Neotropical Ichthyology

Original article https://doi.org/10.1590/1982-0224-2022-0039

Coexistence of endemic peacock basses (*Cichla*) in a Neotropical reservoir (Cichlidae: Cichliformes)

Correspondence:
Geovana de Souza Andrade
geovana21andrade@outlook.com

Geovana de Souza Andrade[1,2] and Fernando Mayer Pelicice[3]

Peacock basses (genus *Cichla*) are predatory fish widely distributed across the Amazon, where two or more species normally coexist in a same drainage. The mechanisms that allow coexistence remain poorly understood, although these species share a number of functional traits and behavioral aspects. To advance on this question, the present study compared population and functional traits of *Cichla kelberi* and *C. piquiti*, based on data collected between 2010 and 2020 in the upper section of the Lajeado Reservoir, Tocantins River. Both species were captured in all sampling sites, frequently in a same sample, but *C. piquiti* was far more frequent and abundant. The species used the same habitats, and co-occurred more often than expected by chance. Species had a similar diet (small-sized fish), reproductive effort, fecundity and fat accumulation, but *C. piquiti* showed larger body sizes, shoaling behavior, a longer reproductive period, and morphology associated with greater swimming potential. Overall, results revealed that these species coexist in the impoundment, with significant overlap in the use of habitats and food resources. Differences in other functional traits may favor their coexistence, possibly involving niche partitioning, which seem to explain the dominance of *C. piquiti* in the impoundment.

Keywords: Co-occurrence, Freshwater fish, Functional trait, Impoundment, Niche.

Submitted February 12, 2022
Accepted July 29, 2022
by Paulo Pompeu
Epub October 03, 2022

Online version ISSN 1982-0224
Print version ISSN 1679-6225

Neotrop. Ichthyol.
vol. 20, no. 3, Maringá 2022

---

[1] Programa de Pós-Graduação em Biodiversidade, Ecologia e Conservação, Universidade Federal do Tocantins. Rua 3, Quadra 17, Jardim dos Ipês, 77500-000 Porto Nacional, TO, Brazil. geovana21andrade@outlook.com (corresponding author).

[2] Empresa Brasileira de Pesquisa Agropecuária, Embrapa Pesca e Aquicultura, Palmas, TO, Brazil.

[3] Núcleo de Estudos Ambientais, Programa de Pós-Graduação em Biodiversidade, Ecologia e Conservação, Universidade Federal de Tocantins. Rua 3, Quadra 17, Jardim dos Ipês, 77500-000 Porto Nacional, TO, Brazil. fmpelicice@mail.uft.edu.br.

Tucunarés (gênero *Cichla*) são peixes predadores amplamente distribuídos pela Amazônia, sendo comum que duas ou mais espécies coexistam em uma mesma drenagem. Os mecanismos que permitem sua coexistência permanecem pouco compreendidos, embora essas espécies compartilhem uma série de traços funcionais e comportamentais. Para avançar nessa questão, o presente estudo comparou uma série de características populacionais e funcionais de *Cichla kelberi* e *C. piquiti*, com base em dados coletados entre 2010 e 2020 no reservatório de Lajeado, rio Tocantins. Ambas as espécies foram capturadas em todos os locais de amostragem, frequentemente em uma mesma amostra, mas *C. piquiti* foi muito mais frequente e abundante que *C. kelberi*. As espécies ocuparam os mesmos habitats, e co-ocorreram mais vezes do que o esperado ao acaso. As espécies apresentaram dieta (composta por peixes de pequeno porte), esforço reprodutivo, fecundidade e acúmulo de gordura semelhantes, mas *C. piquiti* apresentou tamanho corporal maior, comportamento de formar cardumes, período reprodutivo mais longo, e morfologia associada com maior poder de natação. No geral, os resultados revelaram que essas espécies coexistem no represamento, com sobreposição significativa no uso de habitats e recursos alimentares. Diferenças em outros traços funcionais devem favorecer sua coexistência, possivelmente envolvendo partição de nicho, o que parece explicar a dominância de *C. piquiti* no represamento.

Palavras-chave: Co-ocorrência, Nicho, Peixe de água doce, Represamento, Traço funcional.

INTRODUCTION

The ecological niche is a multidimensional description of biological attributes related to the functioning of an organism in a given environment (Hutchinson, 1959; Leibold, Geddes, 2005). Differences in some attributes, such as body size, morphology, feeding resources, and reproductive modes, affect the ecological performance of species, as they determine growth, survival, and recruitment (Violle *et al*., 2007; Winemiller *et al*., 2015). Species with phylogenetic proximity may present similarities and differences in niche attributes, depending on selective forces that induce convergent (*e.g*., environmental filter) or divergent (*e.g*., competition for resources) outcomes. It is expected, however, that closely related species (*i.e*., same genus) possess more niche similarities among themselves than with other groups, as they share similar evolutionary histories. The coexistence of similar species is a matter of great interest in ecology, as biotic interactions can lead some species to live in sub-optimal conditions, affecting their distribution, demography, and functional traits, especially if they compete for resources in a homogeneous environment (*e.g*., Tilman, 1994; Winkelmann *et al*., 2014). Theoretically, competition can drive species to extinction (Hardin, 1960; MacArthur, Levins, 1967), but it is common to observe species coexisting in natural environments even when they share similar resources. The subject is complex, because coexistence can be mediated by multiple factors, such as environmental variation, stochasticity, dispersion, or niche partitioning (Putnam, 1994; Chase, 2003; Connell *et al*., 2004; Lortie *et al*., 2004; Hubbell, 2005; Long *et al*., 2007).

In general, Neotropical fish communities are heterogeneous and highly diverse (Albert *et al*., 2020), representing assemblages of several species coexisting in a same locality (Lowe-McConnell, 1999), including several species of the same genus. Different mechanisms must favor the coexistence of species and populations in species-rich communities (*e.g*., Fernandes *et al*., 2009; Pereira *et al*., 2017; Silva *et al*., 2017; Delariva, Neves, 2020), but the subject has been poorly investigated. The Amazon basin is a special case, as it is home to the greatest fish diversity in the world, at regional and local scales (Dagosta, de Pinna, 2019). Many localities share phylogenetically related species, which have similar niche dimensions and share/compete for the same resources (Barros *et al*., 2017). This is the case of peacock basses (genus *Cichla*), predatory fishes widely distributed across the Amazon. Currently, there are 16 described species (Kullander, Ferreira, 2006; Sabaj *et al*., 2020), but molecular data indicate the existence of only nine valid species and some local varieties (Willis *et al*., 2012). It is common for two or more species and varieties to coexist in a same drainage. For example, *Cichla temensis* Humboldt, 1821, *C. orinocensis* Humboldt, 1821, and *C. intermedia* Machado-Allison, 1971 coexist in the Cinaruco River (Hoeinghaus *et al*., 2003), while *C. monoculus* Agassiz, 1831 and *C. temensis* coexist in the Uatumã River (Santos, Oliveira Jr., 1999). The same is observed in the Tocantins River basin, with the sympatric distribution of the endemics *C. piquiti* Kullander & Ferreira, 2006 and *C. kelberi* Kullander & Ferreira, 2006 (Kullander, Ferreira, 2006); *C. kelberi* is a variety of *C. ocellaris* Bloch & Schneider, 1801 (Willis *et al*., 2012). Although coexistence is a common pattern, *Cichla* species share a number of functional traits and behavioral aspects. In a broader sense, these fish are medium to large size, generalist piscivores, diurnal, nest guarders, limnophilic, and dependent on structured habitats, which may grant similar ecological functioning and performance, but induce, at the same time, some niche overlap and potential competition for resources.

Few studies have investigated the coexistence of *Cichla* species, so the mechanisms that allow their coexistence remain poorly understood. Studies conducted in the Orinoco River basin, Venezuela, revealed that, although *Cichla* species are similar in broad aspects (*e.g*., morphology, feeding, reproduction), differences in niche dimensions affect their ecological performance, abundance patterns, and distribution, possibly favoring coexistence. These species differ in geographic distribution, environmental tolerance, and habitat use (Winemiller, 2001), with a differential use of rivers, lakes, and channels. Seasonal variations in river conditions also affect habitat use, spawning activities, and predator-prey interactions, with effects on ecological performance (Jepsen *et al*., 1997). Body size and condition also differed among *Cichla* species, indicating variations in energy acquisition, allocation, and growth (Jepsen *et al*., 1999; Hoeinghaus *et al*., 2006). However, such comparative studies are lacking in other Amazonian drainages. In the Tocantins River basin, for example, *C. kelberi* and *C. piquiti* (Fig. 1) colonized littoral areas of hydroelectric reservoirs, where they feed on small fish (Novaes *et al*., 2004; Marto *et al*., 2015). In the Lajeado Reservoir, Middle Tocantins, an unpublished study showed that *C. piquiti* is larger, more abundant and dispersed than *C. kelberi* (Andrade, 2018), indicating that *C. piquiti* was more successful in colonizing the impoundment. This pattern is interesting because *C. kelberi* is commonly found in rivers and lakes of the basin (GSA, pers. obs.); moreover, it has invaded several reservoirs and other environments in non-Amazonian drainages (Pelicice, Agostinho, 2009; Catelani *et al*., 2021; Franco *et al*., 2022). Therefore, some ecological factor seems to restrict the population size of *C. kelberi* in Lajeado Reservoir, which may include resources for feeding and reproduction, habitats, and niche adjustments due to negative biotic interactions. Studies that compare population data and niche dimensions are needed to clarify coexistence patterns and associated mechanisms.

Colonization success and coexistence patterns may be explained by differences in functional traits (*e.g*., Barros *et al*., 2017; Delariva, Neves, 2020), as they determine resource use and the degree of niche overlap. The comparison of distribution, feeding, reproduction, and morphology patterns of sympatric species can help to understand ecological interactions and coexistence. In this sense, the present study compared population and functional traits of *C. kelberi* and *C. piquiti* coexisting in the upper section of the Lajeado Reservoir, Tocantins River, to assess potential ecological differences that may explain the coexistence of these species and the apparent dominance of *C. piquiti*. The study analyzed data collected between 2010 and 2020 in order to compare (i) spatio-temporal patterns of distribution and abundance, (ii) co-occurrence and habitat use,

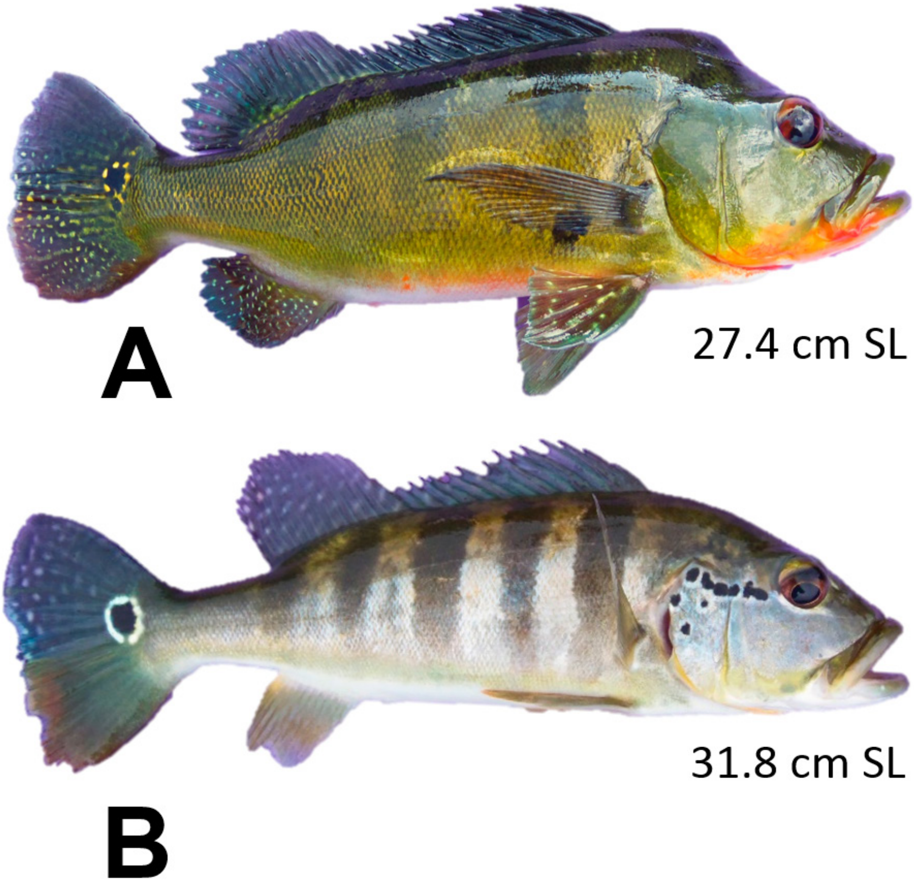

FIGURE 1 | *Cichla kelberi* (**A**) and *C. piquiti* (**B**) captured in the Lajeado Reservoir, Tocantins River, Brazil.

(iii) population structure (length, biomass, and sex ratio), (iv) trophic ecology (diet, fat accumulation, and body condition), (v) reproduction (fecundity, reproductive period, and effort), and (v) ecomorphological patterns related to habitat use, locomotion, and feeding. We hypothesize that *C. piquiti* possess functional traits that grant greater ecological performance if compared to *C. kelberi*, which could explain its dominance and success in the impoundment. We expect to find differences associated with body size, reproduction, feeding, and morphology, as these traits affect the acquisition of energy, survival, and fitness (Mouillot *et al*., 2013; Villéger *et al*., 2017). In particular, we expect that *C. piquiti* presents larger body sizes (*i.e*., competitive superiority), greater reproductive effort and a longer reproductive period (*i.e*., higher recruitment and population size), a more generalist diet (*i.e*., diversified resources, and a greater body condition), and morphology that must enable greater swimming potential (*i.e*., efficient predation and survival) than *C. kelberi*.

MATERIAL AND METHODS

Study area. The Tocantins-Araguaia River basin is a large drainage (*ca*. 800,000 km^2) located inside Brazilian territory, formed by the Araguaia and Tocantins rivers. The Tocantins River is the main channel and extends for 2,500 km. Its sources are located in the central Brazilian plateau and its mouth in the estuarine region of the Amazon River (Ribeiro *et al*., 1995). Currently, the Tocantins River is regulated by seven large hydroelectric dams (Akama, 2017), which altered the natural hydrological regime and impacted fish diversity (Araújo *et al*., 2013; Gilbert *et al*., 2020; Perônico *et al*., 2020).

The present study was carried out in the upper section of the Lajeado Reservoir, Middle Tocantins. This reservoir (630 km^2 surface area) was formed in 2001 after the construction of the Luís Eduardo Magalhães Hydropower Plant. We selected 18 sites distributed along 20 km (municipalities of Porto Nacional and Brejinho de Nazaré), covering the left and right bank of the impoundment, and islands (Fig. **S1**). Although sites were located in the upper end of the reservoir, all had strict lentic conditions, with high water transparency (Secchi disk: 137 ±53 m; range 25 to 262 m). Sampling sites were located in shallow areas of the littoral zone (depths < 2 m), where macrophyte beds (submerged, emerged, and floating) colonize intensively (Noleto *et al*., 2019), which together with submerged trees constitute the main fish habitat. The surface area of each site ranged between *ca*. 0.30 to 1 km^2, but most sites had between *ca*. 0.3 and 0.5 km^2.

Data sampling. Data were collected between March 2010 and March 2020, but with variable frequency in each year. Monthly sampling occurred in three periods: (i) September 2010 to October 2011, (ii) March 2015 to May 2016, and (iii) April 2019 to March 2020. Other samples were collected sporadically in 2012, 2014, and 2017, while 2013 and 2018 were not sampled. In total, we collected 365 samples at 18 sites over the 10 years (Tab. **S2**); in this study, a sample represents a locality within a site sampled for at least for 30 min with controlled effort (*i.e*., number of fishers and time). Sampling took place during the day, between 8:00 a.m. and 6:00 p.m.

Fish were sampled with artificial lures (surface and subsurface action, 10–15 cm total length, white), rods, casting reels, and motorized boat. Baits were continuously cast in different habitats along the littoral zone, controlling the fishing effort (number of fishers and time). We recorded all predation activity towards the baits, which generated two types of records: attacks and captures. Attack records represent fish that attacked the bait but were not caught; these records were only considered when the fish was identified with certainty. Capture records represent fish caught and handled. Some fish were measured (total length, cm) and released alive, while others (*C. kelberi* = 132; *C. piquiti* = 570) were taken to the Núcleo de Estudos Ambientais (Neamb) or to the Laboratório de Ecologia e Triagem (PPGBec) at the Universidade Federal do Tocantins (UFT). In the field, we recorded the habitat in which the captured fish was associated, which included margins (near the shoreline), open areas (no submerged structure), macrophytes (submerged, emergent, and floating plants), logs (submerged trees and branches), and some habitat combinations, because these habitats were frequently mixed (*e.g.*, margin and macrophytes). We also recorded the group behavior of each fish, *i.e.*, whether the fish was independent or associated with definable aggregations (shoals). The formation of shoals has been recorded in Lajeado Reservoir (Caproni, 2017), which are occasional and transient (minutes) aggregations of many fish (dozens) on the water surface, where they seem to be in a state of frenzy, keeping jumping and bursting against the surface. Shoals appear occasionally and unpredictably; when they emerge near the boat, sampling is feasible.

In the laboratory, fish were measured, weighed, and eviscerated to obtain the following variables: total and standard length (TL and SL, cm), total weight (TW, g), body weight (eviscerated, BW, g), gonad weight (GW, g), sex, stage of gonadal development, visceral fat accumulation (g), and the degree of stomach fullness. The stage of gonadal development followed Brown-Peterson *et al.* (2011), adapted to four classes: immature (IMT), development (DES), regressing (REGR), and regenerating (REG). Classification considered the macroscopic conditions of the gonads, such as size, turgidity, irrigation, and color. Ovaries in the development stage were preserved in 70% alcohol; subsamples were removed and weighted to estimate fecundity, by counting the number of vitellogenic oocytes under stereoscopic microscope. To analyze trophic ecology, stomachs were preserved in 70% alcohol and the gastric contents were identified to the lowest taxonomic level under stereoscopic microscope; prey fish were identified following the species list reported in Lucinda *et al.* (2007). For each food item, volume (ml) was measured using graduated cylinders, and for each prey fish, standard length (cm) was measured with a ruler (length was estimated when the posterior part of the body was damaged).

Some individuals were randomly selected for ecomorphological characterization. We measured the following morphometric variables (mm) with a digital caliper: head length (HL); head height (HH); maximum body depth (BD); maximum body width (BW); eye position (EP); eye diameter (ED); mouth height (MH); mouth width (MW); peduncle length (PL); peduncle height (PH); peduncle width (PW); caudal fin length (CL); caudal fin height (CD). The selection of variables and their measurement followed Casatti, Castro (2006), Teixeira, Bennemann (2007), Cardoso *et al.* (2019), and Soria-Barreto *et al.* (2019). Voucher specimens of *Cichla kelberi* (UNT 12498) and *C. piquiti* (UNT 12494) were deposited in the fish collection at the Laboratório de Ictiologia Sistemática, Universidade Federal do Tocantins (UNT), Porto Nacional, Brazil.

Data analysis

Abundance, distribution and coexistence. To investigate abundance trends between *Cichla kelberi* and *C. piquiti*, we calculated mean relative abundance for each site and year, based on the number of individuals in each sample (attack + capture records). For that, we considered only the abundance of *C. kelberi* and *C. piquiti*; other species were excluded (they summed 10% of all fish records, mainly *Serrasalmus marginatus* Valenciennes, 1837, *S. eigenmanni* Norman, 1929, and *Crenicichla lugubris* Heckel, 1840). To investigate distribution patterns and coexistence, we calculated the occurrence of each species across samples and sites. In addition, a null model of species co-occurrence was used to statistically determine if observed co-occurrence patterns (C-score index) could be obtained by chance. The C-score measures the number of checkerboard unities (0 1 or 1 0) in the matrix (Stone, Roberts, 1990). The observed C-score was compared with a distribution frequency of simulated C-scores, calculated after 5,000 randomizations of the original data matrix, using the software EcoSim v.7.0 (Gotelli, Entsminger, 2001), A sequential swap permutation algorithm was used, maintaining the row sum fixed and the column sum equiprobable (algorithm SIM 2; Gotelli, 2000). Nonsignificant C-scores suggest random patterns of species co-occurrence. A significant lower C-score means that species are co-occurring more often than expected by chance, while a significant higher C-score indicates a lower number of co-occurring pairs than expected by chance. Finally, to investigate habitat use, the proportion of fish captured in each habitat was calculated, considering eight habitat configurations: open areas (OP), margins (MG), macrophytes (MC), logs (LG), and the combinations [MC+LG], [MG+MC], [MG+LG], and [MG+MC+LG].

Population structure. To investigate differences in body size between species, we used Analysis of Variance (ANOVA) considering total length (TL, cm) and total weight (TW, cm) as response variables. The distribution of values among size classes was also calculated, considering 5 cm and 250 g intervals for TL and TW, respectively. We calculated the sex ratio (males:females) for each species in each year, and tested differences in mean values with ANOVA, considering species as a factor. Finally, the number of shoals and the number of fish captured in shoals were calculated.

Trophic ecology. To characterize the diet, we considered the volume (ml) of each resource grouped in broader categories: fish (grouped in sub-families, families, and orders), fish remains (unidentified fish and fragments), Mollusca, Decapoda (shrimp), Insecta (Odonata), insect remains (unidentified insects and fragments), and macrophytes. Diet similarity was measured as Bray-Curtis similarity, based on percent volume. The diversity of feeding resources consumed by each species was evaluated using a resource accumulation curve controlled by sampling effort (number of stomachs analyzed). Finally, an Analysis of Covariance (ANCOVA) was used to investigate variations in prey (fish) size between species, considering species as the categorical factor, predator length (SL) as the covariate, and prey length (SL) as the response variable. The proportion (%) of prey larger than 5 cm was also calculated.

ANCOVA was also used to compare fat accumulation and body condition between species, considering the species as the categorical factor. For fat accumulation, body weight was the covariate and visceral fat the response variable; for body condition, standard length was the covariate and body weight the response variable. Covariates and response variables were log-transformed.

Reproduction. The reproductive period was determined based on monthly variations in the frequency of breeding females (gonads in the developing and regressing stages) and in the gonadosomatic index (GSI). The GSI is the product of the division between gonad weight (GW, g) and body weight (BW, g). We used ANOVA to test for differences in reproductive effort (GSI of females in the developmental stage), total fecundity (oocytes/fish), and relative fecundity (oocytes/gram of gonad) between species.

Ecomorphology. We calculated 10 ecomorphological relative indices: head length (HL/SL), eye position (EP/HH), gape size (MH/MW), mouth width (MW/SL), body lateral compression (BD/BW), body depth (BD/SL), peduncle length (PL/SL), peduncle compression (PH/PW), caudal fin height (CH/SL) and caudal fin length (CL/SL). We used ANOVAs to investigate differences in mean values between species. In addition, we investigated variations in ecomorphological indices using a Principal Component Analysis (PCA), based on the correlation matrix.

All statistical analyzes were conducted in Past v. 2.17 (Hammer *et al*., 2001) and Statistica v. 7.1 (Statsoft, 2005). Parametric assumptions were checked for all analyses, and when data were heteroscedastic, the Welch statistic was considered for ANOVAs. The inference of statistical significance followed the concept of statistical clarity of Dushoff *et al.* (2019).

RESULTS

Abundance, distribution, and coexistence. During the study period, we obtained 1,377 fish records (1,140 captures and 237 attacks), of which 258 corresponded to *Cichla kelberi* and 1,119 to *C. piquiti*. Considering all samples (n = 365), *C. kelberi* was present in 39.2%, *C. piquiti* in 81.6%, and no fish was captured in 14%. The species co-occurred in 34.8% of the samples; *C. kelberi* was captured alone in only 4.4%, and *C. piquiti* in 46.8%. Mean relative abundance of *C. piquiti* (mean 0.70) was always higher than *C. kelberi* (mean 0.17) over the years (Fig. 2A) and across sites (Fig. 2B). Null model results indicated that the species co-occurred more often than expected by chance (observed C-score = 2736; mean of simulated C-scores = 4747.3; $p < 0.0024$). Moreover, habitat use was similar between species (Fig. 2C), as most individuals were associated with macrophytes and its combinations with logs and margins. However, *C. kelberi* was more associated with margins (53.7% of all fish) if compared to *C. piquiti* (24.5%).

Population structure. *Cichla kelberi* (n = 204 measured) ranged between 18.1 cm and 44.7 cm TL (Fig. **S3**), with most individuals between 25 and 30 cm (Tab. 1); total weight ranged between 86.34 and 1,313.4 g. *Cichla piquiti* (n = 937 measured) reached larger sizes, ranging between 14 cm and 60 cm TL (Fig. **S3**), with most fish between 20 and 40 cm (Tab. 1); total weight ranged between 54.96 and 3,352.8 g. There was a

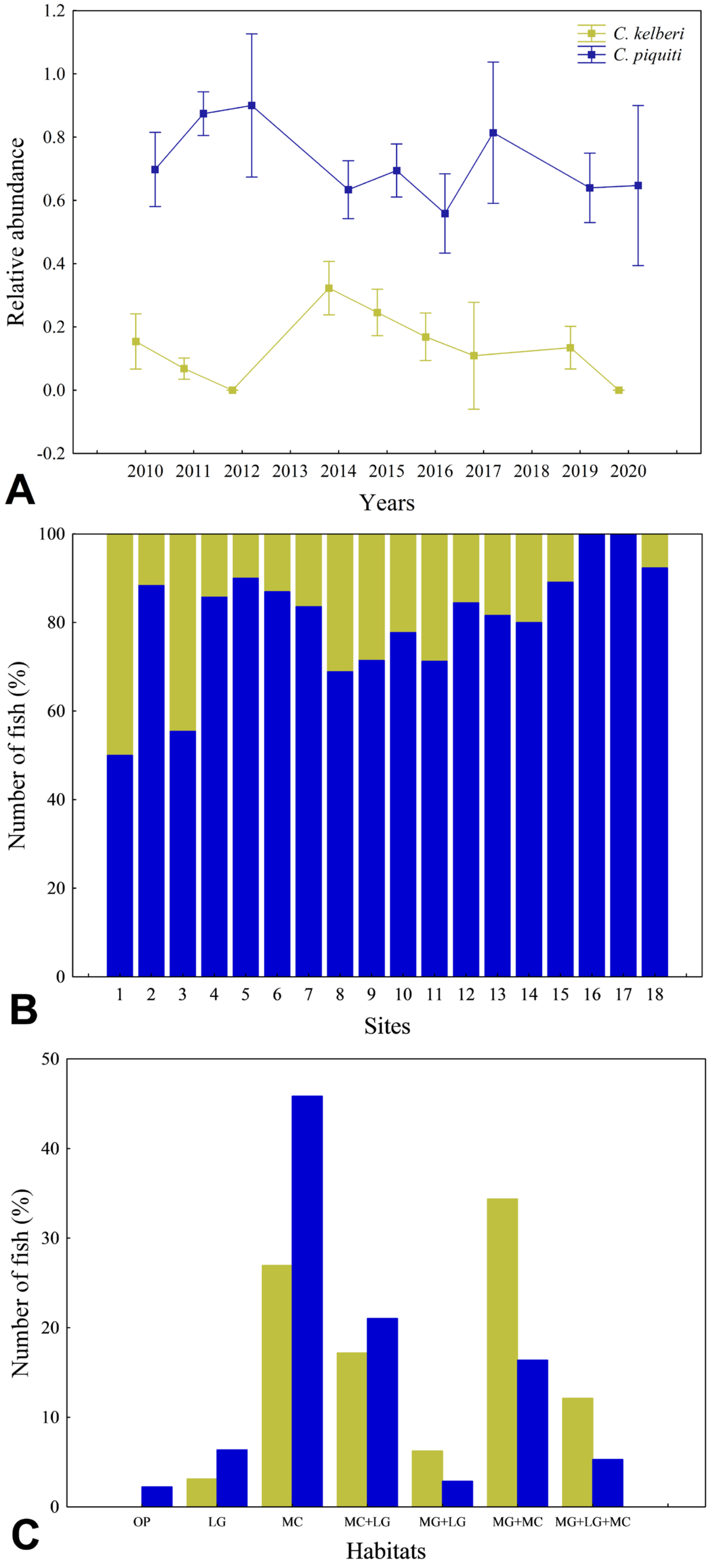

FIGURE 2 | Temporal and spatial variation in the abundance of *Cichla kelberi* and *C. piquiti*. **A.** Mean relative abundance over the years; whiskers represent 95% confidence intervals. **B.** Relative abundance at each sampling site. **C.** Habitat use considering the number (%) of fish captured in each habitat (and some combinations). OP = open areas; MG = margins; MCR = macrophytes; LG = logs.

statistically clear difference in mean TL (ANOVA: Welch $F_{1;1139} = 94.0$; $p < 0.0001$) and TW (ANOVA: Welch $F_{1;699} = 35.81$; $p < 0.0001$) between species, with higher values for *C. piquiti*. Males predominated in both populations, with a mean proportion of 1:1.8 for *C. kelberi* and 1:1.4 for *C. piquiti*; we observed no clear statistical difference in the sex ratio between species (ANOVA: $F_{1;11} = 0.65$; $p < 0.4365$). During the study period, we recorded 35 shoals, totaling 72 fish captured. Of these, *C. kelberi* (5 fish) was present in 8.6 % of the shoals, while *C. piquiti* (66 fish) was present in 85.7%.

Trophic ecology. We analyzed 40 stomachs of *C. kelberi* (12 resources consumed) and 251 of *C. piquiti* (23 resources). Teleost fish represented the main resource consumed, especially Cichlidae, Engraulidae, Serrasalmidae, and different Characiformes (Fig. 3A). Diet similarity between the species was 0.65 (Bray-Curtis). Accumulation curves did not stabilize, but both species consumed a similar number of resources considering a same

TABLE 1 | Size distribution of *Cichla kelberi* and *C. piquiti* among classes of total length (cm) and total weight (g), based on the percentage of fish in each class. Bold indicate more frequent classes.

Classes	*C. kelberi* (%)	*C. piquiti* (%)
Total length (cm)		
0 – 5	0.00	0.00
5.1 – 10	0.00	0.00
10.1 – 15	0.00	0.32
15.1 – 20	1.47	3.52
20.1 – 25	**11.27**	**15.37**
25.1 – 30	**67.65**	**32.12**
30.1 – 35	**18.14**	**24.33**
35.1 – 40	0.49	**13.23**
40.1 – 45	0.98	4.80
45.1 – 50	0.00	2.99
50.1 – 55	0.00	2.45
55.1 – 60	0.00	0.85
Total Weight (g)		
0 – 250	**24.43**	**31.28**
250.1 – 500	**70.99**	**43.23**
500.1 – 750	3.05	**13.01**
750.1 – 1000	0.76	**5.80**
1000.1 – 1250	0.00	1.41
1250.1 – 1500	0.76	1.41
1500.1 – 1750	0.00	1.05
1750.1 – 2000	0.00	1.23
2000.1 – 2250	0.00	0.88
2250.1 – 2500	0.00	0.35
2500.1 – 2750	0.00	0.00
2750.1 – 3000	0.00	0.00
3000.1 – 3250	0.00	0.18
3250.1 – 3500	0.00	0.18

sample size (Fig. 3B). The length of predators and preys were significantly correlated (ANCOVA: $F_{1;222} = 76.84$; $p < 0.0001$), however, there was no clear effect of species ($F_{1;222} = 0.55$; $p < 0.4584$) and the interaction between factors ($F_{1;222} = 0.008$; $p < 0.9272$). Most prey showed SL < 6 cm (Fig. 3C), and prey larger than 5 cm were consumed exclusively by *C. piquiti* (21% of all prey).

There was a clear statistical effect of body weight on fat accumulation (ANCOVA: $F_{1;609} = 17.70$; $p < 0.0001$), but no effect of species ($F_{1;609} = 2.15$; $p < 0.1428$) or the interaction between factors ($F_{1;609} = 2.78$; $p < 0.0958$). There was no clear statistical difference in body condition between species, with an evident effect of standard length on body weight (ANCOVA: $F_{1;688} = 6298.0$; $p < 0.0001$), but no effect of species ($F_{1;688} = 1.30$; $p < 0.2542$) or the interaction between factors ($F_{1;688} = 0.57$; $p < 0.4517$).

Reproduction. There was no clear statistical difference in mean values of GSI (ANOVA: $F_{1;90} = 1.21$; $p < 0.2746$), total fertility (ANOVA: $F_{1;12} = 3.77$; $p < 0.0759$), and relative fertility (ANOVA: $F_{1;12} = 1.17$; $p < 0.3007$) between species. The reproductive period differed between species, considering that females of *C. kelberi* showed higher IGS values between September and December (Fig. 4A); *C. piquiti* presented a long reproductive period, with higher IGS values between January and July (Fig. 4C). Variations in IGS coincided with the frequency of breeding females (Figs. 4B,D).

Ecomorphology. Most ecomorphological indices differed statistically between species, with the exception of peduncle compression (Tab. 2). *Cichla kelberi* showed higher values for most indices, excepting peduncle length, body lateral compression, and caudal fin height. Principal Components Analysis confirmed these differences (Fig. **S4**). The first three components explained 54.4% of data variability, but only the first (25.7%) was related to differences between species. Head length, caudal fin (length), body depth and mouth width were associated with *C. kelberi*, while peduncle length, body lateral compression, and caudal fin height were associated with *C. piquiti*.

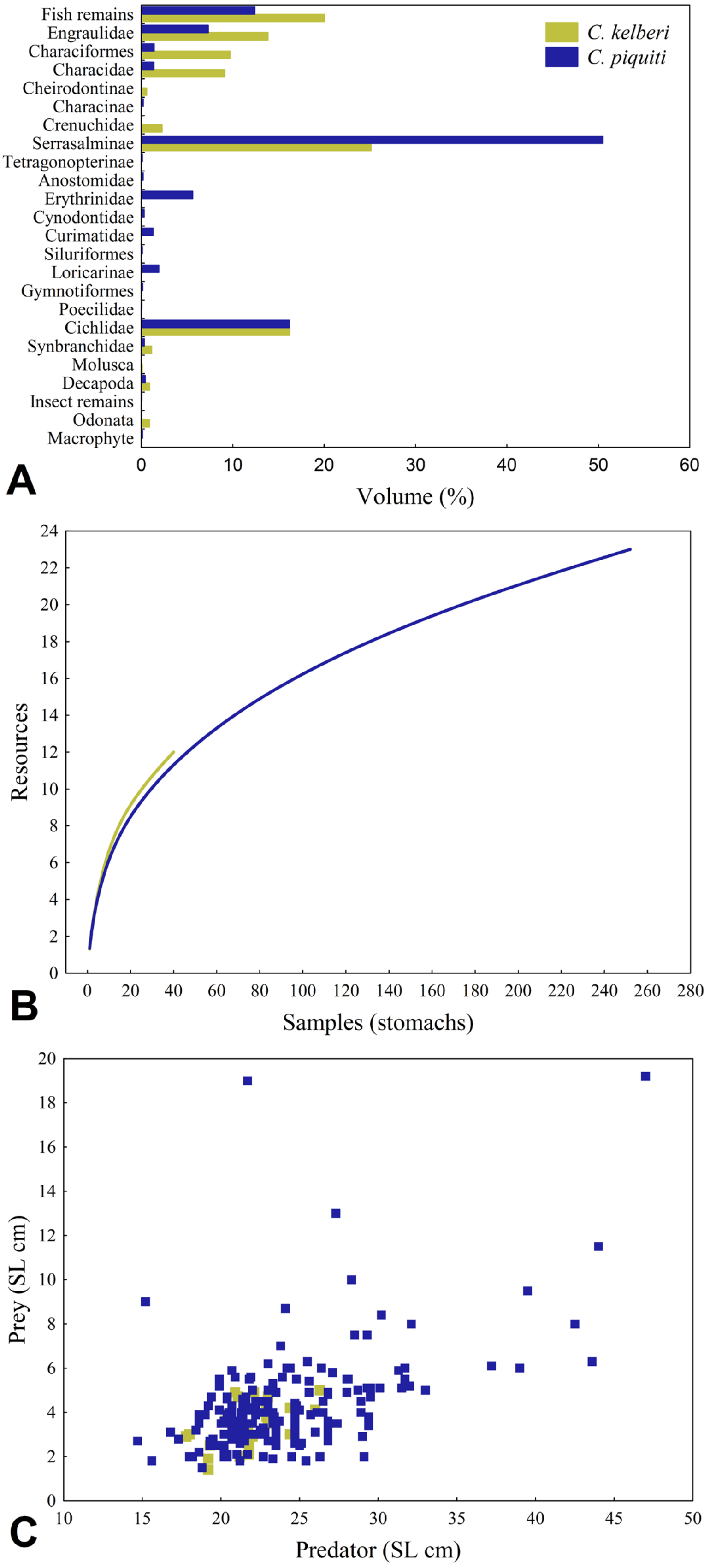

FIGURE 3 | Comparative feeding ecology of *Cichla kelberi* and *C. piquiti*. **A.** Food resources (percentage) consumed by each species, grouped in broad categories. **B.** Resource accumulation curves based on sampling effort (stomachs analyzed). **C.** Relationship between the standard length (cm) of *C. kelberi* and *C. piquiti* (predators) and the standard length (cm) of consumed prey (only fish).

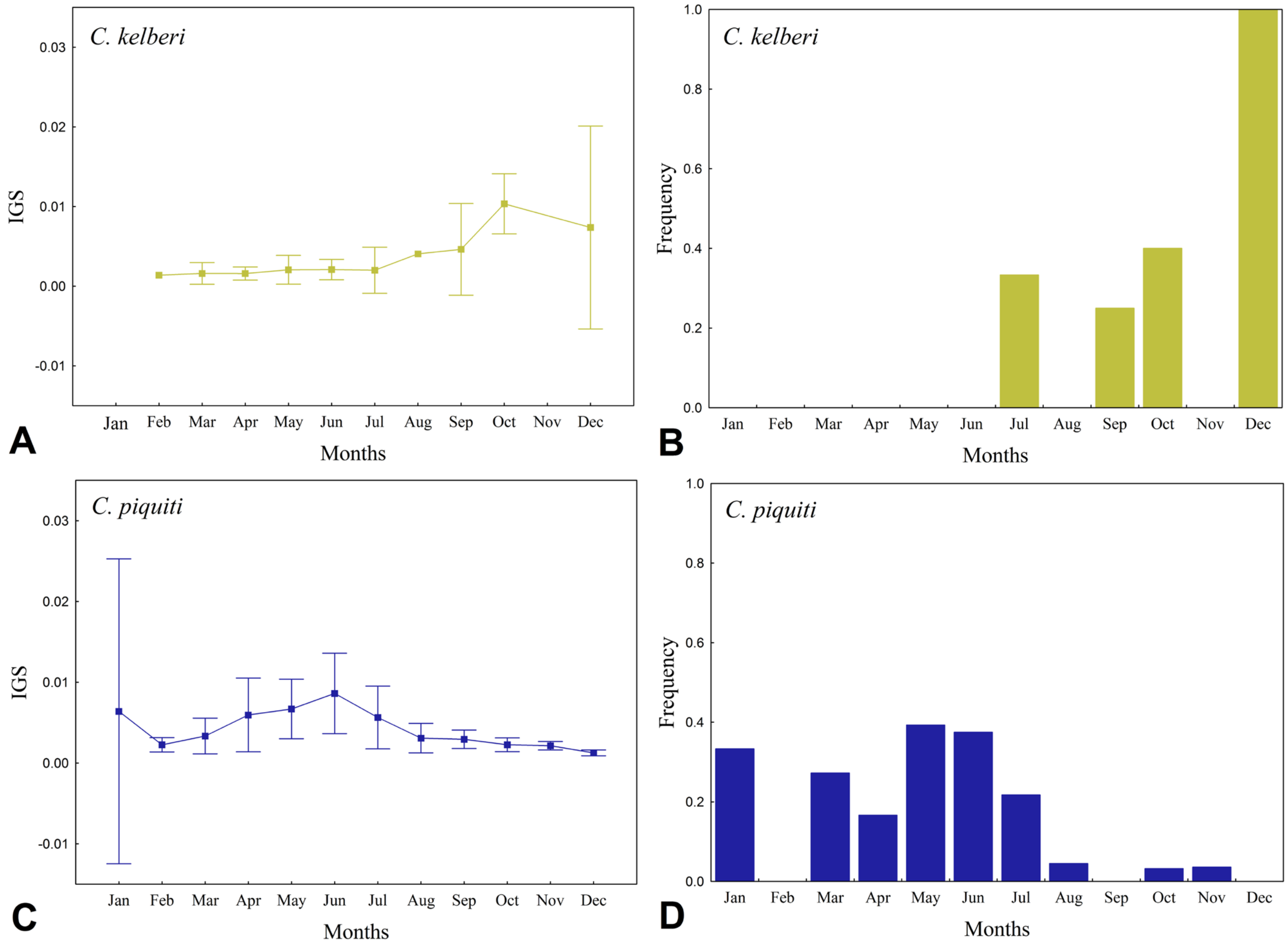

FIGURE 4 | Comparative reproductive ecology of *Cichla kelberi* and *C. piquiti*. Monthly variations in the gonadosomatic index (IGS) and in the frequency (%) of breeding females for *C. kelberi* (**A**, **B**) and *C. piquiti* (**C**, **D**).

TABLE 2 | Differences in ecomorphological indices between *Cichla kelberi* (n = 67) and *C. piquiti* (n = 179), tested by Analysis of Variance (ANOVA).

Variables	$F_{1;244}$	p	Higher values
Head length	73.61	< 0.0001	*C. kelberi*
Eye position	10.24	< 0.0016	*C. kelberi*
Gape size	8.21	< 0.0046	*C. kelberi*
Mouth width	23.97	< 0.0001	*C. kelberi*
Body lateral compression	12.61	< 0.0001	*C. piquiti*
Body depth	132.1	< 0.0001	*C. kelberi*
Peduncle compression	2.82	< 0.0944	
Peduncle length	36.85	< 0.0001	*C. piquiti*
Caudal fin (height)	8.65	< 0.0038	*C. piquiti*
Caudal fin (length)	40.76	< 0.0001	*C. kelberi*

DISCUSSION

Several factors favor the coexistence of phylogenetically related species, which may involve processes related to resource availability, environmental variation, habitat heterogeneity, or niche partitioning (Putnam, 1994). Different *Cichla* species naturally coexist in their respective drainages (Kullander, Ferreira, 2006), or even when introduced (Pelicice *et al*., 2018; Franco *et al*., 2022). However, the mechanisms of coexistence remain poorly understood, and the present study provided new information about this topic, particularly in the context of artificial reservoirs. We compared population and functional traits of *C. kelberi* and *C. piquiti* coexisting in the upper section of the Lajeado Reservoir, Tocantins River, assessing ecological differences that may explain the coexistence of these closely related species and the dominance of *C. piquiti*. Both species were captured in all sampling sites over a decade (2010–2020), indicating that they colonized littoral areas of the impoundment. However, *C. piquiti* was consistently more abundant and frequent than *C. kelberi*, indicating that it was more successful. This pattern points to the existence of ecological restrictions controlling the population size and growth of *C. kelberi*, which is curious, considering that peacock basses usually proliferate in impoundments, and that *C. kelberi* is a powerful invader when non-native (Pelicice *et al*., 2018; Catelani *et al*., 2021; Franco *et al*., 2022). Moreover, these species are ecologically similar in several aspects (*i.e*., generalist piscivores, diurnal, nest guarders, limnophilic), which would grant similar ecological performance in a same environment. However, our detailed examination showed that these species share similarities and differences in multiple niche dimensions (Tab. 3). In general, they overlapped in the use of space and food, but differed in respect to body size, reproduction, morphology, and behavior, which clarify how they use resources and manage to coexist in a same locality. These differences, in particular, seem to grant greater ecological performance to *C. piquiti*, confirming our hypothesis and helping to understand its dominance and success in the impoundment.

One important finding was the significant overlap in the use of space and food. Both species coexist in the littoral zone of the impoundment, where they find refuge and food among macrophyte beds and submerged trees. We recorded both species in all sites, frequently in the same sample, revealing that these fish coexist in a same locality. In fact, null model analysis showed that their co-occurrence patterns are not random, because *C. kelberi* was usually captured together with *C. piquiti*. They also shared habitats, as most individuals were associated with macrophytes, particularly submerged plats (*i.e*., beds of *Najas microcarpa*). In addition, *C. kelberi* and *C. piquiti* were essentially piscivorous, consuming mainly small cichlids, engraulids, characids, and serrasalmids. These fish are opportunistic predators that consume a variety of small fish (Novaes *et al*., 2004; Marto *et al*., 2015), so they must feed on the same pool of prey. We found some differences in diet composition, but they are probably occasional, considering that small fish are highly diverse in this reservoir (Lucinda *et al*., 2007). Differences in sample size must have also affected diet composition (fewer stomachs of *C. kelberi*), especially because accumulation curves indicated similar levels of diet richness. Therefore, results support the idea that these species coexist in the same environment, use the same habitats, and consume similar food resources in the impoundment.

TABLE 3 | Synthesis of population and functional traits analyzed in this study, with indication of differences between species. X = higher values. - = no clear statistical difference.

Trait	*C. kelberi*	*C. piquiti*
(i) Population structure		
Abundance		X
Frequency		X
Total length		X
Total weight		X
Sex ratio	-	-
Shoaling behavior		X
(ii) Feeding		
Composition	-	-
Richness	-	-
Prey length	-	-
Large preys (> 5 cm)		X
Body condition	-	-
Fat accumulation	-	-
(iii) Reproduction		
Period		X
Effort (IGS)	-	-
Relative fecundity	-	-
Total fecundity	-	-
(iv) Ecomorphology		
Head length	X	
Eye position	X	
Gape size	X	
Mouth width	X	
Body lateral compression		X
Body depth	X	
Peduncle compression	-	-
Peduncle length		X
Caudal fin (height)		X
Caudal fin (length)	X	

Parallel to the overlap in the use of space and food, we found relevant differences in a number of traits that affect ecological and demographic performance, indicating that *C. piquiti* has some ecological advantage over *C. kelberi*. In this case, *C. piquiti* showed greater body size (length and weight), a trait associated with competitive superiority (Sanches *et al*., 2012). A large body size grants advantages during predation, considering that these predators consume small fish in the littoral zone; in fact, *C. piquiti* was able to consume larger prey. This trait may also be advantageous for reproduction, especially for territorial fish that build and guard nests – as is the case of *Cichla* species (Winemiller, 2001). In this case, larger fish may be more successful in defending territories and protecting eggs and young from predators. Another factor to consider is the shoaling behavior, a phenomenon virtually restricted to *C. piquiti*. An unpublished study (Caproni, 2017) demonstrated that sub-adults form temporary aggregations in the water column to prey upon small engraulids, indicating that shoals are formed with the specific purpose of feeding, which may enhance the foraging ability and facilitate the capture of this particular prey. This behavior should favor survival, feeding, and recruitment. Moreover, most ecomorphological traits differed between species, with *C. piquiti* having a morphology that must provide greater burst and pursuit speed, *i.e*. elongated body, larger peduncle, and higher caudal fin. *Cichla kelberi*, in turn, had a morphology more related to the life in more structured environments, *i.e*., higher body depth and larger head, in addition to its smaller body size. In fact, *C. kelberi* was captured more frequently close to the margins, which represent shallow habitats with high physical structure, suggesting that its predatory strategy is based more on ambushes than on pursuit. Therefore, a larger body size, the formation of temporary shoals, and specific morphological traits must enhance the ecological performance of *C. piquiti* in the impoundment, favoring activities related to feeding, nesting, and survival.

We also detected sharp differences in the reproductive period, even though most traits related to reproduction did not differ between species (Tab. 3). In this case, species showed a separated reproductive period, with *C. piquiti* reproducing mainly between January and July, and *C. kelberi* reproducing between September and December. In natural environments, the reproduction of *Cichla* is restricted to the low water period (Jepsen *et al*., 1999; Winemiller, 2001; Muñoz *et al*., 2006), a common pattern among cichlids, when the water level is more stabilized and nest building is safer. In the Tocantins River basin, evidence about *Cichla* reproduction in natural conditions is weak (Medeiros *et al*., 2009), but it indicates that reproduction is restricted to the dry season, *i.e*., between May and October. River regulation, however, may have affected these patterns. Lajeado Reservoir, for example, is a run-of-river impoundment that stabilized the water level; this aspect, together with constant warm temperatures, created favorable conditions for continuous reproduction along the year. Changes in reproductive traits were clearly observed in *C. piquiti* (Marto *et al*., 2015; this study), considering that reproductive fish was recorded all over the year, with more activity during the transition between the wet and dry seasons (April to July). *Cichla kelberi*, on the other hand, seemed to keep its reproductive activity restricted to the end of the dry period. Therefore, changes in reproductive tactics may have a significant demographic effect on population recruitment, especially if the reproductive period is expanded, which may constitute an important mechanism determining differences in population size. Future research must investigate possible changes in the reproduction of *C. kelberi*, and its effects on population size.

Differences in niche dimensions favor the coexistence of similar species (Pereira *et al*., 2017), which may arise from multiple factors, including evolutionary (*i.e*., species are naturally different) and ecological processes (*i.e*., interactions inducing differences). Both processes may have played a role in the present case, but ecological drivers deserve further investigation. If we consider that *C. kelberi* has successfully invaded impoundments elsewhere, this fish may be under sub-optimal conditions in Lajeado, pointing to the action of some ecological restriction. Niche partitioning between *C. kelberi* and *C. piquiti* seems a reasonable explanation, considering that these fish share the same environment, habitats, and food resources, which may elicit negative interactions and ecological adjustment. In fact, niche partitioning has been commonly reported for animals and plants (*e.g*., MacArthur, MacArthur, 1961; Putnam, 1994; Jácomo *et al*., 2004), and demographic effects have been observed in fish populations subjected to strong biotic interactions (*e.g*., Agostinho, Júlio Jr., 2002; Di Prinzio, Casaux, 2012; Gois *et al*., 2015; Ganassin *et al*., 2021). Although the present study did not assess competitive interactions, and provided no direct evidence that these species are competing for resources, future studies must investigate the hypothesis that negative interactions between *Cichla* species can affect the ecological performance and recruitment of inferior species (in this case, *C. kelberi*). Comparative studies in river stretches of the Tocantins and Araguaia rivers are needed to check abundance patterns and niche overlap in natural environments, especially because other *Cichla* species seem to partition resources in natural conditions (Jepsen *et al*., 1997). Studies with introduced populations are also fundamental, providing interesting opportunities to investigate ecological patterns in coexisting and isolated populations. These studies would contribute to improve our understanding about mechanisms modulating the coexistence of *Cichla* species in natural and modified environments.

ACKNOWLEDGMENTS

The authors thank the Universidade Federal do Tocantins (UFT), the Núcleo de Estudos Ambientais (Neamb) and the Programa de Pós-Graduação em Biodiversidade, Ecologia e Conservação (PPGBec) for providing infrastructure and support. Financial support was received from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), by providing scholarships for GSA (master thesis, process number 130799/2019 – 0) and research grants for FMP (process number 312256/2020–5).

REFERENCES

- **Agostinho CS, Júlio Jr., HF.** Observation of an invasion of the piranha *Serrasalmus marginatus* Valenciennes, 1847 (Osteichthyes, Serrasalmidae) into the Upper Paraná River, Brazil. Acta Sci. 2002; 24(2):391–95.
- **Akama A.** Impacts of the hydroelectric power generation over the fish fauna of the Tocantins River, Brazil: Marabá dam, the final blow. Oecologia Aust. 2017; 21(3):222–31. https://doi.org/10.4257/oeco.2017.2103.01

- **Albert JS, Tagliacollo VA, Dagosta F.** Diversification of Neotropical freshwater fishes. Annu Rev Ecol Evol Syst. 2020; 51:27–53. https://doi.org/10.1146/annurev-ecolsys-011620-031032
- **Andrade GS.** Abundância e distribuição *Cichla kelberi* e *Cichla piquiti* no reservatório da Usina Hidrelétrica Luís Eduardo Magalhães, Tocantins. [Monografia]. Porto Nacional: Universidade Federal do Tocantins; 2018.
- **Araújo ES, Marques EE, Freitas IS, Neuberger AL, Fernandes R, Pelicice FM.** Changes in distance decay relationships after river regulation: Similarity among fish assemblages in a large Amazonian river. Ecol Freshw Fish. 2013; 22(4):543–52. https://doi.org/10.1111/eff.12054
- **Barros G, Zuanon J, Deus C.** Effects of species co-occurrence on the trophic-niche breadth of characids in Amazon forest streams. J Fish Biol. 2017; 90(1):326–40. https://doi.org/10.1111/jfb.13183
- **Brown-Peterson NJ, Wyanski DM, Saborido-Rey F, Macewicz BJ, Lowerre-Barbieri SK.** A standardized terminology for describing reproductive development in fishes. Mar Coast Fish. 2011; 3(1):52–70. https://doi.org/10.1080/19425120.2011.555724
- **Caproni AA.** Ecologia de *Cichla piquiti* (Perciformes, Cichlidae) associado a cardumes no reservatório de Lajeado, rio Tocantins. [Monografia]: Porto Nacional: Universidade Federal do Tocantins; 2017.
- **Cardoso DC, Dehart P, Freitas CE de C, Siqueira-Souza FK.** Diet and ecomorphology of predator fish species of the Amazonian floodplain lakes. Biota Neotrop. 2019; 19(3):e20180678. https://doi.org/10.1590/1676-0611-bn-2018-0678
- **Casatti L, Castro RMC.** Testing the ecomorphological hypothesis in a headwater riffles fish assemblage of the rio São Francisco, southeastern Brazil. Neotrop Ichthyol. 2006; 4(2):203–14. https://doi.org/10.1590/s1679-62252006000200006
- **Catelani PA, Petry AC, Pelicice FM, García-Berthou E.** When a freshwater invader meets the estuary: the peacock bass and fish assemblages in the São João River, Brazil. Biol Invasions. 2021; 23:167–79. https://doi.org/10.1007/s10530-020-02363-w
- **Chase JM.** Community assembly: When should history matter? Oecologia. 2003; 136:489–98. https://doi.org/10.1007/s00442-003-1311-7
- **Connell JH, Hughes TP, Wallace CC, Tanner JE, Harms KE, Kerr AM.** A long-term study of competition and diversity of corals. Ecol Monogr. 2004; 74(2):179–210. https://doi.org/10.1890/02-4043
- **Dagosta FCP, de Pinna M.** The fishes of the Amazon: Distribution and biogreographical patterns, with a comprehensive list of species. Bull Am Mus Nat Hist. 2019; (431):1–163. https://doi.org/10.1206/0003-0090.431.1.1
- **Delariva RL, Neves MP.** Morphological traits correlated with resource partitioning among small characin fish species coexisting in a Neotropical river. Ecol Freshw Fish. 2020; 29(4):640–53. https://doi.org/10.1111/eff.12540
- **Di Prinzio CY, Casaux RJ.** Dietary overlap among native and non-native fish in Patagonian low-order streams. Ann Limnol. 2012; 48(1):21–30. https://doi.org/10.1051/limn/2011055
- **Dushoff J, Kain MP, Bolker BM.** I can see clearly now: Reinterpreting statistical significance. Methods Ecol Evol. 2019; 10(6):756–59. https://doi.org/10.1111/2041-210X.13159
- **Fernandes R, Gomes LC, Pelicice FM, Agostinho AA.** Temporal organization of fish assemblages in floodplain lagoons: The role of hydrological connectivity. Environ Biol Fishes. 2009; 85(2):99–108. https://doi.org/10.1007/s10641-009-9466-7
- **Franco ACS, Petry AC, Tavares MR, Fátima Ramos Guimarães T, Santos LN.** Global distribution of the South American peacock basses *Cichla* spp. follows human interference. Fish Fish. 2022; 23(2):407–21. https://doi.org/10.1111/faf.12624
- **Ganassin MJM, García-Berthou E, Rodrigues AC, Nascimento CP, Muniz CM, Baumgartner MT *et al*.** The invasion of an alien characiform fish and the decline of a native congener in a Neotropical river-floodplain system. Hydrobiologia. 2021; 848:2189–201. https://doi.org/10.1007/s10750-020-04454-0
- **Gilbert MC, Akama A, Fernandes CC, Albertson RC.** Rapid morphological change in multiple cichlid ecotypes following the damming of a major clearwater river in Brazil. Evol Appl. 2020; 13(10):2754–71. https://doi.org/10.1111/eva.13080

- **Gois KS, Pelicice FM, Gomes LC, Agostinho AA.** Invasion of an Amazonian cichlid in the Upper Paraná River: facilitation by dams and decline of a phylogenetically related species. Hydrobiologia. 2015; 746(1):401–13. https://doi.org/10.1007/s10750-014-2061-8
- **Gotelli NJ.** Null model analysis of species co-occurrence patterns. Ecology. 2000; 81(9):2606–21. Available from: https://ecoevol.ufg.br/adrimelo/div/Gotelli2000-NullModels.pdf
- **Gotelli NJ, Entsminger GL.** EcoSim: null models software for ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear; 2001. Available from: http://garyentsminger.com/ecosim.htm
- **Hammer Ø, Harper DAT, Ryan PD.** Past: Paleontologia statistics software package for education and data analysis. Palaeontol Electron. 2001; 4:1–09. Available from: https://palaeo-electronica.org/2001_1/past/past.pdf
- **Hardin G.** The competitive exclusion principle: An idea that took a century to be born has implications in ecology, economics, and genetics. Science. 1960; 131(3409):1292–97. https://doi.org/10.1126/science.131.3409.1292
- **Hoeinghaus DJ, Layman CA, Arrington DA, Winemiller KO.** Movement of *Cichla* species (Cichlidae) in a Venezuelan floodplain river. Neotrop Ichthyol. 2003; 1(2):121–26. https://doi.org/10.1590/S1679-62252003000200006
- **Hoeinghaus DJ, Winemiller KO, Layman CA, Arrington DA, Jepsen DB.** Effects of seasonality and migratory prey on body condition of *Cichla* species in a tropical floodplain river. Ecol Freshw Fish. 2006; 15(4):398–407. https://doi.org/10.1111/j.1600-0633.2006.00152.x
- **Hubbell SP.** Neutral theory in community ecology and the hypothesis of functional equivalence. Funct Ecol. 2005; 19(1):166–72. https://doi.org/10.1111/j.0269-8463.2005.00965.x
- **Hutchinson GE.** Homage to Santa Rosalia or why are there so many kinds of animals? Am Nat. 1959; 93(870):145–59. https://doi.org/10.1086/282070
- **Jácomo ATA, Silveira L, Diniz-Filho JAF.** Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. J Zool. 2004; 262(1):99–106. https://doi.org/10.1017/S0952836903004473
- **Jepsen DB, Winemiller KO, Taphorn DC.** Temporal patterns of resource partitioning among *Cichla* species in a Venezuelan blackwater river. J Fish Biol. 1997; 51(6):1085–108. https://doi.org/10.1111/j.1095-8649.1997.tb01129.x
- **Jepsen DB, Winemiller KO, Taphorn DC, Olarte DR.** Age structure and growth of peacock cichlids from rivers and reservoirs of Venezuela. J Fish Biol. 1999; 55(2):433–50. https://doi.org/10.1111/j.1095-8649.1999.tb00689.x
- **Kullander SO, Ferreira EJG.** A review of the South American cichlid genus *Cichla*, with descriptions of nine new species (Teleostei: Cichlidae). Ichthyol Explor Freshw. 2006; 17(4):289–398. Available from: https://www.pfeil-verlag.de/wp-content/uploads/2015/05/ief17_4_01.pdf
- **Leibold MA, Geddes P.** El concepto de nicho en las metacomunidades. Ecol Austral. 2005; 15(2):117–29. Available from: http://ojs.ecologiaaustral.com.ar/index.php/Ecologia_Austral/article/view/1460/819
- **Long ZT, Petchey OL, Holt RD.** The effects of immigration and environmental variability on the persistence of an inferior competitor. Ecol Lett. 2007; 10(7):574–85. https://doi.org/10.1111/j.1461-0248.2007.01049.x
- **Lortie CJ, Brooker RW, Choler P, Kikvidze Z, Michalet R, Pugnaire FI *et al*.** Rethinking plant community theory. Oikos. 2004; 107(2):433–38. https://doi.org/10.1111/j.0030-1299.2004.13250.x
- **Lowe-McConnell, RH.** Estudos ecológicos de comunidades de peixes tropicais. São Paulo: EDUSP; 1999.
- **Lucinda PHF, Freitas IS, Soares AB, Marques EE, Agostinho CS, Oliveira RJ.** Fish, Lajeado Reservoir, rio Tocantins drainage, State of Tocantins, Brazil. Check List. 2007; 3(2):70–83. https://doi.org/10.15560/3.2.70
- **MacArthur RH, MacArthur JW.** On bird species diversity. Ecology. 1961; 42(3):594–98. https://doi.org/10.2307/1932254
- **MacArthur R, Levins R.** The limiting similarity, convergence and divergence of coexisting species. Am Nat. 1967; 101(921):377–85. Available from: https://www.jstor.org/stable/2459090

- **Marto VCO, Akama A, Pelicice FM.** Feeding and reproductive ecology of *Cichla piquiti* Kullander & Ferreira, 2006 within its native range, Lajeado Reservoir, rio Tocantins basin. Neotrop Ichthyol. 2015; 13(3):625–36. https://doi.org/10.1590/1982-0224-20140165
- **Medeiros ER, Neuberger AL, Agostinho CS.** Variações sazonais na atividade reprodutiva de peixes na área de influência do reservatório de Peixe Angical. In: Agostinho CS, Pelicice FM, Marques EE, editors. Reservatório de Peixe Angical: bases ecológicas para o manejo da ictiofauna. São Carlos: RiMa; 2009. p.69–76.
- **Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR.** A functional approach reveals community responses to disturbances. Trends Ecol Evol. 2013; 28(3):167–77. https://doi.org/10.1016/j.tree.2012.10.004
- **Muñoz H, Van Damme PA, Duponchelle F.** Breeding behaviour and distribution of the tucunaré *Cichla* aff. *monoculus* in a clear water river of the Bolivian Amazon. J Fish Biol. 2006; 69(4):1018–30. https://doi.org/10.1111/j.1095-8649.2006.01177.x
- **Noleto EV, Barbosa MVM, Pelicice FM.** Distribution of aquatic macrophytes along depth gradients in Lajeado Reservoir, Tocantins River, Brazil. Acta Limnol Bras. 2019; 31:e6. https://doi.org/10.1590/S2179-975X9317
- **Novaes JLC, Caramaschi ÉP, Winemiller KO.** Feeding of *Cichla monoculus* Spix, 1829 (Teleostei: Cichlidae) during and after reservoir formation in the Tocantins River, Central Brazil. Acta Limnol Bras. 2004; 16(1):41–49. Available from: https://ufersa.edu.br/wp-content/uploads/sites/3/2015/02/Feeding-of-Cichla-monoculus-Spix-1829-Teleostei.pdf
- **Pelicice FM, Agostinho AA.** Fish fauna destruction after the introduction of a non-native predator (*Cichla kelberi*) in a Neotropical reservoir. Biol Invasions. 2009; 11(8):1789–801. https://doi.org/10.1007/s10530-008-9358-3
- **Pelicice FM, Azevedo-Santos VM, Esguícero ALH, Agostinho AA, Arcifa MS.** Fish diversity in the cascade of reservoirs along the Paranapanema River, southeast Brazil. Neotrop Ichthyol. 2018; 16(2):e170150. https://doi.org/10.1590/1982-0224-20170150
- **Pereira LS, Mise FT, Tencatt LFC, Baumgartner MT, Agostinho AA.** Is coexistence between non-native and native Erythrinidae species mediated by niche differentiation or environmental filtering? A case study in the upper Paraná River floodplain. Neotrop Ichthyol. 2017; 15(2):e160142. https://doi.org/10.1590/1982-0224-20160142
- **Perônico PB, Agostinho CS, Fernandes R, Pelicice FM.** Community reassembly after river regulation: rapid loss of fish diversity and the emergence of a new state. Hydrobiologia. 2020; 847(2):519–33. https://doi.org/10.1007/s10750-019-04117-9
- **Putnam RJ.** Community Ecology. New York: Chapman & Hall; 1994.
- **Ribeiro MCLB, Petrere Jr. M, Juras AA.** Ecological integrity and fisheries ecology of the Araguaia — Tocantins River basin, Brazil. Regul Rivers Res Manag. 1995; 11(3–4):325–50. https://doi.org/10.1002/rrr.3450110308
- **Sabaj MH, López-Fernández H, Willis SC, Hemraj DD, Taphorn DC, Winemiller KO.** *Cichla cataractae* (Cichliformes: Cichlidae), new species of peacock bass from the Essequibo Basin, Guyana and Venezuela. Proc Acad Nat Sci. 2020; 167(1):69–86. https://doi.org/10.1635/053.167.0106
- **Sanches FHC, Miyai CA, Costa TM, Christofoletti RA, Volpato GL, Barreto RE.** Aggressiveness overcomes body-size effects in fights staged between invasive and native fish species with overlapping niches. PLoS ONE. 2012; 7(1):e29746. https://doi.org/10.1371/journal.pone.0029746
- **Santos GM, Oliveira Jr. AB.** A pesca no reservatório da hidrelétrica de Balbina (Amazonas, Brasil). Acta Amaz. 1999; 29(1):145–63. https://doi.org/10.1590/1809-43921999291163
- **Silva JC, Gubiani ÉA, Neves MP, Delariva RL.** Coexisting small fish species in lotic neotropical environments: evidence of trophic niche differentiation. Aquat Ecol. 2017; 51(2):275–88. https://doi.org/10.1007/s10452-017-9616-5
- **Soria-Barreto M, Rodiles-Hernández R, Winemiller KO.** Trophic ecomorphology of cichlid fishes of Selva Lacandona, Usumacinta, Mexico. Environ Biol Fishes. 2019; 102:985–96. https://doi.org/10.1007/s10641-019-00884-5

- **Statsoft.** Statistica (data analysis software system). Version 7.1. Tulsa: StatSoft Inc. 2005.
- **Stone L, Roberts A.** The checkerboard score and species distributions. Oecologia. 1990; 85:74–79. https://doi.org/10.1007/BF00317345
- **Teixeira I, Bennemann ST.** Ecomorfologia refletindo a dieta dos peixes em um reservatório no sul do Brasil. Biota Neotrop. 2007; 7(2):67–76. https://doi.org/10.1590/s1676-06032007000200007
- **Tilman D.** Competition and biodiversity in spatially structured habitats. Ecology. 1994; 75(1):2–16. https://doi.org/10.2307/1939377
- **Villéger S, Brosse S, Mouchet M, Mouillot D, Vanni MJ.** Functional ecology of fish: current approaches and future challenges. Aquat Sci. 2017; 79:783–801. https://doi.org/10.1007/s00027-017-0546-z
- **Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I *et al*.** Let the concept of trait be functional! Oikos. 2007; 116(5):882–92. https://doi.org/10.1111/j.2007.0030-1299.15559.x
- **Willis SC, Macrander J, Farias IP, Ortí G.** Simultaneous delimitation of species and quantification of interspecific hybridization in Amazonian peacock cichlids (genus *Cichla*) using multi-locus data. BMC Evol Biol. 2012; 12:1471–2148. https://doi.org/10.1186/1471-2148-12-96
- **Winemiller KO.** Ecology of peacock cichlids (*Cichla* spp.) in Venezuela. J Aquaric Aquat Sci. 2001; 9:93–112.
- **Winemiller KO, Fitzgerald DB, Bower LM, Pianka ER.** Functional traits, convergent evolution, and periodic tables of niches. Ecol Lett. 2015; 18(8):737–51. https://doi.org/10.1111/ele.12462
- **Winkelmann K, Genner MJ, Takahashi T, Rüber L.** Competition-driven speciation in cichlid fish. Nat Commun. 2014; 5(3). https://doi.org/10.1038/ncomms4412

AUTHORS' CONTRIBUTION

Geovana de Souza Andrade: Conceptualization, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing-original draft, Writing-review and editing.

Fernando Mayer Pelicice: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Supervision, Visualization, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENT

The collections took place under Sistema de Autorização e Informação em Biodiversidade (license SISBIO 25774–4), approved by the Ethics Committee on the Use of Animals (CEUA) of the Universidade Federal do Tocantins (process number 23.101.001.818/2019–25).

COMPETING INTERESTS

The authors declare no competing interests.

HOW TO CITE THIS ARTICLE

- **Andrade GS, Pelicice FM.** Coexistence of endemic peacock basses (*Cichla*) in a Neotropical reservoir (Cichlidae: Cichliformes). Neotrop Ichthyol. 2022; 20(3):e220039. https://doi.org/10.1590/1982-0224-2022-0039

Neotropical Ichthyology

OPEN ACCESS

SBI
Official Journal of the
Sociedade Brasileira de Ictiologia