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Changes in ecosystem functions generated by fish populations after the introduction of a non-native predator (*Cichla kelberi*) (Perciformes: Cichlidae)

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The introduction of non-native predators is a matter of great concern, but their impacts on ecosystem functions remain poorly understood. We investigated how changes in fish diversity following the invasion of *Cichla kelberi* affected ecosystem functions generated by fish populations. Fish assemblages were sampled in macrophyte patches in a Neotropical impoundment over a 5-year period, before and after the introduction of the predator. We assigned seven ecosystem functions (26 trait-states) to each fish species, and examined how these functions behaved after the invasion. We collected 577 fish belonging to 25 species. Species richness, fish biomass and main species declined significantly over periods. The biomass of ecosystem functions changed significantly over time, and most trait-states declined. Few trait-states were lost, but all functions had at least one trait-state reduced by more than 85%. A null model analysis showed that changes in functions were not driven by species identities, while species richness correlated positively with total biomass and with most functions, suggesting that the loss of taxa and biomass drove observed changes in ecosystem functions. Our study provided evidence that community disassembly associated with the invasion of *C. kelberi* translated to the decline of several ecosystem functions, affecting energy mobilization and transference.

Keywords: Biological invasion, Energy transference, Fish diversity, Reservoir.

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A introdução de predadores não-nativos tem gerado grande preocupação, mas seus impactos sobre a geração de funções ecossistêmicas permanecem pouco investigados. O presente estudo investigou como mudanças na diversidade de peixes, associadas com a invasão de *Cichla kelberi*, afetaram funções ecossistêmicas geradas por populações de peixes. As assembleias de peixes foram amostradas em bancos de macrófitas em um grande reservatório Neotropical durante um período de cinco anos, antes e depois da introdução do predador. Um conjunto de funções ecossistêmicas (26 *trait-states*) foi atribuído a cada espécie de peixe, e examinamos como as funções se comportaram depois da invasão. Foram coletados 577 peixes pertencentes a 25 espécies. Registramos declínio significativo da riqueza de espécies, biomassa total e biomassa das principais espécies ao longo dos períodos. A biomassa das funções ecossistêmicas mudou significativamente ao longo do tempo, e a maioria dos *trait-states* declinou. Poucos *trait-states* foram perdidos, mas todas as funções tiveram pelo menos um *trait-state* reduzido em mais de 85%. Uma análise de modelos nulos mostrou que as mudanças nas funções não foram impulsionadas pela identidade das espécies, enquanto que a riqueza de espécies correlacionou positivamente com a biomassa total e com a maioria das funções, sugerindo que a perda de espécies e biomassa impulsionou as mudanças observadas nas funções ecossistêmicas. Nosso estudo apresenta evidências de que a desestruturação da comunidade, associada com a invasão de *C. kelberi*, se traduziu no declínio de várias funções ecossistêmicas, afetando a mobilização e transferência de energia.

Palavras-chave: Diversidade de peixes, Invasão biológica, Reservatório, Transferência de energia.

INTRODUCTION

Ecosystem functions are ecological, biological and physical/chemical processes that maintain ecosystem functioning (Naeem *et al*., 1999; Hooper *et al*., 2005; Naeem *et al*., 2012). They include, for example, energy transfer, pollination, decomposition, primary production, biomass accumulation, population control, nutrient cycling, and climate regulation, among many others. Organisms generate or affect the performance of these functions through a set of functional traits, often defined as effect traits (Lavorel, Garnier, 2002; Cadotte *et al*., 2011; Raffard *et al*., 2017), *i.e*., a set of phenotypic attributes linked to trophic relationships, metabolic processes, behavioral aspects, and interactions with the environment that affect ecosystem functioning. Much recent research effort has been devoted to understanding how biodiversity, and especially biodiversity loss, affects ecosystem functioning. Although results can vary depending on ecological context and spatial and temporal scales, in general, there is compelling evidence that species and functional diversity of local communities strongly affect ecosystem functioning (Cadotte *et al*., 2011; Cardinale *et al*., 2012; Hooper *et al*., 2012; Naeem *et al*., 2012; Balvanera *et al*., 2014; Tilman *et al*., 2014; Daam *et al*., 2019).

In aquatic and riparian ecosystems, fishes contribute to various ecosystem functions through the assimilation of energy and matter from different sources, the production, accumulation and transfer of biomass, dispersal of seeds, population control, and nutrient cycling, among others (Holmlund, Hammer, 1999; Correa *et al*., 2007; Hoeinghaus *et al*., 2009; Flecker *et al*., 2010; Pendleton *et al*., 2014). However, fish diversity is being eroded in freshwater ecosystems worldwide, with anthropogenic impacts and introduction of non-native fishes acting as major drivers of biodiversity loss. In general, invasive fishes affect ecological interactions, habitat structure and biogeochemical cycles, causing the loss of taxonomic and functional diversity in natural communities (Cucherousset, Olden, 2011). In the Neotropics, the continuous invasion of multiple species has impaired the structure and functioning of freshwater ecosystems (Vitule *et al*., 2009), induced biotic homogenization (Toussaint *et al*., 2016; Bezerra *et al*., 2019) and threatened fish diversity (Pelicice *et al*., 2017). The introduction of predatory fish is a matter of great concern, as they reduce or extirpate local populations, permanently changing the structure of fish assemblages (Eby *et al*., 2006; Sharpe *et al*., 2017; Marshall, 2018). However, the understanding of how human activities impair ecosystem functions generated by fish populations remains incipient (Holmlund, Hammer, 1999; Nash *et al*., 2013), including the impacts caused by non-native predators. Invasive predators are expected to induce strong effects on ecosystem functions due to strong demographic effects on prey populations.

The introduction of *Cichla* species, also known as peacock bass in English or tucunaré in Portuguese, provides a well-known system for assessing invasive predator effects on ecosystem functioning. Native to the Amazon basin (Kullander, Ferreira, 2006), these predators are appreciated by sport fishing and aquaculture activities (Britton, Orsi, 2012), which led to the introduction of several species to different freshwater ecosystems around the world (Ortega *et al*., 2015; Sastraprawira *et al*., 2020*). Cichla* are voracious predators that consume small fish and invertebrates (Bacheler *et al*., 2004; Fugi *et al*., 2008; Mendonça *et al*., 2018), with strong potential to disturb the invaded community, particularly in reservoirs (Zaret, Paine, 1973; Latini, Petrere Jr., 2004; Pelicice, Agostinho, 2009; Sharpe *et al*., 2017; Carvalho *et al*., 2021; Franco *et al*., 2021). However, their effects on ecosystem functioning remain poorly known, with the classic work by Zaret, Paine (1973) the only study reporting consequences on ecosystem functions and services. This limitation is not restricted to the invasion of *Cichla*, since studies on biological invasions have devoted more attention to changes in taxonomic diversity (Olden *et al*., 2018), possibly due to the difficulty of measuring ecosystem functions in the field.

In this context, the present study investigated how the invasion of *Cichla kelberi* Kullander & Ferreira, 2006 affected ecosystem functions generated by fish assemblages associated with aquatic macrophytes in a tropical reservoir (Rosana Reservoir, Paranapanema River, Brazil). Previous studies have shown drastic changes in taxonomic diversity after the introduction (Pelicice, Agostinho, 2009), and provided evidence that the invader caused these changes (Pelicice *et al*., 2015). No study, however, has investigated how the loss of biodiversity affected ecosystem functioning, and this study examined temporal changes in the composition and performance of ecosystem functions before and after the introduction of the predator. Adapting methodology established by functional ecology, *i.e*., assignment of functional traits (*e.g*., Violle *et al*., 2007; Mouillot *et al*., 2012), we assigned a set of ecosystem functions to each species. Specifically, we classified species into seven functions (26 trait-states) related to the transfer of energy, matter and genetic information in the system. The study investigated the hypothesis that changes in fish diversity after the invasion of *C. kelberi* affected the generation of ecosystem functions, causing the erosion of functions due to strong demographic effects (*i.e.*, population decline) and the loss of some prey species. Furthermore, the approach developed for this study serves as a model for initial investigations of effects of changing biodiversity on ecosystem functioning in poorly studied regions where traditional functional trait approaches are not suitable due to data limitations.

MATERIAL AND METHODS

Study area. Rosana Reservoir is the last of a series of reservoirs that regulates the discharge of the Paranapanema River, one of the main tributaries of the Upper Paraná River. The dam was closed in 1986 for hydroelectric production and created a shallow reservoir with 276 km^2 of surface area. Aquatic macrophytes, especially *Egeria densa* and *E. najas*, readily colonized shallow areas (Pelicice *et al*., 2005). Currently, 65 fish species are recorded in the reservoir, of which 23 are non-native (Pelicice *et al*., 2018).

The first record of *C. kelberi* (initially identified as *C. monoculus*) in the basin occurred in 2001 in Capivara Reservoir, which is located approximately 150 km upstream of Rosana Reservoir (Orsi, Britton, 2014). The first record in Rosana Reservoir occurred in 2005 (Pelicice, Agostinho, 2009), but according to local fishermen, the species had been captured in the reservoir since 2004. Dispersal from Capivara Reservoir, or even new clandestine fish releases, are possible causes for the introduction of *C. kelberi* in Rosana Reservoir. Currently, the species has invaded almost all of the reservoirs of the Paranapanema River (Pelicice *et al*., 2018). Previous studies analyzed the structure of fish assemblages in Rosana Reservoir and their response to the invasion of *C. kelberi* (Pelicice, Agostinho, 2009; Ferrareze, Nogueira, 2015; Pelicice *et al*., 2015). These studies reported significant changes in abundance, richness and composition, mainly of small fishes associated with aquatic macrophytes. Pelicice *et al.* (2015), in particular, provided evidence that the loss of fish diversity in macrophyte patches was associated with the invasion of *C. kelberi*.

Fish sampling. Fish assemblages were monitored in an arm of the transition zone of Rosana Reservoir (22º34’07”S 52º33’34”W), upstream from Euclides da Cunha Paulista district, São Paulo State. The arm occupies approximately 40 ha, with shores massively colonized by *E. densa*. For more information about the study area and the fish fauna, see Pelicice *et al.* (2005). Sampling was carried out over six periods between 2003 and 2007 during warm months (> 30 ºC). The first sampling period occurred in the summer of 2003, before *C. kelberi* invaded the reservoir (hereafter referred to as ‘Pre’). Five other sampling periods started one year after the introduction of *C. kelberi*, and occurred during the summer/autumn and spring seasons between 2005 and 2007 (hereafter referred to as ‘Post-1’ through ‘Post-5’). In total, we collected 123 samples with approximately 20 samples per period (see Tab. **S1**).

Fish were collected in mixed patches of *E. densa* and *E. najas*, distributed along both shores of the study area. Sampling methodology consisted of a 1 m^2 throw trap, with collections occurring during daylight hours (07:00–18:00). The trap was comprised by a rectangular aluminum frame (1.0 x 1.0 x 1.5 m) with 0.5 cm mesh covering all sides except for the superior and inferior ends. A boat was silently positioned above *Egeria* patches and used as a platform for trap deployment. Immediately following boat positioning, the trap was quickly thrown into the water and pressed to the bottom. Macrophytes were then removed from the trap with a metal fork and were washed and weighed in the field (fresh mass, g). Next, fish inside the trap were collected with a sieve (0.90 x 1.5 m) and an aluminum dip-net (49 x 49 cm), both with 0.5 cm mesh. The sieve was handled until three procedures captured no fish. The dip-net was hauled inside the trap area until 10 successive hauls resulted in no additional capture. All collected individuals were preserved in 10% formalin and taken to the laboratory, where they were identified, counted and weighted (g). Species identification was based on Graça, Pavanelli (2007) and Ota *et al.* (2018). Voucher specimens were deposited in the Coleção Ictiológica do Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura (Nupélia), Universidade Estadual de Maringá, Maringá (see Tab. **S2**).

Categorization of ecosystem functions. Linking biodiversity to ecosystem functioning is often aided by functional approaches that quantify phenotypic traits of species related to various aspects of performance that mediate ecosystem processes (Naeem *et al*., 1999; Lavorel, Garnier, 2002; Violle *et al*., 2007; Raffard *et al*., 2017). A significant limiting factor for functional traits-based approaches is the quantification or availability of relevant traits, especially for specious communities in comparatively poorly studied regions such as the Neotropics (Vitule *et al*., 2017). For this reason, we developed a new method for initial investigations of effects of changing biodiversity on ecosystem functioning that is particularly suitable for regions where traditional functional trait approaches are inhibited due to the lack of and/or infeasibility of generating traditional functional traits data. The method consists of directly assigning ecosystem functions performed by each species (trait-states), with the magnitude of performance of each function in a community determined by relative biomass of each species and summed across all species contributing to a particular function. Trait-state assignments are fixed, meaning that spatial, temporal and intra-specific variations were not considered (*e.g*., Isbell *et al*., 2011; Raffard *et al*., 2017). We used biomass as a measure of functional intensity (*i.e*., performance), with the assumption that greater biomass implies greater functioning. Although the relationship between biomass and ecosystem functioning is variable (*e.g*., terHost, Munguia, 2008), some studies show positive associations (Barnes *et al*., 2016; Vargas-Larreta *et al*., 2021).

Based on previous works, particularly Holmlund, Hammer (1999), Groot *et al.* (2002), Eby *et al.* (2006), Flecker *et al.* (2010), and Bauer, Hoye (2014), we defined seven ecosystem functions described by 26 trait-states related to the transfer of energy, matter and genetic information in the system (Tab. 1). Trait-states were assigned to each species based on information available in the literature. The Energy Source ecosystem function was quantified based on species' diet, primarily following data published by Casatti *et al.* (2003) and Pelicice, Agostinho (2006). We considered the proportion of resources consumed grouped into classes: algae, plant, invertebrate, vertebrate, organic material/ detritus. Other functions were assigned in terms of presence (1) or absence (0), and indicate whether the species directly contributes to the ecosystem function or not (see Tab. **S2**).

TABLE 1 | Ecosystem functions generated by fish populations considered in the present study. We defined a number of trait-states to describe each function, which were then assigned to each fish species.

Ecosystem function	Trait-states	Description
Energy source	Algae Vegetal Invertebrates Vertebrates Organic matter/detritus	Function related to the components of the system (sources) from which fishes mobilize energy, matter and nutrients.
Habitat	Terrestrial Bottom Column Littoral	Function related to the environment where fishes mobilize energy.
Regional flow (migration)	Prey Herbivory Predator Genetic exchange	Function related to the transference of energy, matter or genetic information between distant habitats, performed by migratory animals. These animals may feed during migration, or become prey, establishing energy links between habitats. The function refers to the delivery (prey) and mobilization (herbivory, predation) of energy between habitats.
Regional flow (local)	Aquatic prey Predator Terrestrial prey	Function related to the transference of energy and matter between distant habitats, performed by local animals. Animals residing in a given location may interact with passengers (as prey or predators), establishing energy links between habitats. In this case, the function refers to the delivery (prey) or mobilization (predation) of energy between the resident and the passenger.
Plant Disperser	Propagule disperser	Function related to the dispersal of seeds, fruits or propagules.
Ecosystem Engineering	Bioturbation/Cycling Predation Herbivory	Function related to the control of physical-chemical conditions of the environment via trophic, behavioral and metabolic relationships, which affect the availability of nutrients (bottom-up control). The function is also related to the control of lower trophic levels by high consumption rates (top-down control).
Services	Food Sport fishing Bait Ornamental Aquaculture	Ecosystem services (provisioning and cultural) generated by fish species.

Data analysis. We used generalized linear models (GLM) to test whether species richness, total biomass, biomass of dominant species (the nine most abundant species, including *C. kelberi*) and the biomass of each trait-state differed among periods (Pre against Post-1, 2, 3, 4 and 5). We selected Poisson and Gamma models with a log link function to account for overdispersion in discrete (*e.g.*, species richness) and continuous data (all other variables), respectively. When models were significant, we performed a post-hoc linear contrast between Pre and each Post-period. In order to assess the magnitude of variation, we calculated the "loss" or "gain" in biomass for each trait-state calculated as the percent difference (decline or increase) between mean biomass values in the first (Pre) and last (Post-5) periods. Trait-states registered in Pre but absent in Post-5 were considered as lost, while trait-states absent in Pre but registered in Post-5 were considered as gained.

Ecological null modeling was used to test whether the observed ecosystem functions were different than expected based on chance given the number of species and relative biomass in the assemblages. This analysis distinguishes whether the pattern of change in estimated trait-states is due to species richness and biomass alone or whether the identities of species plays an important role in determining ecosystem functioning. This analysis controls for the 'sampling effect' (*i.e.*, higher ecosystem functioning with greater diversity due to the likelihood of including a species that strongly contributes to ecosystem functioning; Huston, 1997) and species identities, which can have significant impacts on ecosystem function regardless of biomass (*e.g.*, rare species that contribute strongly to ecosystem functioning; Pendleton *et al.*, 2014). Species richness and the biomass distribution were held constant for each sample and null assemblages were generated by randomly assigning species identities (*i.e.*, suite of trait values) for each species in an assemblage. We ran 1,000 permutations for each sample in each time-period, and trait-states were calculated for each random assemblage based on the species identity (*i.e.*, trait values) assigned to each biomass in the sample. For each trait-state, the mean of observed values was compared with the null distribution, and p-values were calculated as the probability that the null was as or more extreme than the observed values (*i.e.*, direct null hypothesis test; Veech, 2012).

We also evaluated the decay of assemblage similarity over time, considering the composition of species and trait-states, and the relationship between taxonomic diversity (species richness) and the diversity of ecosystem functioning. Composition similarity (Bray-Curtis distance, biomass-based) was compared between each Post period and the Pre period. Spearman's non-parametric correlation was used to assess relationships between species richness and (i) total biomass, (ii) functional richness, quantified as the number of ecosystem functions performed by an assemblage, and (iii) functional intensity, quantified as biomass. For these analyses, samples were combined within periods and trait-states were combined within their respective ecosystem function in order to represent the overall composition of species and ecosystem functions in each period.

Analyses were performed using Statistica 7.1 (Statsoft, 2005), Past 2.17 (Hammer *et al.*, 2001) and R 2.13.1 (R Development Core Team, 2011). GLMs were performed using the *glm* function from the *stat* package, and post-hoc comparisons were conducted using the *emmeans* package (Lenth, 2018). The inference of statistical significance followed Dushoff *et al.* (2019).

RESULTS

Assemblage structure and populations. In total across all sampling events, we collected 577 individuals belonging to 25 species (see Tab. **S2**). In the period that preceded the introduction of *C. kelberi* (Pre), we collected 256 individuals representing 17 species, with a total biomass of 395.68 g. After the introduction (Post-1 to 5), we captured an average of 321 individuals of 21 species, with an average biomass of 681.28 g. There was a progressive and statistically clear reduction in species richness (Fig. 1A) and total biomass (Fig. 1B) over the periods (Tab. 2). Considering the most abundant species, the majority showed statistically clear changes in biomass (Tab. 2). Some showed oscillatory trends, such as *Roeboides descalvadensis*, *Metynnis lippincottianus*, and *C. kelberi*, but the majority declined progressively (Fig. 2). Some species were extirpated, such as *Hemigrammus marginatus*, *R. descalvadensis*, *Serrasalmus marginatus*, *Serrapinnus notomelas*, *Eigenmannia trilineata*, and *Hyphessobrycon eques* (Fig. 2).

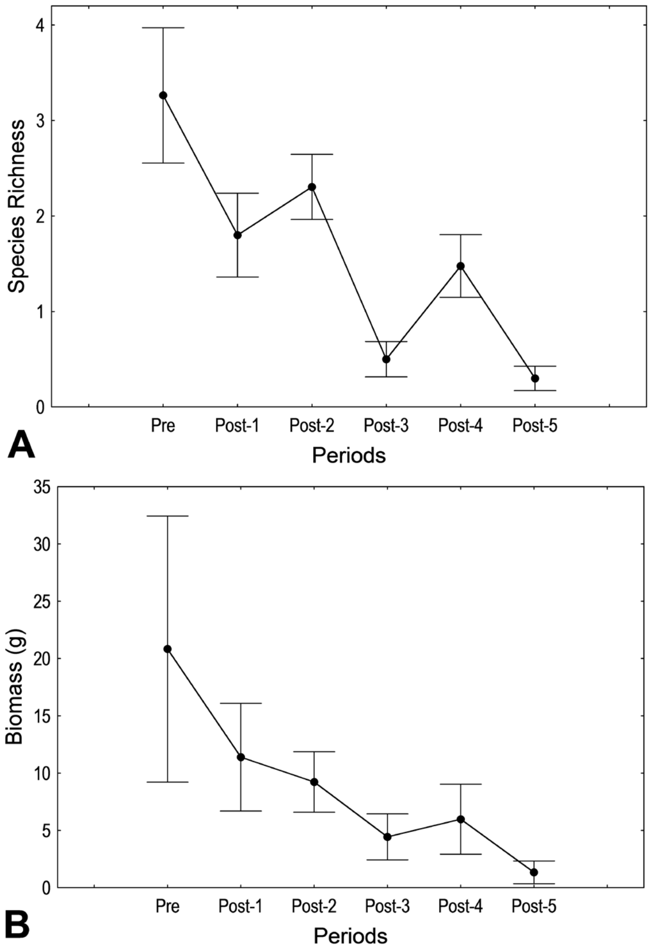

FIGURE 1 | Species richness (**A**) and total biomass (**B**) in fish assemblages associated with macrophyte beds in Rosana Reservoir, before (Pre) and after (Post 1 to 5) the introduction of *Cichla kelberi*. Mean ± standard error.

TABLE 2 | GLM results contrasting Pre and Post periods, considering the structure of fish assemblages (species richness, total biomass), main species and ecosystem functions (trait-states). A post-hoc linear test contrasted the Pre period with each Post-period (p values).

	Post-1	Post-2	Post-3	Post-4	Post-5	DF	Deviance	p
Assemblage structure								
Species richness	0.052	0.427	<0.001	0.004	<0.001	5	84.77	<0.001
Total biomass	0.986	0.998	0.344	0.807	0.003	5	34.72	0.008
Main species								
Hemigrammus marginatus	<0.001	0.014	<0.001	<0.001	<0.001	5	76.04	<0.001
Metynnis lippincottianus	0.998	0.671	0.946	0.997	0.762	5	44.38	0.133
Roeboides descalvadensis	0.007	0.361	<0.001	0.9839	<0.001	5	167.65	<0.001
Serrasalmus marginatus	1.000	0.993	0.922	0.993	0.001	5	76.04	0.002
Serrapinnus notomelas	<0.001	0.002	<0.001	0.0026	<0.001	5	146.68	<0.001
Satanoperca pappaterra	1.000	1.000	0.968	0.239	0.741	5	45.41	0.243
Cichla kelberi	0.009	0.818	0.002	1.000	0.428	5	141.87	<0.001
Eigenmannia trilineata	0.992	<0.001	<0.001	<0.001	<0.001	5	248.47	<0.001
Hyphessobrycon eques	<0.001	<0.001	<0.001	<0.001	<0.001	5	276.11	<0.001

➡

TABLE 2 | (Continued)

	Post-1	Post-2	Post-3	Post-4	Post-5	DF	Deviance	p
Ecosystem functions **Energy source**								
Algae	0.993	0.695	0.096	0.161	0.021	5	35.72	0.009
Plants	1.000	0.995	0.323	0.037	0.009	5	39.57	0.001
Invertebrates	0.859	0.992	0.221	0.848	0.003	5	38.32	0.009
Vertebrates	1.000	1.000	0.999	0.998	0.044	5	22.29	0.061
Organic matter and detritus	0.994	0.984	1.000	0.911	0.187	5	33.69	0.050
Habitat								
Terrestrial	0.990	0.992	0.161	0.965	<0.001	5	119.22	0.001
Bottom	1.000	0.973	0.921	0.973	0.232	5	21.46	0.254
Water column	0.991	1.000	1.000	0.858	0.893	5	10.83	0.785
Littoral	0.986	0.998	0.358	0.711	0.003	5	35.06	0.009
Regional flow (migration)								
Prey	0.943	0.999	1.000	0.997	1.000	5	18.23	0.782
Herbivory	0.699	0.318	1.000	1.000	0.984	5	68.28	0.036
Predator	0.097	0.446	0.097	0.090	0.097	5	140.65	<0.001
Genetic exchange	0.943	0.999	1.000	0.997	1.000	5	18.23	0.782
Regional flow (local)								
Aquatic prey	0.874	0.969	0.046	0.460	0.012	5	44.86	0.009
Predator	0.982	0.727	0.998	0.991	0.037	5	56.33	0.006
Terrestrial prey	0.872	1.000	0.010	0.314	0.001	5	88.93	<0.001
Plant Disperser								
Propagule disperser	0.774	0.987	0.053	0.163	0.013	5	43.41	0.004
Ecosystem Engineering								
Bioturbation/Cycling	1.000	1.000	0.884	0.122	0.526	5	56.86	0.089
Predator	0.022	0.867	0.005	0.935	0.528	5	117.66	0.002
Herbivory	1.000	0.678	0.947	0.997	0.768	5	44.74	0.136
Services								
Food	0.942	0.974	1.000	0.842	0.752	5	22.42	0.110
Sport fishing	0.022	0.867	0.005	0.935	0.528	5	117.66	0.002
Bait	0.999	0.809	0.000	0.799	0.000	5	174.84	<0.001
Ornamental	0.871	0.991	0.311	0.659	0.007	5	33.13	0.020
Aquaculture	0.873	0.765	0.607	1.000	0.979	5	28.39	0.427

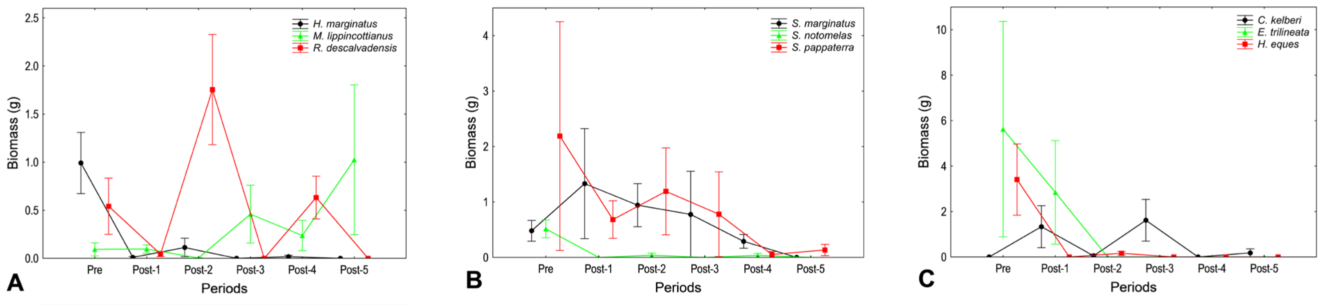

FIGURE 2 | Biomass of the most abundant fish species associated with macrophyte beds in Rosana Reservoir, before (Pre) and after (Post 1 to 5) the introduction of *Cichla kelberi*. Mean ± standard error. **A.** *Hemigrammus marginatus*, *Metynnis lippincottianus*, *Roeboides descalvadensis*; **B.** *Serrasalmus marginatus*, *Serrapinnus notomelas*, *Satanoperca pappaterra*; **C.** *Cichla kelberi*, *Eigenmannia trilineata*, and *Hyphessobrycon eques*.

Ecosystem functioning. We recorded statistically clear changes in the intensity of ecosystem functioning over time (Tab. 2). With the exception of the functions Regional Flow (migration) and Ecosystem Engineering, most trait-states lost biomass over time (Fig. 3A–G). For the ecosystem functions Energy Source, Habitat, Regional Flow (local), Plant Disperser and Services, most or all trait-states declined (Tab. 2).

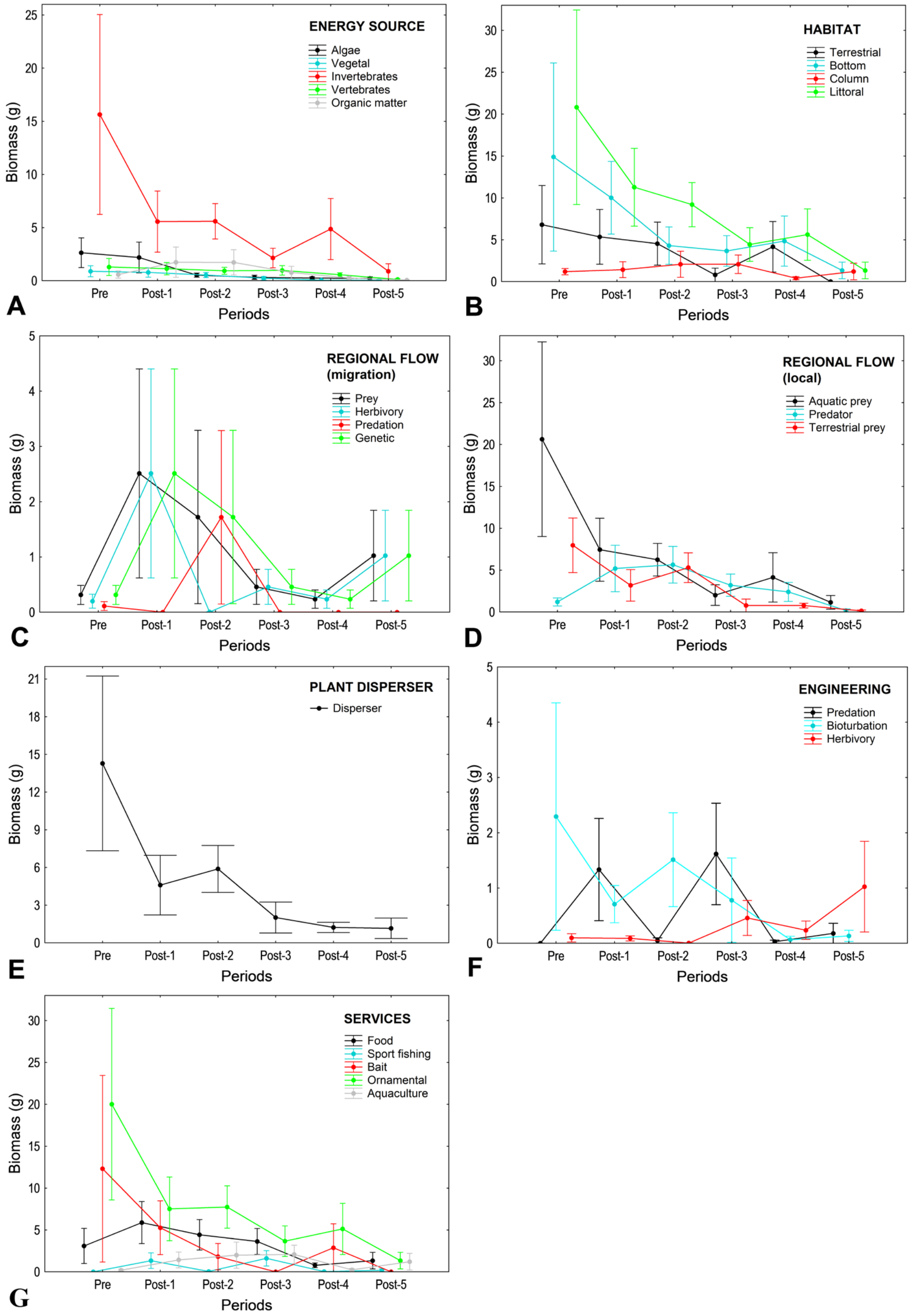

FIGURE 3 | Ecosystem functions generated by fish populations associated with macrophyte beds in Rosana Reservoir, before (Pre) and after (Post 1 to 5) the introduction of *Cichla kelberi*. Mean ± standard error. Ecosystem functions: **A.** Energy Source; **B.** Habitat; **C.** Regional Flow (migration); **D.** Regional Flow (local); **E.** Plant Disperser; **F.** Engineering; **G.** Services.

No ecosystem function was totally lost, but all functions had at least one trait-state reduced by more than 85% of the original intensity (Tab. 3). All trait-states of the Energy Source function declined by more than 90%. The Regional Flow (migration) function lost the *Predator* trait-state, but *Prey* and *Genetic Exchange* increased by more than 200%, while *Herbivory* increased by more than 400%. The Ecosystem Engineering function declined by more than 94% in the *Bioturbation/Cycling* trait-state, but *Herbivory* experienced a 900% increase. The Services function lost the *Bait* trait-state, but *Aquaculture* increased by more than 500% (Tab. 3).

Results from null modeling indicate that in almost all cases (trait-states in different periods) the observed intensity of ecosystem functioning in a time period was not different from expected based on the randomly generated distribution (see Fig. **S3**). In general, this indicates that the observed changes in the intensity of ecosystem functions were driven by the loss of taxa and biomass, not changes in species identities *per se*.

TABLE 3 | Increasing (positive values) and decreasing (negative values) trends in the intensity of ecosystem functions (trait-states) generated by fish populations, calculated from the variation in fish biomass between the first (Pre) and last (Post-5) periods. "+" = function added, absent in Pre but present in Post; "-" = function lost, present in Pre but absent in Post-5.

Ecosystem functions	%
Energy source	
Algae	-91.5
Plants	-94.2
Invertebrates	-94.3
Vertebrates	-90.9
Organic matter and detritus	-90.7
Habitat	
Terrestrial	-
Benthic	-91
Water column	0.6
Littoral	-93.6
Regional Flow (migration)	
Prey	209
Herbivory	409.8
Predator	-
Genetic exchange	226.2
Regional Flow (local)	
Aquatic prey	-94.4
Predator	-85.1
Terrestrial prey	-98.3
Plant Disperser	
Propagule disperser	-91.9
Ecosystem Engineering	
Bioturbation/Cycling	-94.1
Predator	+
Herbivory	936.5
Services	
Food	-56.6
Sport fishing	+
Bait	-
Ornamental	-93.3
Aquaculture	504.3

Taxonomic and functional similarity (based on biomass) progressively declined over time (Fig. 4). Taxonomic similarity showed lower values, and approached zero in the last period. Species richness correlated positively with total biomass (Fig. 5A), but not with the richness of ecosystem functions (Fig. 5B). Species richness was also positively correlated with the intensity (biomass) of the Energy Source, Habitat, Regional Flow (Local), Plant Disperser, and Services functions (Fig. 6A–G).

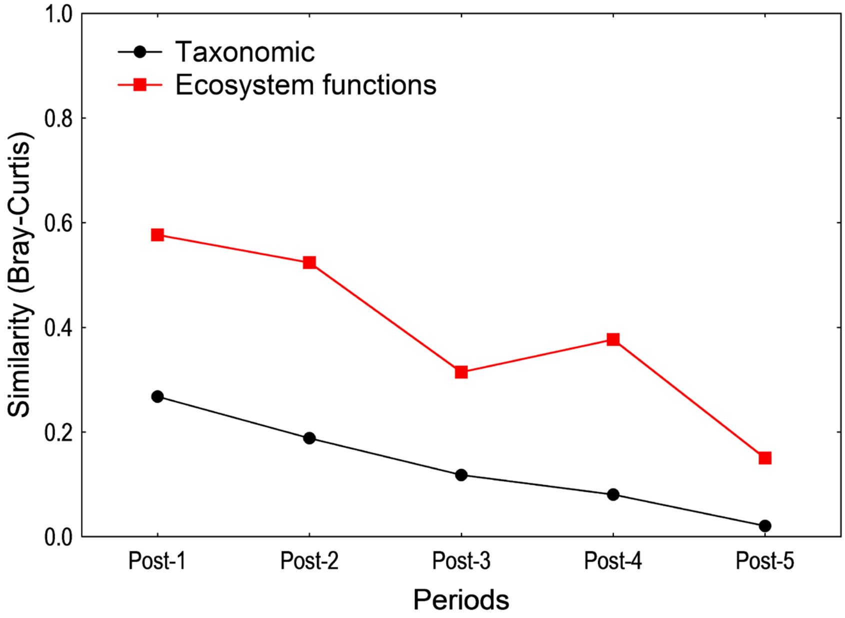

FIGURE 4 | Temporal decay of taxonomic and functional similarity (Bray Curtis, biomass-based) during the study period, calculated as the composition similarity of the Pre period against each Post period.

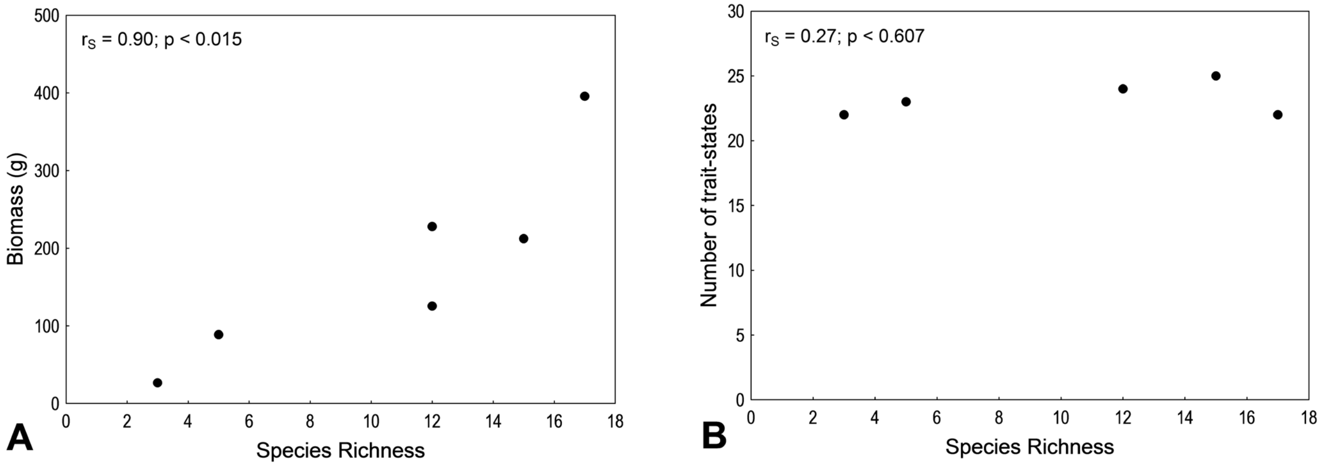

FIGURE 5 | Correlations between species richness and (**A**) total biomass and (**B**) number of ecosystem functions performed by fish populations. The significance of correlations was tested through Spearman's non-parametric correlation.

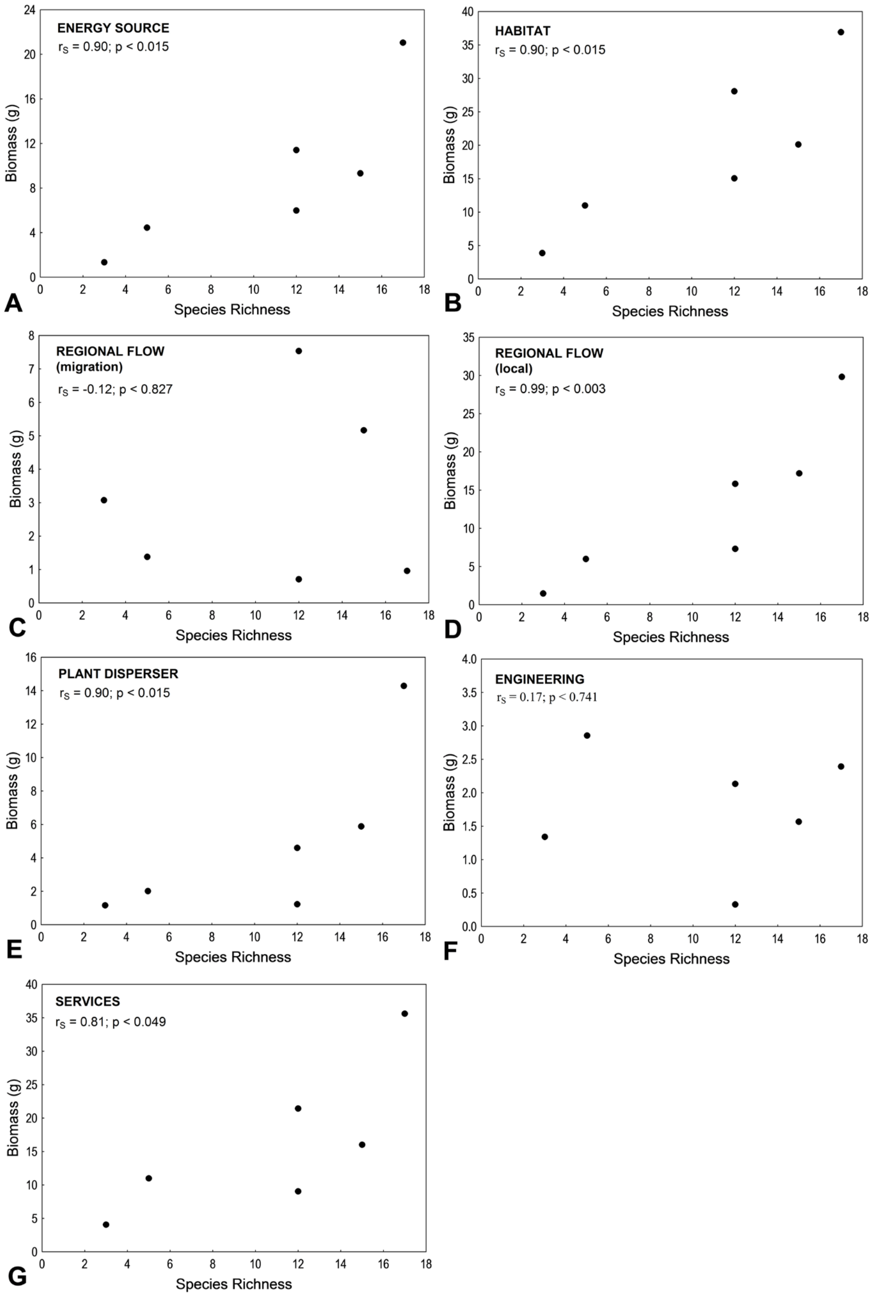

FIGURE 6 | Correlations between species richness and the intensity of ecosystem functions performed by fish populations. The significance of correlations was tested through Spearman's non-parametric correlation. Ecosystem functions: **A.** Energy Source; **B.** Habitat; **C.** Regional Flow (migration); **D.** Regional Flow (local); **E.** Plant Disperser; **F.** Engineering; **G.** Services.

DISCUSSION

Non-native fishes have the potential to cause significant disturbances to the invaded ecosystem, especially in modified environments (Rahel, 2007; Johnson *et al.*, 2008). Studies have reported a myriad of consequences that emerge from fish invasions (*e.g.*, Leprieur *et al.*, 2008; Olden *et al.*, 2018; Toussaint *et al.*, 2018; Bezerra *et al.*, 2019), but the effects on ecosystem functions remain poorly investigated. This topic has high theoretical and practical relevance (Hooper *et al*., 2012; Naeem *et al*., 2012; Balvanera *et al*., 2014), because biodiversity generates essential ecosystem functions and non-native species have the potential to erode biodiversity. In this sense, our work investigated how changes in fish diversity following the invasion of *Cichla kelberi* affected ecosystem functions potentially generated by fish species associated with macrophyte beds in Rosana Reservoir. Considering a set of ecosystem functions (7 functions based on 26 trait-states), we were able to demonstrate that ecosystem functions were significantly altered after the introduction, supporting the hypothesis that species losses and especially strong demographic effects (*i.e*., population declines) translated to the erosion of ecosystem functioning. Our findings also indicate that the loss of ecosystem functioning was not associated with the loss of specific taxa, but with a severe process of community disassembly where the invasion coincided with a sharp decline in species richness and fish abundance (Pelicice, Agostinho, 2009). Thus, our results demonstrate that the invasion of *C. kelberi* was followed by the loss of fish diversity and the functional simplification of the ecosystem, affecting aspects related to the transfer of energy, matter and genetic information.

This study covered processes related to the origin, assimilation and flow of matter/energy between components and compartments of the ecosystem. The Energy Source function referred to the connection between fish and the energy source (*e.g*., algae, invertebrates), whereas the Habitat function referred to the environment where the energy is obtained (*e.g*., water column, benthos). Both functions were drastically reduced after the invasion of *C. kelberi*, which must affect the transfer of matter and energy through the system. The Energy Source function was the most affected, with a decline of more than 90% for each trait-state. It is important to note that fish species in macrophyte beds are small-sized and feed predominantly on invertebrates in shallow littoral environments (Casatti *et al*., 2003; Pelicice, Agostinho, 2006). This link is important, because invertebrates assimilate energy from sources that may be inaccessible for fishes (*e.g*., macrophyte, debris, periphyton, algae; Covich *et al*., 1999; Benetti *et al*., 2014). The loss of this link likely affects the structure of food webs in littoral habitats, with negative effects on higher trophic levels, such as larger fish species and terrestrial predators. Concerning the Habitat function, the *Littoral* state declined by more than 90%, whereas the *Terrestrial* state was completely lost. These trait-states were shared by many small-sized species, specifically *Astyanax lacustris*, *Crenicichla britskii*, *Cichlasoma paranaense*, *Eigenmannia trilineata*, *Gymnotus carapo*, *Hemigrammus marginatus*, and *Oligossarcus pintoi*. The decline of the littoral link has high potential to affect food webs in the reservoir, since littoral areas play a key role for biodiversity in Neotropical reservoirs (Agostinho *et al*., 2016). The complete loss of the terrestrial link, in turn, affects the connection between aquatic and terrestrial environments, impairing the flow of matter and energy between environments (*e.g*., consumption of terrestrial invertebrates, predation of fish by birds).

Our study also investigated functions related to the transference of matter/energy between distant sites. The Regional Flow (migration) function considered fish that could migrate to other locations, whereas Regional Flow (local) considered local fish species that interact with migratory species. Studies indicate that migrants have strong effects on ecosystem functioning, as they link distant environments through energy flows (Flecker *et al*., 2010; Bauer, Hoye, 2014; Uno, Power, 2015). However, Regional Flow (via migration) was not affected by the invasion, probably because fish species associated with macrophyte beds are small and sedentary (Casatti *et al*., 2003; Pelicice *et al*., 2005), indicating that this function was not generated by the pre-invasion fauna. Regional Flow (via local), on the other hand, was significantly affected, since small fish serve as prey for young and adult migratory species (Bozza, Hahn, 2010). Each trait-state reduced by more than 85%, implying a reduction in the supply of prey for aquatic and terrestrial migrants. Although we have not recorded migratory fish species in the macrophyte beds, there are eight migratory fish species found in Rosana Reservoir (Pelicice *et al*., 2018). Therefore, the loss of local prey may negatively affect populations of migratory fishes, if they visit macrophyte beds during their migratory movements or if they use these habitats as nursery grounds. Furthermore, migratory prey not found in macrophyte beds may subsidize *C. kelberi* populations (*e.g*., Hoeinghaus *et al*., 2006) and thus contribute to increased effects of *C. kelberi* on ecosystem functions performed by fish assemblages in macrophyte beds.

The dispersal of seeds, fruits and animal propagules is essential for the maintenance of communities, and many fish species perform this function in Neotropical environments (Correa *et al*., 2007). Many fish species that occurred in macrophyte beds in Rosana Reservoir consume small seeds, and may have a potential role as seed dispersers. Following invasion by *C. kelberi*, the Plant Disperser function declined by more than 90%. The decline of this function, therefore, points to potential negative effects on the dispersal and recruitment of aquatic and terrestrial plants (Silveira, Weiss, 2014; Costa-Pereira, Galetti, 2015). The invasion also affected the Ecosystem Engineering function, specifically functions related to population and biomass control (top-down processes), and bioturbation and nutrient cycling (bottom-up processes). The *Bioturbation/Cycling* trait-state reduced by 94% after the invasion, primarily associated with the decline and extirpation of the benthic consumer *Satanoperca pappaterra* from macrophyte beds (Hahn, Cunha, 2005; Cassemiro *et al*., 2008). The loss of this function can decrease the mobilization of nutrients stored in the sediment, with potential negative effects on primary and secondary production (Biles *et al*., 2002; Adámek, Marsálek, 2013). The *Predation* trait-state did not differ between periods, but it appeared in the system after invasion as it is a function performed almost exclusively by *C. kelberi*. As previous noted, *C. kelberi* is a voracious predator with potential to induce strong top-down control. This function oscillated over time and followed variations in the abundance of the invader (Pelicice *et al*., 2015). The *Herbivory* trait-state experienced a substantial increase (> 900%), associated with the increase in biomass of *M. lippincottianus*, which is a non-native herbivore that spread in macrophyte beds after the invasion of *C. kelberi*.

The study also recorded changes in potential ecosystem services (Services function) generated by fish populations. The main trait-states affected were those related to the provision of ornamental and bait fish resources, because fishes found in macrophyte beds are small-sized. However, the provision of other services showed increasing trends after the invasion. The *Aquaculture* trait-state increased by more than 500%, and was related to increased biomasses of four species: *A. lacustris*, *C. kelberi*, *M. lippincottianus* and *O. niloticus* (the last three are non-native). The *Sport Fishing* trait-state emerged only after the introduction of *C. kelberi*, and represents the provisioning of a new service (sport fishing) much appreciated by some sectors of society (*e.g*., tourism, sport-fishing industry, anglers). However, it should be noted that this trait-state was represented by low biomass throughout the study period, in contrast to the effects of the invasive piscivore on the loss of fishing resources with potential to support consumption, ornamental and bait services. Britton, Orsi (2012) contrasted economic benefits and environmental costs associated with the use of non-native species in sport fishing and aquaculture activities, and concluded that some species provide economic services for some sectors, but they usually do that at the expense of environmental, economic and social sustainability in the long-term. Another aspect is that populations of non-native *Cichla* tend to oscillate and support unproductive fisheries in reservoirs, since these predators reduce prey populations to very small sizes, which constrain the population growth of the invader (Fugi *et al*., 2008). These tradeoffs must be considered in the assessment of socioeconomic costs and benefits derived from the introduction of *Cichla* in non-Amazonian reservoirs. Illegal introductions continue to occur and different species are now widespread in many basins (Pelicice *et al*., 2018; Sastraprawira *et al*., 2020); recently, legislation amendments have been proposed to protect non-native fish stocks and foster fishing activities (Magalhães *et al*., 2018).

Several results from prior studies of the relationship between biodiversity and ecosystem functioning indicate that changes in taxonomic diversity are associated with changes in the performance of ecosystem functions (Cadotte *et al*., 2011; Balvanera *et al*., 2014; Daam *et al*., 2019). Modern ecology has devoted substantial attention to understand how biodiversity affects ecosystem functioning, principally in light of the strong effects of human activities on the structure of most natural communities (Cardinale *et al*., 2012; Tilman *et al*., 2014). In our study, population declines and loss of species following invasion of *C. kelberi* triggered a profound process of community disassembly in littoral macrophyte beds (Pelicice, Agostinho, 2009). In fact, results from the null model analysis indicated that the decline of ecosystem functions was not associated with the loss of particular species, but rather is likely a consequence of wholesale changes in taxonomic diversity, biomass and decay of community similarity due to the voracious nature of *C. kelberi*. Although we observed the erosion of ecosystem functions (*i.e*., complete loss or significant reductions in the intensity of many trait-states), species richness was not correlated with the richness of ecosystem functions. In fact, none of the seven functions were totally lost, and even in situations of low species richness (*i.e*., three species), most functions remained in the area – indicating functional redundancy among fish species in these assemblages. Although the assessment of functional redundancy is highly dependent on the number of traits (Petchey, Gaston, 2006), our study considered a reasonable number of trait-states (n = 26), suggesting that many species share functions (often multiple functions). Redundancy is a common phenomenon in communities, as species overlap in various niche dimensions (Hooper *et al*., 2005). When many species perform the same function, they may replace each other in cases of species loss, maintaining the provisioning of ecosystem functioning (Chapin III *et al*., 2000). However, although no ecosystem function was lost, results indicated that most trait-states changed significantly (*i.e*., increased, declined or disappeared) after the invasion, pointing to a strong functional simplification of the studied system. Moreover, the erosion of taxonomic diversity implies a reduction in functional resilience because the loss of species reduces the redundancy in functions, making the system vulnerable to disorganization and novel disturbances (Tilman, 1997; Chapin III *et al*., 2000).

The loss of ecosystem functions threatens the maintenance of ecosystems, as functions are responsible for the mobilization, assimilation, and transference of energy (Mouillot *et al*., 2012; Naeem *et al*., 2012). Therefore, studies on biological invasions should pay more attention to the effects invaders have on ecosystem functions generated by the resident biota. This is difficult, especially where functional traits data are not available or are particularly challenging to quantify (*e.g*., Vitule *et al*., 2017). In this study, we used a novel method, derived from the traditional approach of functional ecology (*e.g*., Mouillot *et al*., 2012; Toussaint *et al*., 2016), to indirectly assess the presence and performance of ecosystem functions by assigning trait-states directly to species. Admittedly, indirect assessments have natural limitations, as the function and performance of species are not measured in realistic scenarios. However, indirect assessments, such as the one we present here, can provide an initial understanding of potential ecosystem consequences of biodiversity loss or for development of hypotheses for traditional traits-based studies. Such studies can be particularly useful to initiate biodiversity-ecosystem functioning research in poorly studied and species-rich regions like the Neotropics. Studies using indirect assessments of ecosystem functioning should be followed by direct assessments of ecosystem functioning, measuring empirically how non-native species affect the generation of these functions in invaded ecosystems (*e.g*., Tilman *et al*., 1997; Balvanera *et al*., 2014; Allen *et al*., 2016).

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ETHICAL STATEMENT

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COMPETING INTERESTS

The authors declare no competing interests.

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