awareness among the local population and visitors are of great importance for conservation efforts to become effective and to avoid future introductions (Lima *et al.*, 2010).

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**Francisco Antônio Rodrigues Barbosa:** Funding acquisition, Investigation, Methodology, Project administration, Validation, Visualization, Writing–review and editing.

**Rafael Pereira Leitão:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing–original draft, Writing–review and editing.

## Neotropical Ichthyology



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