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ORIGINAL ARTICLE

Cannibalism facilitates and sustains the invasion of top-predator fish (Cichlidae: *Cichla*) in human-modified ecosystems

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Abstract

1. The strategies that allow invasive alien species to perpetuate themselves in the long term are still poorly understood in invasion science. Considering top predators, a key issue is how they overcome the prey decline which they have caused during the invasion process. We investigate factors related to the persistence, impacts and long-term success of the emerging peacock bass (Cichlidae: *Cichla*) invasion, a fish native to the Amazon biome that has been introduced globally.
2. We analysed a robust temporal database that includes comparisons (1994–2002 vs. 2015–2017) on the diet of *Cichla ocellaris*, the abundance of this invader, its prey and competitors in a human-modified ecosystem. In addition, we compare the frequency of cannibalism (presence or absence) between native versus non-native populations, and between natural versus human-modified ecosystems in the American continent. Four hypotheses were tested: (i) prey and competitor populations decrease through time as a result of predation impacts; (ii) cannibalism is size- and density-dependent, and increases after native prey decline; (iii) cannibalism is more frequent in non-native populations; and (iv) the abundance of invader decreases over time because of reduced resources and increased cannibalism.
3. Our results revealed that the impacts of introducing this predator into communities are temporally cumulative and continue to evolve even after 70 years since its introduction. These impacts have led to dramatic reductions in prey availability, resulting in widespread cannibalism. Adult individuals preying on juveniles in areas with higher abundances of peacock bass indicated that cannibalism is size- and density-dependent. Cannibalism was more frequent in non-native populations and in human-modified ecosystems. A complex feedback process (reproduce and cannibalise frequently) may be responsible for overcoming long-term resource scarcity, and the cannibalism may not be a regulatory force strong enough to surpass the reproductive success of the population.

4. Our findings at the local and continental scale converge to confirm the cannibalism as an adaptive invasiveness strategy that facilitates the invasion process and makes populations self-sustainable in the long term, which may jeopardise the efficacy of management actions for these top predators introduced globally.

KEYWORDS
intraspecific predation, invasiveness, long-term impacts, reservoirs, trophic plasticity

1 | INTRODUCTION

Biological invasions are one of the main global problems that threaten biodiversity and ecosystem services (Bezerra, Freitas, et al., 2019; Mollot et al., 2017; Simberloff et al., 2013; Vitule et al., 2009). Humans are simultaneously responsible for it, threatened by it and able to stop it (Bellard et al., 2022). An important concept in this research field is the invasion process which consists of the consecutive stages that invasive alien species (IAS) go through: transport, introduction, establishment and spread (Colautti & Macisaac, 2004; Jeschke et al., 2022). During this process, a non-native species needs to overcome a series of biotic, environmental and physiological barriers to be able to establish and spread in a new environment (Blackburn et al., 2011). The success or failure in overcoming these barriers depends, among other factors, upon (i) the propagule pressure– species are more likely to establish if many individuals are released simultaneously and if multiple introductions occur over long periods (Lockwood et al., 2005); (ii) a series of traits that enhance their establishment potential–invasiveness (e.g., generalist diet and broad tolerance to environmental conditions); and (iii) the susceptibility of the ecosystem–invasibility (e.g., anthropogenic disturbance; Hui et al., 2016). Understanding the characteristics that may facilitate or inhibit the establishment of a non-native species is essential to predict their occurrence and impacts, and to increase the accuracy of conservation strategies.

Globally, at least 551 species of non-native freshwater fish have been reported as established in 3120 basins, with the common carp (*Cyprinus carpio* Linnaeus, 1758), rainbow trout (*Oncorhynchus mykiss* Walbaum, 1792) and brown trout (*Salmo trutta* Linnaeus, 1758) being the most introduced species (Bernery et al., 2022). A common and well-documented trail of ecological impacts follows the IAS, including the decline and extirpation of native populations (Franco, Petry, García-Berthou, et al., 2022; Pelicice & Agostinho, 2009; Sharpe et al., 2017), food-web disruption (Bezerra et al., 2018), biotic homogenisation (Bezerra, Ribeiro, et al., 2019; Villéger et al., 2011), changes in the composition of functional traits (Le Hen et al., 2023) and disease emergence (Zaret & Paine, 1973). These impacts affect ecosystem services and functions (e.g., water supply, food, productivity, fishing) and generate billion-dollar economic losses (Haubrock et al., 2022; Leal et al., 2021). However, the strength and direction of the impact of an IAS depend upon the taxonomic group and trophic position, with predators associated with greater impacts (Mollot et al., 2017; Oficialdegui et al., 2023).

Currently, the emerging invasion of the peacock basses, a group of fish of the genus *Cichla* Bloch & Schneider 1801 originated from the Amazon biome (Franco et al., 2021; Kullander & Ferreira, 2006; Willis et al., 2007; Winemiller, 2001) has been highlighted. Peacock basses are top predatory fish of medium-to-large size reaching ≤1 m in length (Winemiller et al., 2021). They inhabit both lentic and lotic environments (Jepsen et al., 1997) and are generally sedentary, although they exhibit potential for longer-distance movements (Hoeinghaus et al., 2003). Notably, they employ an equilibrium reproductive strategy, with both parents actively participating in nest building and offspring care (Guedes et al., 2021). Peacock basses have been and continue to be introduced worldwide since the 1940s, being already detected in the Americas, Europe, Oceania, the Middle East, Asia and Africa (Franco, Petry, Tavares, et al., 2022; Sastraprawira et al., 2020). These introductions occur mostly because they move collective passions and are much appreciated by aquarists as a consequence of their exuberant colours, strong clash with fishermen when hooked, quality of meat for consumption and control of forage species (Sastraprawira et al., 2020). Most of the invasive populations occur in human-disturbed environments (e.g., reservoirs), where changes in abiotic conditions and the reduction of native diversity increase the invasibility of the ecosystem (Havel et al., 2005; Johnson et al., 2008; Muniz et al., 2021). These cumulative and interactive impacts between reservoirs and IAS lead to temporal changes in ecological networks and resource availability, and consequently in the degree of invasibility of the ecosystem. Besides the occurrence and potential impacts, most studies disregard the long-term persistence of non-native populations. Even though theoretical models predict fluctuations in abundance and even in the intensity of their impacts, as "boom and bust" predictions (e.g., the zebra mussel; Strayer et al., 2017, and the mosquitofish *Gambusia* sp.; Sloterdijk et al., 2015), the mechanisms that sustain a non-native population in the long-term are poorly understood within the invasion science. Considering top predators, another key issue is to determine which invasion strategies they present to overcome the resource decline which they caused and persist in the long term.

Most studies on the effects of invasive species have been brief and lack a temporal context (reviewed by Strayer et al., 2006). Even when considered, temporal research involving IAS has focused on the cumulative impacts of invasions (e.g., Sharpe et al., 2017; Taabu-Munyaho et al., 2016), and future predictions

and susceptibility of environments to new invasions (Franco, Lorini, et al., 2022; Vilizzi et al., 2021), rather than on possible changes in the invasiveness strategy. Over time, IAS show evolutionary adjustments, which include (but are not limited to) morphological changes, hybridisation, niche shift, changes in ecological traits and trophic plasticity (Haubrock et al., 2021; Mooney & Cleland, 2001). It is expected that the trophic plasticity–the ability to alter the feeding matrix–may facilitate successful establishment among IAS as intra- and/or inter-specific competition is reduced and/or diet is adjusted to match changes in the availability of resources in the invaded habitat (Balzani et al., 2021; Cheng et al., 2017; Rolla et al., 2020). Understanding changes in feeding ecology is important, as it is closely related to the population dynamics of the predator and its prey (Braga et al., 2012). The collapse of fish prey is a persistent impact of the introduction of *Cichla* species (Sharpe et al., 2017) and increases over time from their introduction (Franco et al., 2021). The selective pressure exerted by *Cichla* spp. on their prey is limited by the morphology of their digestive tract (Burress & Wainwright, 2020; Santos et al., 2011), which means that many sympatric species are not proportionally consumed. Therefore, switching fish prey types, once a preferable one becomes extirpated, may not be biologically viable (Gill, 2003), and/or switching from a piscivorous diet to an omnivorous diet with lower protein quantity (e.g., invertebrates and plants) may (Glassic et al., 2023) or may not (Sankian et al., 2017) be an energetically appropriate choice. Cannibalism–the act of eating an individual of the same species–seems to be one of the main keys to understand how peacock basses maintain resilient populations over long periods of time, even after resources are exhausted.

Cannibalism has long intrigued researchers and has been recorded for 390 teleost species from 104 families (Pereira, Agostinho, et al., 2017; Pereira, Keppeler, et al., 2017). Cannibalistic behaviour is associated with a wide variety of taxa, habitats and life-history strategies, but it is particularly well-represented in piscivorous and parental care-giving species (Smith & Reay, 1991). Many factors affect cannibalism, such as predator and prey density, nutritional state, food availability, genetic relatedness, refuge, escape response, size disparity, light and environmental disturbances (Pereira, Agostinho, et al., 2017; Pereira, Keppeler, et al., 2017; Polis, 1981; Smith & Reay, 1991). These forms of cannibalism are thought to provide adaptive benefits to cannibals under a range of circumstances, primarily by allowing parents to allocate parental efforts more optimally: energy from eating (some of) one's current offspring can be redirected to other offspring, or to parental growth, survival and, ultimately, to other future reproductive activity (Bose, 2022). However, cannibalism is an important source of mortality and can affect population abundance, dynamics and structure, depending on the species and circumstances in which it occurs (Claessen et al., 2004; Polis, 1981; Rosenheim & Schreiber, 2022). Cannibalism of peacock bass seems to be more frequent in non-native populations in environments disturbed by dams (e.g., Fugi et al., 2008; Santos et al., 2011) than in populations within their native distribution range (Aguiar-Santos et al., 2018; Jepsen et al., 1997). These untested evidences suggest that cannibalism may be an adaptive invasiveness strategy to overcome prey reduction and maximie population resilience over time in the invaded environment.

In order to understand the factors related to the long-term persistence, impacts and success of the invasion of the predatory peacock basses, we analysed a robust database that includes (i) the diet of *Cichla ocellaris* and (ii) the abundance of *Cichla* spp., their prey and competitors between two periods (1994–2002 vs. 2015–2017) in a tropical reservoir (Southeastern Brazil). This is one of the first known translocations of *Cichla* outside its native range, which occurred more than 70 years ago (~1945; Santos et al., 2008). Additionally, we compiled primary data to determine the best local predictors of cannibalism (e.g., time since introduction, body size, prey availability and *Cichla* population density); and secondary data on the trophic ecology of peacock bass populations in the American continent to determine the frequency of cannibalism in native versus non-native populations. Four hypotheses were tested: (H1) prey and competitors populations decrease through time as a result of the peacock bass introduction (i.e., long-term impact); (H2) on a local scale, cannibalism is size- and density-dependent, and increases following the decrease in prey populations (long-term invasiveness strategy); (H3) on a continental scale, cannibalism is more frequent in non-native populations in human-modified environments (e.g., reservoirs); and (H4) the abundance of *C. ocellaris* decreases over time as a result of reduced resources and increased cannibalism. This study, based on one of the broadest temporal perspectives available in the literature, not only for the genus *Cichla* but also for other neotropical invasive fish, aims to contribute to the understanding of invasion dynamics and its long-term adverse effects, discouraging further introductions of top predators.

2 | METHODS

2.1 | Study area

Lajes reservoir (22°42′–22°50′ S; 43°53–44°32′ W) is a 30 km^2 impoundment, located at 415 m above sea level (a.s.l.) in Rio de Janeiro State, Brazil. This reservoir was constructed between 1905 and 1908 for hydroelectric purposes, damming streams and diverting small rivers of the East Hydrographic Basin (Brazilian Committee on Dams, 2011). The reservoir can be divided into two environments along its longitudinal axis: lotic and lentic zones. The lotic ecotone is located upstream of the reservoir and is characterised by shallow depths (2.0–6.1 m), colder (17.6–25.8°C) and turbid waters (~1.4–97.3 NTU) owing to the influence of water discharges from tributaries (Guedes et al., 2020). The lentic zones have deeper waters (11–45 m) of higher temperature (21.1–31.1°C) and lower turbidity (1.6–4.2 NTU). Lentic conditions predominate along the longitudinal extent of the reservoir, owing to low connectivity with natural tributaries and the dendritic morphology of the system, associated with a high retention time (≈300 days) (Araújo et al., 2022; Araújo & Santos, 2001; Guedes et al., 2020). Water transparency (euphotic

zone = 9.2 m) is also high, with a predominance of oligo-mesotrophic conditions (Guedes & Araújo, 2022). Lajes reservoir accounts for one of the oldest introductions of peacock basses outside the Amazon basin (~1945; Santos et al., 2008) involving a translocation of the yellow peacock bass (recently recognised as *Cichla ocellaris* sensu lato; Willis et al., 2012). More recently (between 2005 and 2010), another peacock bass was introduced in this reservoir, the blue peacock bass *Cichla piquiti* (Santos et al., 2016), found in low abundances with potential hybrids between the two species.

2.2 | Data collection

We evaluated the abundance of *C. ocellaris*, its prey and competitors in the reservoir through fish collections during a monthly sampling programme in the two zones (lentic and lotic) between 1994 and 2002 (period I; after ~53 years since introduction) and between 2015 and 2017 (period II; after ~71 years), totalling 532 samples (Table S1). In each sampling unit, gillnets (35 × 2.8 m; mesh of 15–110 mm between adjacent nodes) were installed at the sunset of the first day and retrieved the following morning after ~14 hr of fishing. Water temperature (°C) was measured using a U–52 G multiparameter probe (Horiba). Water transparency (cm) was obtained with a Secchi disk. Monthly rainfall (mm) and water level (m a.s.l.) data were obtained from a local hydrometeorological station (V-3–485) and provided by the hydroelectric company Light Energia S.A. For the evaluation of the diet, *C. ocellaris* (Figure 1) was also sampled through complementary methods, such as purse seines, casting nets, and fishing during a monthly sampling programme. Of a total of 394 stomachs were investigated (254 period I, 140 period II; Table S2), 198 presented some food content, and among these, 101 contained identifiable food items (excluding fish remains). Only stomachs with food content were used in the statistical analyses. Therefore, for each specimen of *C. ocellaris* with stomach contents, we had abiotic (temperature, transparency, precipitation and water level) and biotic (abundance of *Cichla*, prey and competitors) data collected simultaneously. Further information on the sampling methods also can be found in Guedes et al. (2020). Vouchers were deposited in the Ichthyological Collection of the Fish Ecology Laboratory, Universidade Federal Rural do Rio de Janeiro (LEP–UFRRJ no. 1613–1626; Araújo & Guedes, 2023).

FIGURE 1 Adult male *Cichla ocellaris* captured in the Lajes Reservoir, Guandu River Basin (Southeastern Brazil).

2.3 | Diet analysis

Specimens were kept on ice in the field and then transferred to the laboratory, measured (total length, TL), weighed (g) and dissected for diet analyses. Data from the peacock bass diet in the first period (1994–2002) was retrieved from previous publications (Santos et al., 2001). For both periods, food items were identified using a stereoscopic microscope, counted (*n*) and weighed (g). Fish were identified at the genus level, terrestrial arthropods (Odonata and Hemiptera) were grouped into the class "insects," and shrimp (*Macrobrachium* sp.) were grouped into "crustaceans." The digested remains were recorded once per stomach to report their presence/absence. The intraspecific predation data of *C. ocellaris* during period I was free from interference of *C. piquiti*, as the species was introduced later. In period II, any individual of the genus *Cichla* detected in the analysed stomachs was accounted as cannibalism, since it was difficult to differentiate *C. ocellaris* and *C. piquiti*. However, it is important to highlight that the probability of the occurrence of *C. piquiti* in the diet of *C. ocellaris* is low, since for every 11 specimens of *Cichla* captured in the Lajes Reservoir between 2015 and 2017, only one was identified as *C. piquiti*, indicating that this species occurs in low abundances and frequencies in the systems. Furthermore, our intra-specific predation data also do not distinguish between filial, intra-cohort and inter-cohort cannibalism.

2.4 | Cannibalism on a continental scale

A literature review was performed using the Web of Science, Scopus, Scielo, Google Scholar and Brazilian Digital Library of Theses and Dissertations databases to gather information on the frequency of occurrence (presence or absence) of cannibalism in the *Cichla* diet. We used keyword combinations (e.g., Cichla, tucunaré, pavón, peacock bass, diet, feeding, alimentação, alimentación) in different languages (Portuguese, Spanish, English and French) to detect the largest possible number of regional publications on the trophic ecology of the genus. The review was performed between January and December 2022. Articles were retained using the following criteria: (i) sample size of ≥20 peacock bass and/or stomachs from a single site; and (ii) taxonomically defined prey, excluding articles that referred to food items only as "fish" or "fish remains." The presence of cannibalism in the diet was detected when the terms "*Cichla*," or "cannibalism," or "intraspecies predation" were explicit in the results and/or discussion. The absence of cannibalism in the diet was interpreted when the terms mentioned above were not present, as well as by the absence of prey referred to as Cichiliformes/Cichlidae/Cichlinae/Cichla. Whenever more than one study was available for the same location, we retained the most recent one. From the retained studies, we gathered data

on the (i) presence or absence of cannibalism, (ii) population origin (native or non-native) and (iii) ecosystem type (natural vs. human-modified). Natural ecosystems include rivers and lakes, whereas human-modified ecosystems include artificial channels, and locations with upstream and downstream influences from dams. A total of 36 populations of *Cichla* (17 native, 19 non-native; Figure 2; Table S3) was recorded, most of them located within South America (Brazil, Guyana, Peru and Venezuela), but also in Central (Panama and Puerto Rico) and North America (USA).

2.5 | Data analysis

In order to quantify the diet of the peacock bass, we calculated the: (i) frequency of occurrence (%FO)–the number of stomachs containing a particular prey type, divided by the total number of non-empty stomachs; (ii) biomass percentage (%*W*)–the mass of each prey type, expressed as a percentage of the total biomass of all the stomach contents; and (iii) relative prey abundance (%*N*)–the abundance of each prey type, expressed as a percentage of the total abundance of all the stomach contents (Hyslop, 1980). From these metrics, we calculated the Index of Relative Importance (IRI; Pinkas, 1971) of the food items, where IRI = %FO (%*N* + %*W*). The percentage IRI (%IRI) was calculated by dividing the IRI values from each food item by the sum of all IRI values and multiplying the result by 100. A permutational analysis of variance (PERMANOVA; function "adonis2" in the *vegan* package; Oksanen et al., 2019) was used to compare dietary matrices between environments (lentic vs. lotic) and periods (1994–2002; 2015–2017). PERMANOVA is a geometric partitioning of the variation in a multivariate data cloud defined from a dissimilarity or similarity measure, and with statistical inferences performed in a distribution-free environment using permutational algorithms (Anderson, 2017). The biomass data were previously transformed (square root) and the triangular matrix was constructed using Bray–Curtis similarity distance. The PERMANOVA was applied using 9999 permutations and square sum (partial) to calculate the *p*-values. Whenever significant differences were detected ($p < 0.05$), paired comparisons were conducted between the groups.

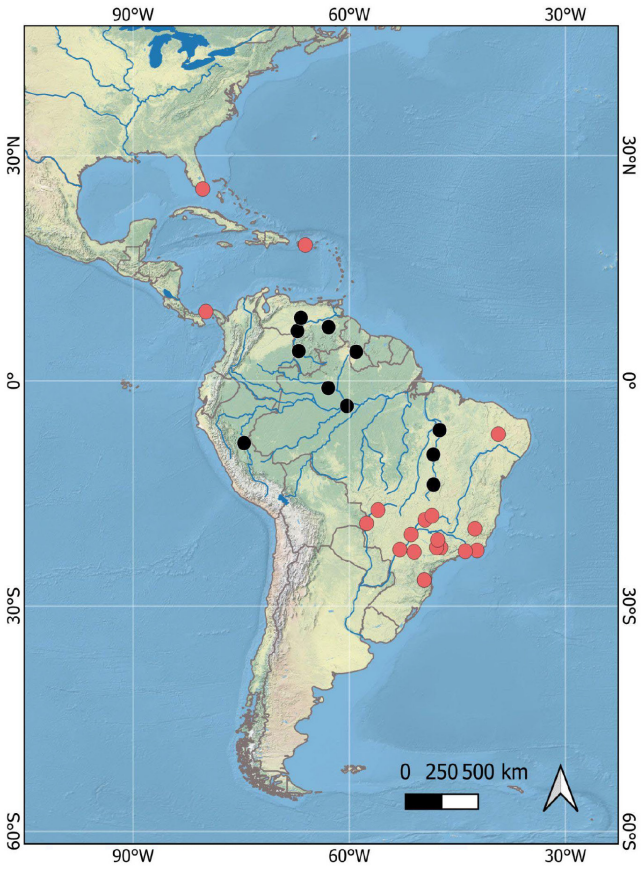

FIGURE 2 Distribution of native (black circles) and non-native (orange circles) populations of *Cichla* included in this study (more details in Table S3).

A two-way ANOVA on aligned ranks transformation (ANOVA ART) was used to compare the abundance of *Cichla*, its prey and competitors between environments and periods. This approach, implemented via the art function in the *ARTool* package in R (Kay & Wobbrock, 2020), is particularly beneficial for data that do not meet the assumptions of classical ANOVA, such as normality and homogeneity of variances. The "alignment" process of the data, as described by Wobbrock et al. (2011), is a preprocessing step in which data are aligned for each effect (either main or interaction) before rank assignment. This alignment ensures that the effects of other factors are removed, allowing for a more direct and isolated analysis of the effect of interest. After alignment, effects are estimated as marginal means and then "stripped" from the response variable, leaving only the desired effect for analysis (Wobbrock et al., 2011). When significant differences were detected, a posteriori Tukey's honestly significant difference (HSD) tests were conducted at the 0.05 confidence level.

In order to determine the most likely predictors of cannibalism at a local scale, machine learning (ML) models based on random forests (Breiman, 2001) and Boruta algorithms (Kursa & Rudnicki, 2010) were applied. We used the cannibalism biomass (i.e., the weight of the *Cichla* item) observed in the diet of each *C. ocellaris* specimen captured in the Lajes reservoir as the response variable. We used as potential predictors a set of explanatory variables related to the phenotype (body size), environmental conditions (temperature and transparency), hydrology (rainfall and water level), time since introduction, gonadosomatic index (GSI–proxy for reproductive period; Guedes et al., 2021), the abundance of *C. ocellaris* in the environment (proxy for intraspecific competition), abundance of other piscivorous fish in the environment (proxy for interspecific competition; e.g., *Hoplias malabaricus* Bloch, 1794), and availability of resources in the environment (abundance of the main prey consumed in the diet). The ML models were applied to: (i) determine the effects of all relevant explanatory variables, rather than just the non-redundant ones; and (ii) detect nonlinear and interactive relationships between the variables. The Boruta approach coupled with the random forest allows comparison of the importance of the real predictor variables with those of random so-called shadow variables using statistical testing and several runs of random forests (Degenhardt et al., 2019). Variables

that are relevant for prediction will have large *Z*-values, whereas variables that are not associated with the outcome have *Z*-values close to zero (Degenhardt et al., 2019; Kursa & Rudnicki, 2010). For this analysis, we used 999 trees, level of significance $p < 0.05$ and multiple comparisons adjustment using the Bonferroni method in the *Boruta* package (Kursa & Rudnicki, 2010).

In order to determine whether the presence/absence of cannibalism is affected by population origin (native or introduced) and ecosystem type (natural vs. human-modified) on a continental scale (Americas), we used generalised linear models (GLM) assuming a binomial error distribution (*logit* function). A χ^2 test was used to test for differences between independent variables at the 0.05% significance level. Residual diagnoses, assumptions and model adequacy (Figure S1) were investigated using the "simulateResiduals" function in the *DHARMa* package (Hartig, 2022). All statistical analyses were performed using the R language and environment, version 3.6.3 (R Core Team, 2023).

3 | RESULTS

3.1 | Diet

The *C. ocellaris* diet was dominated by fish prey, with >90% of the total IRI, while other items (eggs, insects, crustaceans and plants) had smaller contributions (Table 1). The consumed fish prey belonged to nine of the 30 genera identified as potential prey recorded in the Lajes reservoir (Figure 3). Cannibalism was predominant in the lentic zones (IRI = 82.41%; Table 1) and lowest in lotic zones (35.62%), mostly associated with adult individuals preying on conspecific juveniles. Moreover, juvenile individuals of only 9.6 cm TL were also recorded preying conspecifics. The consumption of insects (19.37%), crustaceans (6.05%) and native fish (genera *Astyanax*, *Oligosarcus*, *Hoplias* and *Gymnotus*) was higher in lotic zones (37.26%), whereas lentic zones recorded a higher consumption of the non-native tilapia (*Coptodon*; 13.4%). Regarding temporal changes in diet, there was an increase in the cannibalism with increasing time of introduction, from period I (1994–2002; IRI = 62.6%) to period II (2015–2017; IRI = 89.3%). Tilapias (period I = 19.9% and period II = 1.73%) and the native characid *Astyanax* (period I = 8.87% and period II = 0.73%) were, respectively, the second and third most consumed fish prey, but their consumption has decreased in importance over time (Table 1). Peacock bass diet changed significantly between environments (Pseudo–$F = 2.37$; $p = 0.041$) and periods (Pseudo–$F = 3.31$; $p = 0.009$), with interactions among these two factors (Pseudo–$F = 3.20$; $p = 0.006$) according to a PERMANOVA (Table 2). Paired comparisons for the interaction indicate significant spatial changes (i.e., lentic vs. lotic zones) occurring only in period II ($t = 2.01$; $p = 0.006$; Table 2).

TABLE 1 Index of relative importance (IRI; in %) of the *Cichla ocellaris* diet matrix: total (all environments and periods) and categorised by periods (1994–2002 and 2015–2017) and environments (Lentic and Lotic).

		Periods		Environments	
Food category	Total	1994–2002	2015–2017	Lentic	Lotic
Fishes					
Cichla	76.38	62.63	89.30	82.41	35.62
Coptodon	10.58	19.90	1.73	13.40	1.57
Astyanax	4.57	8.87	0.73	0.31	33.34
Crenicichla	0.17	0.08	0.29	0.28	
Pimelodella	0.07	0.27		0.11	
Rhamdia	0.05	0.17		0.07	
Oligosarcus	0.09	0.34			1.07
Gymnotus	0.04		0.12		0.43
Hoplias	0.20		0.90		2.45
Fish eggs	0.32	1.54		0.56	
Insects	6.63	5.30	6.23	2.64	19.37
Crustaceans	0.74	0.48	0.67	0.01	6.05
Plants	0.16	0.43	0.03	0.16	0.10

3.2 | Abundance of *Cichla ocellaris*, prey and competitors in the environment

The prey recorded in the diet of the *C. ocellaris* and the competing piscivores showed different patterns of decreased or increased abundances in the reservoir between the periods and environments, with significant interaction among those factors (Figure 3; Table 3). The native Characiformes *Astyanax*, *Hoplias* and *Oligosarcus* had the highest abundances in the lotic zone ($p < 0.01$; Table 3) and a significant decrease over time ($p < 0.01$). The native catfishes *Pimelodella* and *Rhamdia*, and the knifefishes *Gymnotus*, rare prey in the peacock bass diet (Table 1), showed an increase in abundance over time ($p < 0.01$), but exhibited different patterns of abundance between zones of the reservoir (Figure 3). The cichlids *C. piquiti* and *Crenicichla* had an increase in abundance over time ($p < 0.01$), whereas tilapia (*Coptodon*), the main prey at the lentic zone, showed a temporal decline in abundance ($p < 0.01$). *Cichla ocellaris* had higher abundances in the lentic zone ($p < 0.01$), and an increase in abundance over time (Table 3; Figure 3).

3.3 | Predictors of cannibalism in local and continental scale

Boruta's variable selection method identified, among the 10 original variables, four relevant predictors of the cannibalism in *C. ocellaris* on a local scale (Figure 4). The average importance *Z*-scores ranged from 3.1 to 10.7 for the selected variables, and the best local predictors for cannibalism were predator body size (10.7), *C. ocellaris* abundance (6.9), time since its introduction (4.5), and prey abundance (3.1). At a continental scale, the presence of cannibalism was more frequent in non-native populations (GLM; $p < 0.001$; Table 4) and in human-modified ecosystems ($p < 0.001$; Table 4).

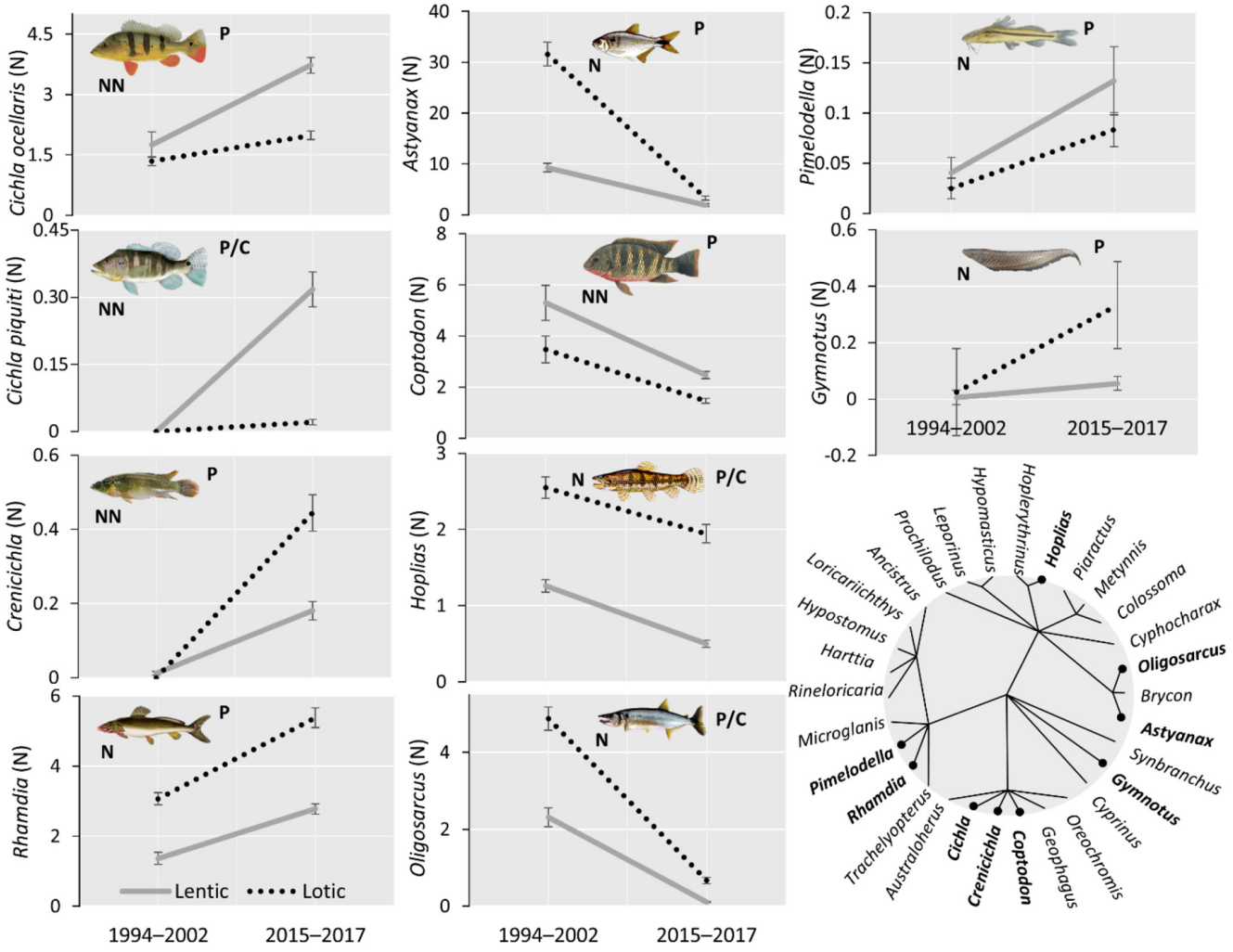

FIGURE 3 Mean and standard error of the abundance of *Cichla ocellaris*, its prey (P) and competitors (C) in the different environments (Lentic, continuous grey line; Lotic, dotted black line) between 1994–2002 and 2015–2017. Dendrogram illustrates the genera of the fish assemblage captured in the Lajes reservoir with the genera preyed by *C. ocellaris* highlighted in bold. N, native; NN, non-native.

TABLE 2 Results from PERMANOVA comparing differences in the diet (based on biomass) of *Cichla ocellaris* between environments and periods.

Source	df	MS	Pseudo-*F*	*p*
Environments	1	8380	2.37	**0.041**
Periods	1	11,680	3.31	**0.009**
Environments × Periods	1	11,308	3.20	**0.006**
Residual	194	3526		
Total	197			
Pairwise test for the interactions				
Environments × Periods				
Lentic × Lotic (1994–2002)			1.09	0.276
Lentic × Lotic (2015–2017)			2.01	**0.006**

Note: Significant differences ($p < 0.05$) are highlighted in bold.
Abbreviations: df, degree of freedom; MS, mean square.

TABLE 3 Results (*F*-values) of a two-way ANOVA on aligned ranks transformation (ANOVA ART) comparing the abundance of prey and competitors between environments (lentic × lotic) and periods (1994–2002 × 2015–2017).

ANOVA ART	Environments	Periods	Environments × periods
Astyanax	46.6***	122.6***	43.0***
Cichla ocellaris	13.9**	62.9***	17.1***
Crenicichla	14.0**	31.2***	15.7***
Cichla piquiti	40.6***	16.3***	40.6***
Coptodon	1.5	14.4***	0.6
Gymnotus	33.9***	126.8***	91.1***
Hoplias	31.9***	5.0*	0.8
Oligosarcus	78.4***	218.9***	31.9***
Pimelodella	6.97**	21.6***	5.70*
Rhamdia	48.7***	54.0***	2.1

*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

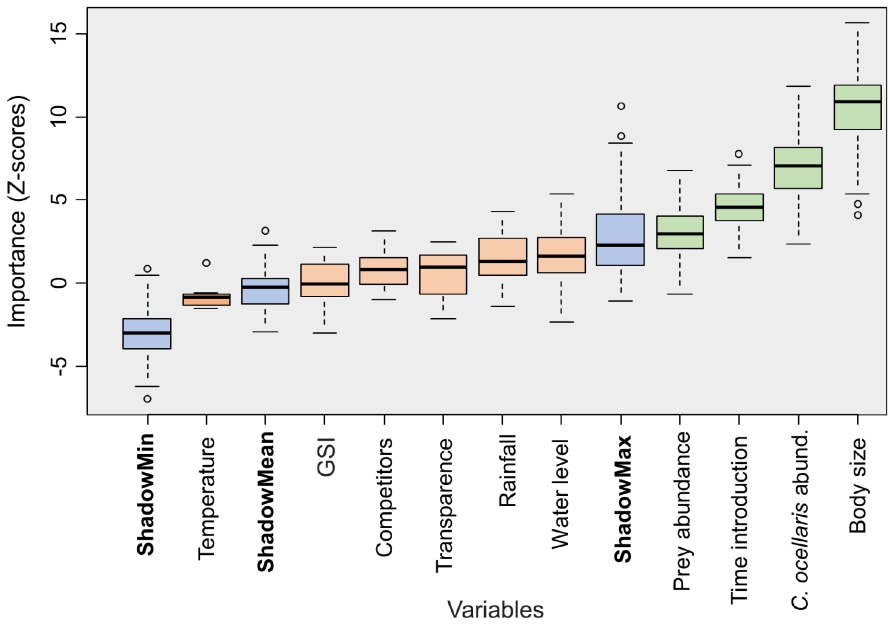

FIGURE 4 Results of the Boruta algorithm applied to random forests comparing the importance (*Z*-score) of different variables to determine the best predictors of the cannibalism rate of *Cichla ocellaris* in the Lajes reservoir. Green boxplots represent the confirmed variables, whereas blue boxplots correspond to minimal, mean and maximum *Z*-score of a shadow attribute. Orange boxplots represent *Z*-scores of rejected variables.

Source	df	Deviance	Residuals df	Dr	Pr(>x^2)
Null			35	49.8	
Origin	1	17.4	34	32.4	<0.0001
Ecosystem type	1	13.7	33	18.7	<0.001
Origin × Ecosystem type	1	0.71	32	18.0	0.39

Abbreviations: df, degrees of freedom, Dr, deviance residual, Pr(>x^2), *p*-value associated with the chi-square test.

TABLE 4 Results from an analysis of deviance for binominal generalised linear models (GLMs) comparing the presence/absence of cannibalism in *Cichla* spp. according to population origin (native or introduced) and ecosystem type (natural vs. human-modified) in the American continent.

4 | DISCUSSION

Our findings highlighted for the first time the variation in the prevalence of cannibalism in the peacock bass diet using a long-term time frame in a human-modified system. The cannibalism has increased over time reaching 89% of the IRI of prey consumed by the peacock bass after ~71 years since introduction. These high levels of cannibalism seem to be related to the increase in invader abundance over time of introduction, with adults preying on conspecific juveniles in lentic areas under a background scenario of decreased native prey species. Analyses of the patterns of cannibalism in the diet of the genus *Cichla* in the American continent have demonstrated that the presence of cannibalism was related to non-native populations introduced into human-modified ecosystems (i.e., dammed systems, artificial channels). Regardless of the increase in cannibalism and the decrease in prey abundance in the community, the abundance of the invader did not show any sign of decrease through time. In summary, we demonstrate that cannibalism in peacock bass populations is affected by the time since introduction, hydrological conditions (lotic or lentic), body size, prey abundance, predator invader abundance, origin (native or introduced) and ecosystem (natural or human-modified).

4.1 | Long-term impacts

A clear pattern observed in our studies was the decrease over time in many prey species and competitors (especially Characiformes) probably in response to a long-term impact exerted by the non-native peacock basses through predation, which corroborates H1. These findings also corroborate many other studies describing the impacts of peacock basses (Franco, Petry, García-Berthou, et al., 2022; Leal et al., 2021; Pelicice & Agostinho, 2009; Pelicice et al., 2015; Sharpe et al., 2017), but adding further evidence based on a long-term perspective. The degree of impact of predation directed at certain taxa is related to the behaviour and morphology of the predator. The peacock bass uses the pursuit and stalking feeding tactics to capture prey (Brejão et al., 2013), ingesting them through suction by using the wide opening of the prognostic protractile mouth. Their cardiform teeth (premaxillary and pharyngeal) are typical of species that swallow whole prey with little evidence of chewing (Santos et al., 2011). This type of capture strategy limits the size of prey that can be captured and ingested (Gill, 2003). Therefore, a large part of the potential prey biomass available in the Lajes reservoir cannot be preyed upon by peacock basses owing to morphological limitations. Small-bodied fish, such as *Astyanax*,

Oligosarcus and/or juveniles of large-sized species (e.g., *Hoplias* and the *Coptodon*), are more prone to predation, whereas species with bone carapace and large rustles (e.g., *Rhamdia* and *Pimelodella*) tend to be less preyed. Thus, the selective pressure exerted by the peacock bass on certain taxa or ontogenetic phases can influence the assemblages' structure, size and density of the prey populations (Jepsen et al., 1997; Santos et al., 2001; Sharpe et al., 2017). In addition to the high rates of individual consumption, which are crucial for explaining the predatory impact of the peacock bass (Carvalho et al., 2021), its impacts can occur indirectly through increase interspecific competition with other piscivores (Fugi et al., 2008), as they prey on competitors (Pereira et al., 2015) and/or cascade changes in trophic webs that affect distinct taxonomic groups (Zaret & Paine, 1973). Therefore, our findings indicate that the impacts of introducing a top predator fish into communities are temporally dynamic and cumulative, with changes continuing to manifest even after ~70 years since their introduction.

4.2 | Long-term invasiveness strategy

A subsequent and fundamental question is to understand how invasive top predators maintain sustainable populations even after depleting preferred trophic resources. Our results highlight that, on a local scale, cannibalism increased after prey populations decreased, with adult individuals preying on juveniles in lentic zones with higher abundances of peacock bass, supporting H2 that cannibalism is size- and density-dependent. Higher abundances of peacock bass in lentic environments, when compared to lotic environments, have already been reported at local (Guedes et al., 2020) and continental scale (Franco et al., 2021). However, the distribution of non-native species is asymmetrical within the lentic environments; for example, peacock bass and tilapias reached higher densities in shallow (0–7 m) and physically complex littoral habitats, whereas deep areas harbour lower densities of these species (Guedes & Araújo, 2022). Equilibrium strategy cichlids (sensu Winemiller, 1989) are often found in higher abundances near complex and hydrologically stable habitats which they use for nesting and parental care (Guedes et al., 2021; Mims & Olden, 2012). It is precisely here that cannibalism–a behaviour that seems antagonistic to care–begins.

Cannibalism as an adaptive strategy to low resource availability is frequently reported in fishes (Pereira, Agostinho, et al., 2017; Pereira, Keppeler, et al., 2017), frogs (Measey et al., 2015), raptors (Allen et al., 2020) and even in human primates (Lee, 2019), making it one of the most widespread phenomena of trophic plasticity in the animal kingdom. This intriguing behaviour confers adaptive benefits (e.g., survival, energy reserves, competition reduction) in a variety of circumstances of prey scarcity and several hypotheses aim to address this issue (as reviewed by Bose, 2022). However, the detection of this phenomenon may face a temporal gap. At Gatun Lake (Panamá), for example, the introduction of the peacock bass has caused severe changes at the community level (Zaret & Paine, 1973). Even considering these impacts, cannibalism was not observed at early years leading Zaret (1977) to propose that different colour patterns may act as inter- and intra-specific signs to inhibit intra-specific predation. However, previous studies (e.g., Gomiero & Braga, 2004; Santos et al., 2001) as well as our findings, refute this hypothesis and demonstrate that cannibalism within the group of peacock basses is common and generalised in non-native populations. Our findings are consistent with the optimal foraging theory (Polis, 1981) which predicts that cannibalism increases with the decrease in the quality and/or quantity of alternative prey.

Body size is positively correlated with cannibalism owing to the prevalence of adult individuals preying on juvenile conspecifics. Although less frequent, cannibalism in *C. ocellaris* also occurred among juveniles, with individuals >9.6 cm TL preying on even smaller conspecifics, which may indicate a widespread cannibalism within the population. Size-dependent cannibalism has also been identified in other species outside their natural distribution range, such as the brown trout *Salmo trutta*, rainbow trout *Oncorhynchus mykiss* (Musseau et al., 2017), Guabina *Gobiomorus dormitor* (Bedarf et al., 2001), pikeperch *Sander lucioperca* (Ribeiro et al., 2021) and lionfish *Pterois volitans* (Dahl et al., 2018), reflecting the ontogenetic dietary shifts in these species. Although juveniles (smaller TL) predominantly feed on a non-piscivorous diet (e.g., insects, crustaceans), adults (larger TL) prey on juveniles of their own species, especially when the abundance of young-of-the-year is high (Bedarf et al., 2001; Dahl et al., 2018; Dörner et al., 2007; Eigaard et al., 2014; Gomiero & Braga, 2004; Heermann & Borcherding, 2013; Pereira, Agostinho, et al., 2017; Pereira, Keppeler, et al., 2017; Preciado et al., 2015), indicating a strong relationship between cannibalism and reproductive period. Unlike native populations in more preserved ecosystems at the Amazon, which exhibit a seasonal and more defined reproductive cycle, non-native populations of peacock basses show a considerable reproductive plasticity in dammed systems, with multiple events throughout the year (Guedes et al., 2021). The prolonged reproductive period reflects in a production of juvenile conspecifics which may act as a viable food resource available throughout the year and, consequently, also reflects in a generalised cannibalistic behaviour in non-native populations. This complex retro-feeding (i.e., reproduce and cannibalise frequently) can overcome resource scarcity in reservoirs, and make non-native populations self-sustaining in the long term, which may jeopardise the efficacy of management actions for these top-predator invaders.

4.3 | Cannibalism in native versus non-native populations

Cannibalism is more frequent in non-native populations and in human-modified environments across the American continent, corroborating H3. Pereira, Agostinho, et al. (2017), Pereira, Keppeler, et al. (2017) revised fish cannibalism, suggesting that intraspecific predation was more common in non-native populations

of *Cichla*. Here, from a dataset compiled from Lowe-McConnell (Lowe-Mcconnell, 1969) to the present study, we were able to confirm this assumption for the first time. Cannibalism may be associated with the additive and synergistic impacts of habitat degradation and biological invasions for various reasons. Firstly, because natural and diversified ecosystems tend to sustain more complex trophic interactions and greater resistance to invasions (i.e., Biotic Resistance Theory; Elton, 1958; Gu et al., 2023). This can translate into greater availability of native prey (lower cannibalistic propension) in the diet and a lower abundance of predators. In general, cannibalism is more frequent in communities with lower species richness (Pereira, Keppeler, et al., 2017). Secondly, because habitat degradation can weaken trophic networks and modify available ecological niches, creating opportunities for invasive species (i.e., Empty Niche Hypothesis; Daly et al., 2023; Elton, 1958). In the case of peacock bass, this effect seems to manifest particularly through the conversion of lentic and lotic areas caused by the construction of dams (the main impact mapped in our database), which supports greater abundances of this invader when compared to natural systems (Espínola et al., 2010; Franco et al., 2018), and by the disruption of trophic webs and depletion of resources during the establishment process discussed previously. Greater prevalence of cannibalism in artificial reservoirs versus rivers was also observed for the invasion of the top predator *Sander lucioperca* in Portugal (Ribeiro et al., 2021). Therefore, the greater frequency of cannibalism in human-modified ecosystems and in non-native populations may be associated with intensified intraspecific competition in invasive populations where predator densities are high and resources are limited, favouring the development of plasticity invasiveness strategies to reduce competition, such as cannibalism.

This may indicate that cannibalism not only promotes self-sustaining populations in the long-term, but is also an invasiveness trait that may facilitate the process of invasion in a series of contexts. Rudolf et al. (2010) observed through predictive models that cannibalism can trigger dispersion by changing the spatial distribution of conspecific prey. This prediction could be tested in future studies within the context of naivety theory (Kovalenko et al., 2010; Pereira et al., 2019; Sharpe et al., 2021), verifying when, where and if juveniles recognise invasive predators of their own species as a threat, and exhibit evasion/dispersal behaviour. Cannibalism can facilitate the invasion process not only for fish (e.g., Javidpour et al., 2020; Via, 1999). In new nutritionally stressful environments, cannibalism employed by the red flour beetle (*Tribolium castaneum* Herbst, 1797) can provide a nutritional advantage, allowing for colonisation and expansion of the population (Via, 1999). The ctenophore *Mnemiopsis leidyi* Agassiz, 1865, an invader in several seas around the world, uses mass reproduction events to build nutrient reserves to overcome critical periods of prey scarcity during long winters in its non-native distribution range (Javidpour et al., 2020). In summary, our findings at local and continental scales converge in the same direction: cannibalism can be an adaptive invasiveness strategy against the reduction of resources imposed by the interactive impacts between biological invasions and habitat modification.

Analysing cannibalism based solely on its presence or absence provides a limited view of the phenomenon. More informative measures, such as the abundance, frequency or weight of prey, could offer a richer understanding, potentially revealing a more significant effect of the origin and the environment. However, these aspects could not be evaluated as a consequence of variability in the presentation of results in the consulted studies. Furthermore, the data were collected in various contexts, including environments recently degraded or those with a long history of degradation, and in both lentic and lotic areas. The time since species introduction and the time since environmental impact may be crucial factors in detecting cannibalism, but diversity in sampling methods prevented a more in-depth analysis of this effect. These limitations in the consulted studies highlight the importance of a more standardised and meticulous methodology in data collection and analysis, aiming for a more accurate understanding of the impact and complexities of cannibalism in invasive and disturbed environments.

4.4 | Cannibalism as a self-regulating mechanism?

Even though studies indicate that invasive species may experience fluctuations through time that may lead to their local extinction (e.g., "boom and bust"; Strayer et al., 2017), this does not seem to be the case for *C. ocellaris* in the Lajes reservoir. Despite the cannibalism rate increase over an 18-year period, our findings did not corroborate our hypothesis H4 of population decline of peacock basses resulting from an intra-specific regulatory force exerted by cannibalism. As a form of density-dependent mortality, cannibalism functions as a self-regulating mechanism in many populations (Rosenheim & Schreiber, 2022). Conversely, the energy gained through conspecific consumption can have a positive effect on fecundity and survival, resulting in a population increase in a special case of biostability known as the 'lifeboat mechanism' (Getto et al., 2005; Van den Bosch et al., 1988). This effect is equivalent to positive feedback, in which the costs of cannibalism associated with mortality are lower than the benefits associated with additional reproduction (Claessen et al., 2004). The increase in the abundance of invasive predators over time has already been observed for different species (Castaldelli et al., 2013; Strayer et al., 2017). Furthermore, the increase in cannibal abundance in a context of generalised intraspecific predation may also be related to several factors that could not be excluded in our study and deserves further analyses. One of them is the recent introduction of another conspecific, the blue peacock bass *C. piquiti* (Santos et al., 2016), which could have contributed to this increase in the abundance of the genus. Even though they are captured in low abundances, the high potential for hybridisation within the genus is already recognised in the scientific literature (Willis et al., 2012). One of the possible outcomes of the process of introgression may be heterosis, which is the production of hybrids with increased function of

any biological quality. Another possibility that could explain the increase in *Cichla* abundance despite the high increase in cannibalism rate is the potential for novel introductions which could have taken place in the reservoir considering that this is a species highly prized in sport fisheries and that is a fishing club on the spot. The continuous propagule pressure may be responsible for local populational increase since novel individuals are introduced. Our study was not designed to exhaust all of the possibilities related to the cannibalism, and thus novel studies may further elucidate the patterns described herein.

5 | CONCLUSIONS

The impacts of introducing the top predator *C. ocellaris* into communities are temporally dynamic and cumulative, with changes continuing to manifest even after 70 years since their introduction. These impacts led to dramatic reductions in prey availability, resulting in widespread cannibalism. A complex feedback process (i.e., reproduce and cannibalise frequently) may be responsible for circumventing long-term resource scarcity in human-modified system. Adult individuals preying on juveniles in lentic areas with higher abundances of peacock bass, indicated that cannibalism is size- and density-dependent on a local scale. Considering a broad geographical context in the American continent, cannibalism was more frequent in non-native populations in human-modified environments, indicating that intraspecific predation is an adaptive strategy that can facilitate the invasion process. Cannibalism may not be an efficient regulatory force strong enough to surpass the reproductive success of the population. In conclusion, our findings cover broad temporal and spatial scales yet converge in the same direction: cannibalism can be an adaptive invasiveness strategy to the reduction of resources imposed by the interactive impacts between species introduction and habitat degradation, promoting self-sustainable populations in the long term, and complicating the management of invasive top predators.

AUTHOR CONTRIBUTIONS

Conceptualisation: GHSG. Developing methods: GHSG, LNS, AFGNS, ACSF, FGA. Conducting the research: GHSG, LNS, AFGNS. Data analysis: GHSG, ACSF. Data interpretation: GHSG, ACSF. Preparation figures & tables: GHSG. Writing: GHSG, ACSF, LNS, AFGNS, FGA.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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