

Seasonality and interspecific competition shape individual niche variation in co-occurring tetra fish in Neotropical streams

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Abstract

The drivers of intraspecific niche variation and its effects on species interactions are still unclear, especially in species-rich Neotropical environments. Here, we investigated how ecological opportunity and interspecific competition affect the degree of individual trophic specialization and the population niche breadth in tetra fish. We studied the four ecologically similar species (*Psalidodon* aff. *gymnodontus*, *P. aff. paranae*, *P. bifasciatus*, and *Bryconamericus ikaa*) in subtropical headwater streams (three sites with two co-occurring species and three sites with only one species). We sampled fish in two contrasting seasons (winter/dry and summer/wet) and quantified their trophic niches using gut content analysis. *Psalidodon bifasciatus* was the only species distributed over all the sampled streams. We observed seasonal differences in population trophic niche breadth of *P. bifasciatus* just when this species co-occurred with *P. aff. gymnodontus*. These findings confirm the complex nature of the effects of interspecific competition, depending, for instance, on the identity of the competitor. The degree of individual specialization of *P. bifasciatus* was higher in the winter, and it was not influenced by the presence of another species. Conversely, the other two *Psalidodon* species studied presented greater individual specialization in the summer, when fish consumed a higher proportion of allochthonous items (terrestrial insects and seeds), and there were no effects only for *B. ikaa*. Herein, our results suggest that seasonality in food-resource availability is a major driver of niche variation and it has the potential to play an important role in how these similar tetra species interact and coexist.

Abstract in Portuguese is available with online material.

KEYWORDS

co-occurrence, freshwater, gut contents, individual specialization, southern Brazil, trophic niche breadth

1 | INTRODUCTION

Traditionally, ecological niches have been measured at the population level, indirectly assuming that individuals are functionally

equivalent (Bolnick et al., 2003). However, in the last two decades it has been widely recognized that intrapopulation niche variation is common in nature and has relevant implications for diverse ecological and evolutionary processes (Araújo et al., 2011; Bolnick

et al., 2003, 2011; Ingram et al., 2018). Individual niche specialization occurs when generalist species are composed of specialist individuals that use only narrow subsets of the total niche population (Bolnick et al., 2003). Essentially, documenting individual specialization in nature allows us to better understand how organisms use and partition resources across different organizational levels (Bolnick et al., 2003; Evangelista et al., 2014). However, the causes of intraspecific niche variation and how it may affect species interactions are still unclear (Costa-Pereira et al., 2018; Hart et al., 2016), especially in highly diverse environments (Araújo & Costa-Pereira, 2013), such as the Neotropical freshwaters.

Foraging theory and recent empirical evidence indicate that intra- and interspecific competition and ecological opportunity (i.e., diversity of available resources, sensu Araújo et al., 2011) are major factors driving niche variation within populations (Araújo et al., 2011; Costa-Pereira et al., 2018). Regarding interspecific competition, the niche variation hypothesis states that ecological release from competing species leads to population niche expansion largely via increased between-individual variation (Van Valen, 1965). However, there are conflicting results in the empirical literature, as interspecific competition has a negative or positive effect on the degree of individual specialization (Araújo et al., 2011; Bolnick et al., 2010; Costa-Pereira, Araújo et al., 2019). In turn, empirical evidence strongly suggests that intraspecific competition favors individual niche variation (Araújo et al., 2011; Svanbäck & Bolnick, 2007). The optimal foraging theory assumes that individuals tend to consume energetically favorable food (Stephens & Krebs, 1986). Because intraspecific competition tends to decrease the availability of preferred resources, individuals are expected to diverge in their trophic niches by consuming alternative items (Svanbäck & Bolnick, 2005). Therefore, resource depletion by both conspecifics and heterospecifics can affect niche variation (Araújo et al., 2011; Svanbäck & Bolnick, 2005), but this effect also depends on environmental prey availability.

Ecological opportunity is also an important driver of individual niche variation. The diversity of available prey can vary independently of the number or abundance of competing species (Araújo et al., 2011; Costa-Pereira et al., 2018). Considering both seasonal resource dynamics and consumer niche variability, empirical studies support the hypothesis that the degree of individual specialization

should increase with periods of greater resource diversity (Araújo et al., 2011; Costa-Pereira et al., 2017). In Neotropical freshwater ecosystems, higher ecological opportunity during rainy and hot periods often leads to a greater population trophic niche breadth and higher individual variation (Costa-Pereira et al., 2017; Cunha et al., 2018; Neves et al., 2018; Quirino et al., 2017; Silva et al., 2017).

Subtropical streams are dynamic and diverse environments markedly affected by seasonal variation in temperature and precipitation (Dudgeon, 2008). The winter is the dry period, when resource diversity is mainly supported by autochthonous inputs (Pujarra et al., 2017). In turn, rains are concentrated in the summer, when resource diversity increases substantially due to inputs of allochthonous materials (Lisboa et al., 2015; Tonin et al., 2017). These marked seasonal variations in resource availability in subtropical streams are expected to shape population and individual niches in line with the optimal foraging theory. However, their effects should also depend on the magnitude of interspecific competition (Costa-Pereira et al., 2017).

In Neotropical streams, several ecologically similar fish species co-occur and potentially compete for common resources. How these species interact locally has been widely studied in an interspecific perspective; however, ecological studies have rarely taken into account intraspecific variations (Baldasso et al., 2019; Neves et al., 2015; Pini et al., 2019). Among these similar co-occurring species, small characids (tetra fish) exhibit a striking diversity in morphology and life history across species, but also conspicuous variation within populations (Bonato et al., 2017; Garita-Alvarado et al., 2018; Silva et al., 2017). South American small-sized characids, mainly *Asyanax*, *Psalidodon*, and *Bryconamericus* species, are omnivorous generalist fish commonly found in the water column of streams (Bonato et al., 2017; Delariva & Neves, 2020; Neves et al., 2018). Characid species are considered as opportunistic foragers due to their ability to shift their diets according to the seasonal abundance of resources (Corrêa et al., 2011; Juncos et al., 2015; Neves et al., 2018; Silva et al., 2017). Still, due to their ecological similarities, characid species exhibit high diet similarity and thus are expected to compete for food resources with each other. Finally, considering that streams are threatened environments due to anthropogenic pressures (Castro & Polaz, 2020), knowing the factors that influence the species' niche is essential for the management and conservation of these ecosystems.

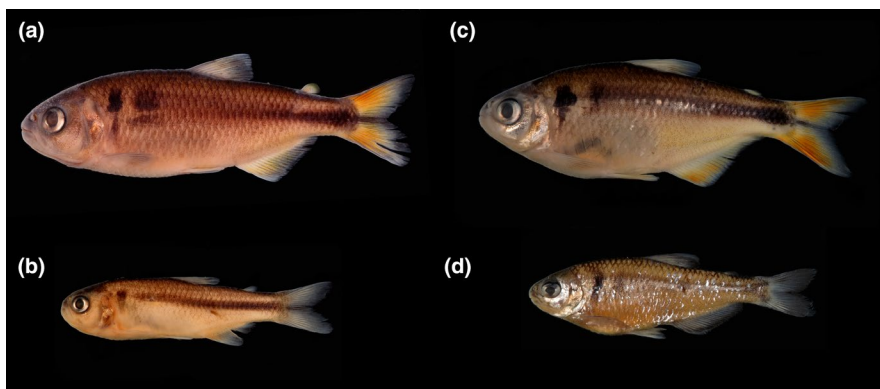


FIGURE 1 Species studied: (a) *Psalidodon* aff. *gymnodontus* (UFRGS 25,725, 95.4 mm SL); (b) *Psalidodon* aff. *paranae* (UFRGS 26,232, 48.0 mm SL); (c) *Psalidodon bifasciatus* (UFRGS 26,235, 85.0 mm SL); and (d) *Bryconamericus ikaa* (UFRGS 26,246, 49.0 mm SL)

Here, we studied trophic niche variation across individuals and populations of four species of tetra fish (genera *Psalidodon* and *Bryconamericus*) in Neotropical headwater streams. Due to their morphological (Figure 1; Baumgartner et al., 2012), resource, and microhabitat use similarities, species from these genera have high competitive potential. First, we described the diet of these species and tested how seasonality affects individual trophic specialization and population niche variation. We expected that in the summer, tetras would exhibit a wider trophic population niche and greater trophic specialization at the individual level, due to a greater diversity of available feeding resources. Then, we focused on one widely distributed species (Delariva et al., 2018), *Psalidodon bifasciatus*, which is found both in streams with and without other characid species, to test the effects of seasonality and interspecific competition on individual specialization. Then, based on the niche variation hypothesis (Van Valen, 1965), we expected to observe narrow population niches and lower individual niche specialization in populations of *P. bifasciatus* co-occurring with potential interspecific competitors.

2 | METHODS

2.1 | Study area

The Piquiri and Iguaçu rivers are direct tributaries of the Paraná River, the second largest basin in South America (Agostinho et al., 2000). This area is considered of great ecological relevance and high priority of action due to the fish richness and high degree of endemism (~70% of the fish species in Iguaçu River Basin, Baumgartner et al., 2012). In addition, the fish fauna is highly threatened by anthropogenic pressures from the construction of hydroelectric projects, agriculture, and urbanization, which highlights the need for conservation (Parolin et al., 2010). Originally, vegetation was composed by seasonal semideciduous forest and mixed ombrophilous forest. However, currently forested areas are mostly confined to conservation areas protected by law, such as parks and biological reserves. The climate of this ecoregion is humid subtropical Cfa (Köppen, 1936), with hot humid summers and cool and dry winters (Baumgartner et al., 2012). The mean annual precipitation in this region varies between 1,275 and 2,250 mm. The mean minimum and maximum temperatures range between 4 and 10°C in winter, and 23 and 33°C in summer (Baumgartner et al., 2012).

2.2 | Sampling

We sampled six headwater streams (2nd and 3th orders—Figure S1, Table S1) and collected all small characid species found: *Psalidodon* aff. *paranae* (Eigenmann, 1914), *Psalidodon bifasciatus* (Garavello & Sampaio, 2010), *Psalidodon* aff. *gymnodontus* (Eigenmann, 1911), and *Bryconamericus ikaa* Casciotta, Almirón & Azpelicueta, 2004 (Figure 1). *Psalidodon* species were recently relocated to the genus *Psalidodon* by Terán et al. (2020), and until then, they were

recognized as *Astyanax* aff. *gymnodontus*, *Astyanax* aff. *paranae*, and *Astyanax bifasciatus*. Characidae species are the most abundant species in the sampled streams, and their abundance varied from 55.4% to 83.3% of the fish assemblage. In addition to their high abundance, we choose to investigate these species due to their phylogenetic proximity and morphological similarity that make them potential competitors. In our samples, *P. bifasciatus* was abundant in streams with co-occurrence characid species (mean numerical abundance: 40.5%) and highly abundant in streams without the presence of another Characidae species (77.9%). *Psalidodon* aff. *gymnodontus* (relative abundance 49.5%), *P.* aff. *paranae* (5.6%), and *B. ikaa* (12.9%) were restricted to one location each (S1, S3, and S2, respectively). In summary, our study design includes three sites (S1, S2, and S3) with two characid species co-occurring (*P.* aff. *gymnodontus* × *P. bifasciatus*, *P.* aff. *paranae* × *P. bifasciatus*, *B. ikaa* × *P. bifasciatus*, respectively), and three sites (S4, S5, and S6) with only characid species (*P. bifasciatus*). Due to clear ecological (i.e., trophic, behavioral, microhabitat use) and morphological differences between characid and other taxonomic families, we did not consider other species of Siluriformes and Cyprinodontiformes as potential direct interspecific competitors. In addition, we did not observe any predatory species of Characidae species, as well as in previous studies carried out in streams in the study region (Baldasso et al., 2019; Delariva et al., 2018; Neves et al., 2015).

We sampled fish in July (winter) and December (summer) 2017. According to the historical climate series of the region, 2017 represents a typical year with cold and dry winter, and hot and rainy summer (Figure S2). There is solid evidence that seasonal variation in precipitation drastically alters the diversity and abundance of resources for fish (Correa & Winemiller, 2014; Novakowski et al., 2008; Soares et al., 2013; Tonin et al., 2017), including streams in our study region (Pujarra et al., 2017). In each season, we realized one sampling event per stream. We conducted the fish sampling in reaches of 50 m using electrofishing with three passes of 40 min. After capture, specimens were anesthetized, fixed in 10% formalin, and preserved in 70% alcohol. We collected fish with authorization from the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) (license number 25039-1) and approved by the Ethics Committee on Animal Use of the Universidade Federal do Rio Grande do Sul (CEUA – 32,734) in accordance with protocols in their ethical and methodological aspects for the use of fish.

2.3 | Laboratory procedures

We identified specimens in the laboratory according to specific identification keys (Baumgartner et al., 2012; Ota et al., 2018). To avoid bias caused by ontogenetic variations, we selected 403 adult individuals (Table S2). Voucher specimens were deposited in the fish collection of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul.

We analyzed the stomach contents under stereoscopic and optical microscope, and feeding items were identified to the lowest

possible taxonomic level, using specific literature for the algae (Bicudo & Bicudo, 1970) and invertebrates (Mugnai et al., 2010). We quantified the proportion of feeding items in each individual's diet following the volumetric method (Hyslop, 1980) using graduated test tubes and a glass counting plate (Hellawell & Abel, 1971).

2.4 | Data analysis

2.4.1 | Population niche breadth

We performed all statistical analyses in R version 3.5.2 (R Core Team, 2019). To investigate seasonality in population niche breadth, we used a permutational analysis of multivariate dispersions (PERMDISP; Anderson, 2006). PERMDISP was applied based on the distance of samples (diet of individuals) from the centroid of the group (species–season). In this case, distance to the centroid (D), obtained by the average of the distance of the individuals of each group (species/season) to centroid, corresponds to a metric analogous to population niche breadth (Correa & Winemiller, 2014), that is, in populations with high D value, individuals tend to vary more from diet to average population. The distance to the centroid of group defined a priori (species/season) was calculated using a principal coordinate analysis (PCoA). Calculation of the centroid of the group was performed using the dissimilarity measure of Bray–Curtis, allowing the comparison of the average dissimilarity in n -individual observations within the group. To test the null hypothesis that niche breadth did not differ among the groups, we calculated a statistical F to compare the average distance of each sample to the centroid of the group. Subsequently, we obtained P-values through 9,999 permutations of the residues of least squares (Anderson, 2006). We made post hoc pairwise comparisons among species and between seasons using Tukey's honest significant difference method. Finally, when PERMDISP revealed seasonal differences in the population niche breadth, we performed a similarity percentage analysis (SIMPER) using Bray–Curtis dissimilarity (Clarke, 1993) to identify feeding items that contributed most to the intraspecific dissimilarity between the seasons. We run PERMDISP and SIMPER in the *vegan* package (Oksanen et al., 2019).

2.4.2 | Individual specialization

First, we calculated for each individual the proportional similarity index (PS_i ; Schoener, 1968) using the following formula:

$$PS_i = 1 - 0.5 \sum_j |p_{ji} - q_j| = \sum_j \min(p_j, q_j)$$

where the variable p_{ji} describing the proportion of the j th all resources category in individual i 's diet, q_j , is the proportion of the j th resource category in the population's niche. Then, the population-wide prevalence of individual specialization (IS) is then measured by the average

of individuals' PS_i values. IS measures the average overlap between individuals' niche and the population niche (Bolnick et al., 2002; Schoener, 1968). As proposed by Bolnick et al. (2007), instead of IS we used a more intuitive metric of individual specialization: $V = 1 - IS$. High values of V (closer to 1) indicate that individuals are more specialized (Bolnick et al., 2007). We performed these metrics using the *RInSp* package (Zaccarelli et al., 2013).

2.4.3 | Drivers of individual specialization and population trophic niche

To test the effects of interspecific competition and seasonality on the degree of specialization and trophic niche breadth, we focused on *P. bifasciatus* due to its wide distribution (three sites: allopatric; three sites: in co-occurrence with other Characidae species). We constructed generalized linear mixed model (GLMM) with beta family distribution, including PS_i values and D (distance to centroid, PERMDISP) as response variables; seasons (summer or winter) and presence of potential competitor (other Characidae species; as category variable) and their interaction as fixed factors, and site as a random factor. We did visual inspection of residual plots to check model assumption, and the models were performed using the *glmmTMB* package (Brooks et al., 2017). To identify differences in individual specialization between seasons and species, we perform a generalized linear model (GLM) using beta family distribution in *betareg* package (Cribari-Neto & Zeileis, 2010), which was designed for analyzing the proportional data with values bounded between 0 and 1.

3 | RESULTS

3.1 | Diet composition

We analyzed the diet of a total of 403 individuals. Tetra fish consumed a wide diversity of feeding items (38), ranging from aquatic invertebrates to leaves and seeds (Table S2). In terms of frequency of occurrence, the most common items consumed by species were aquatic insects (43.4%), sediment/detritus (11.6%), seeds/leaves (17.1%), and Hymenoptera (8.1%). The rarest were Acarina (0.16%), Conchostraca (0.16%), Hemiptera nymphy (0.16%), Plecoptera adult (0.16%), Bivalvia (0.08%), and Oniscidae (0.08%). In general, *Psalidodon* species consumed greater proportions of allochthonous resources in the summer (*P. aff. gymnodontus*: 73.6%; *P. bifasciatus*: 75.7%; *P. aff. paranae*: 55.5%), except *B. ikaa* (Table S2). *Psalidodon aff. gymnodontus* was classified as omnivorous and consumed predominantly items of allochthonous origin in both seasons, leaves (29.9%) and seeds (26.7%) in the winter, and there was an increase in the consumption of Coleoptera (22.2%) and Hymenoptera (12.1%) in the summer. *Psalidodon aff. paranae* presented an insectivorous habit, whose consumption in the winter was based on aquatic insects (45.6%) and Hymenoptera (29.8%), and in the summer, Coleoptera (34.1%) and Auchenorrhyncha (13.4%). *Psalidodon bifasciatus* consumed mainly aquatic insects (27%)

and sediment/detritus (20.5%) in the winter, and seeds (61.3%) in the summer, and due to this substitution, it was classified as omnivorous. *Bryconamericus ikaa* exhibited an insectivorous habit with high consumption of aquatic insects in both seasons (Table S2), mainly Ephemeroptera (44.7% in the winter and 18.2% in the summer) and Trichoptera (19.6% in the winter and 16% in the summer).

3.2 | Population niche breadth

Overall, there was no influence of seasonality on population niche breadth of species (PERMDISP; Table 1; Figure 2; Table S3), except for *P. aff. gymnodontus* and *P. bifasciatus* in "S1" and *P. aff. paranae* in "S2." Specifically, in the stream "S1," in the winter, *P. bifasciatus* exhibited a greater trophic niche breadth (0.61, Table 1) and decreased in the summer (0.52). Already, *P. aff. gymnodontus* presented a lower value (0.58) in the winter and increased in the summer (0.63). Also, in the stream "S2" *P. aff. paranae* significantly broadened its alimentary spectrum in the summer (winter: 0.35; summer: 0.61), but there was no significant seasonal difference for *P. bifasciatus*. In other streams, no significant differences were observed in trophic niche breadth of *P. bifasciatus* between the seasons (Table 1). In general, according to the SIMPER analysis, seasonal differences observed in the diet of the species were related to the higher consumption of seeds in summer (Table S4).

3.3 | Individual specialization

The degree of individual specialization in *P. bifasciatus* was influenced by seasonality (β : -0.99 ; $p < .001$), but not by co-occurrence with characid species (β : 0.39 ; $p = .07$; Table 2; Figure 3). In general,

TABLE 1 Results of permutational analysis of multivariate dispersions (PERMDISP) applied to diet data of the tetra fish (Pag = *P. aff. gymnodontus*; Pap = *P. aff. paranae*; Pbi = *P. bifasciatus*; Bik = *B. ikaa*.) collected during the winter and summer seasons

Site	Species	Average distance to centroid		F	p
		Winter	Summer		
S1	Pag	0.58	0.63	$F_{1,89} = 6.10$.010
	Pbi	0.61	0.52	$F_{1,37} = 5.54$.028
S2	Pap	0.35	0.61	$F_{1,8} = 11.67$.001
	Pbi	0.6	0.58	$F_{1,45} = 0.20$.675
S3	Bik	0.52	0.59	$F_{1,29} = 1.90$.196
	Pbi	0.53	0.58	$F_{1,74} = 3.78$.053
S4	Pbi	0.55	0.55	$F_{1,31} = 0.00$.985
S5	Pbi	0.58	0.57	$F_{1,34} = 0.04$.825
S6	Pbi	0.6	0.6	$F_{1,38} = 0.00$.970

Note: Average distance from the centroid (D), F statistics, and p -values estimated by 9,999 randomizations. The significant ($p < .05$) effects are given in bold.

P. bifasciatus presented high individual specialization in the winter (Figure 3, Table 2). Conversely, the other two *Psalidodon* species (*P. aff. gymnodontus*, *P. aff. paranae*, and *B. ikaa*) exhibited higher individual specialization in the summer (Figure 3, Table 3). There were no effects of seasonality on the degree of individual specialization only for *B. ikaa* (Table 3).

4 | DISCUSSION

Tetra fish presented seasonal diet variation mainly associated with greater consumption of allochthonous resources in the summer. However, this temporal variation did not result in differences in population trophic niche breadth across seasons, except for *P. aff. paranae* and for *P. bifasciatus* when in co-occurrence with *P. aff. gymnodontus*. In turn, the degree of individual specialization of the studied species differed largely between seasons. In agreement with the optimal foraging theory, *P. bifasciatus* exhibited greater individual specialization in the winter regardless of the presence of potential competitors. It suggests a possible preference of *P.*

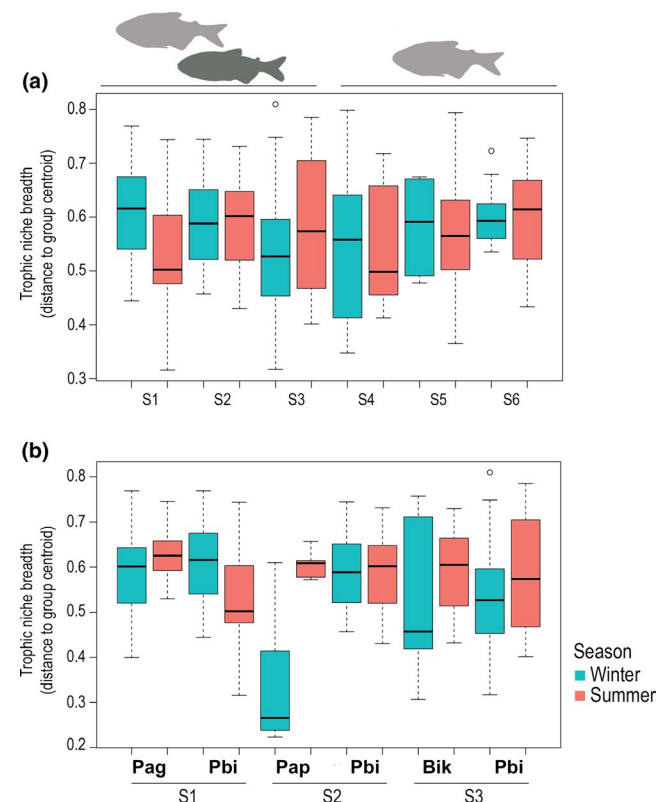


FIGURE 2 (a) Boxplot of population trophic niche breadth (estimated as distance to centroid, PERMDISP) of *P. bifasciatus* (Pbi) in streams with co-occurring characid species (S1, S2, and S3) and in allopatry (S4, S5, and S6). B) Population trophic niche breadth of three characid fish species (Pag = *P. aff. gymnodontus*; Pap = *P. aff. paranae*) in co-occurrence with *P. bifasciatus* collected during the winter and summer seasons. Box lower and upper endpoints represent the 25th and 75th quartiles, respectively. The horizontal bar inside each box represents median diet breadth

Predictor	Trophic niche breadth (D)			Individual specialization (PS _i)		
	Estimate (SE)	z	p	Estimate (SE)	z	p
Intercept	0.29 (0.06)	4.65	<.001	-1.07 (0.19)	-5.58	<.001
Season	0.01 (0.09)	0.15	.88	-0.99 (0.16)	-6.06	<.001
Number of co-occurring species	-0.05 (0.09)	-0.60	.55	0.39 (0.22)	1.79	.07
Interaction	0.07 (0.12)	0.54	.59	-0.14 (0.26)	-0.54	.59

Note: The significant ($p < .05$) effects are given in bold.

TABLE 2 Effects of seasonality, presence of interspecific competitors, and their interaction on the population trophic niche breadth (D: distance to centroid) and PS_i values of the *Psalidodon bifasciatus* in Neotropical headwater streams, southern Brazil, in the winter and summer seasons

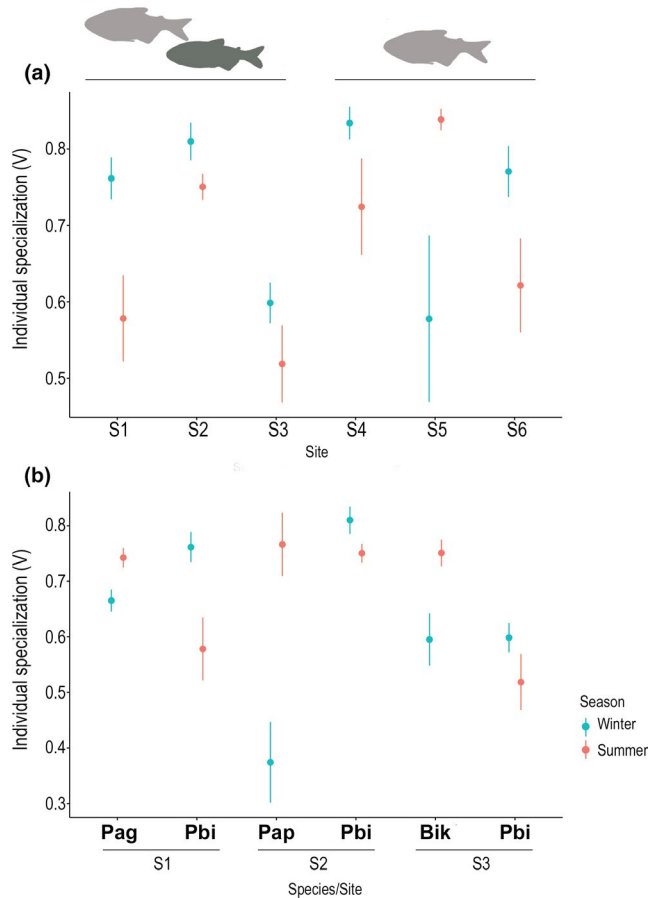


FIGURE 3 (a) Differences in individual specialization (V) of *P. bifasciatus* (Pbi) in streams with co-occurring characid species (S1, S2, and S3) and in allopatry (S4, S5, and S6). (b) In individual specialization (V) of three characid fish species (Pag = *P. aff. gymnodontus*; Pap = *P. aff. paranae*) in co-occurrence with *P. bifasciatus* collected during the winter and summer seasons. Error bars were generated based on observed values of 1-PS_i

bifasciatus for autochthonous resources (i.e., aquatic invertebrates), which has been corroborated by stable isotope analyses (unpublished data). The other two *Psalidodon* species exhibited increased individual specialization in the summer, which may be related to the seasonal increment in resource diversity during this season, mainly allochthonous resources. The absence of seasonal difference in the

TABLE 3 Effects of seasonality on PS_i values of the tetra fish (Pag = *P. aff. gymnodontus*; Pap = *P. aff. paranae*; Pbi = *P. bifasciatus*; Bik = *B. ikaa*) collected in Neotropical headwater streams, southern Brazil, in the winter and summer of 2017

Predictor variable	Estimate (SE)	z	p
Intercept	-0.63 (0.12)	-5.46	<.001
Season (Summer)	-0.33 (0.18)	-1.84	.066
Species (Pap)	1.07 (0.41)	2.64	.008
Species (Pbi)	-0.30 (0.14)	-2.09	.037
Species (Bik)	0.24 (0.25)	0.97	.331
Season (Summer): Species (Pag)	-1.09 (0.59)	-1.85	.065
Season (Summer): Species (Pbi)	0.48 (0.21)	2.28	.023
Season (Summer): Species (Bik)	-0.17 (0.37)	-0.46	.647

Note: We modeled PS_i values of species with beta regression (R function *betareg*). Model: PS_i ~ Season*Species. The significant ($p < .05$) effects are given in bold.

degree of individual specialization of *B. ikaa* may be related to the high consumption of aquatic insects in both seasons. These findings reinforce the key role that seasonal environmental variation plays in shaping niche variation both within and between species, which may have important implications for how species interact temporally, mainly for congeneric species.

Environmental prey availability in Neotropical streams is strongly determined by the continuous precipitation in the austral summer (Novakowski et al., 2008). Specifically, although high precipitation increases water flow and hinders establishment of macrobenthic community, it increments the input of allochthonous food resources (i.e., terrestrial invertebrates, fruits, seeds), and, consequently, boosts the diversity of available resources (Pujarra et al., 2017; Quirino et al., 2015). According to the foraging theory, this seasonal increment in ecological opportunity would result not only in a population niche expansion but also lead to an overall increase in individual trophic variation (Araújo et al., 2011; Costa-Pereira et al., 2017). Surprisingly, here we did not observe seasonal differences in the population trophic niche breadth, but there were seasonal variations on the degree of individual specialization of species. This pattern

is in line with the expected by the individual release hypothesis, in which individual niche expansion is offset by decreased variation among individuals, so the population niche remains unchanged (Bolnick et al., 2010). Thus, according to the optimal foraging theory, if an initially heterogeneous population experiences reduced environmental prey availability, all individuals can become more generalist and begin to include previously neglected food items in their diets (Stephens & Krebs, 1986).

In periods of higher diversity of available resources, the degree of individual specialization is expected to increase (Araújo et al., 2011; Costa-Pereira et al., 2017; Cunha et al., 2018; Lowe-McConnell, 1999). Indeed, this pattern was observed for *P. aff. gymnodontus* and *P. aff. paranae*. These species exhibited greater individual specialization in the summer (greater ecological opportunity). However, we acknowledge this result is based on the presence of these species in only one stream (*P. aff. gymnodontus* in S1 and *P. aff. paranae* in S2), and therefore, future studies should expand the spatial scale of these investigations. On the other hand, *P. bifasciatus*, the most widely distributed species in our system (Delariva et al., 2018), exhibited a distinct response with greater individual specialization in the winter (dry season). This surprising result

indicates that higher ecological opportunity may not always strongly favor individual niche variation as predicted by foraging theory and observed in most of the empirical studies. For example, the relative importance of ecological opportunity in determining individual specialization in communities can be relatively weak when compared to other ecological interactions (i.e., intraspecific competition, predation) (Costa-Pereira et al., 2018).

The distinct pattern of individual specialization displayed by *P. bifasciatus* suggests that there may be other drivers of niche variation beyond seasonality. In this sense, interspecific competition can reduce the ecological opportunity because profitable common resources are depleted by heterospecific competitors (Evangelista et al., 2014). The stream "S1" was the only case where the population trophic niche of *P. bifasciatus* differed significantly between seasons. Specifically, *P. bifasciatus* expanded significantly its trophic niche in the winter. However, contrarily, in the same stream *P. aff. gymnodontus* expanded its niche in the summer. This species-specific pattern can be related to relative abundance and competitive pressure. Interestingly, in this stream, *P. aff. gymnodontus* had higher abundance than *P. bifasciatus*, while in another streams, *P. bifasciatus* had higher abundance than another characid species.

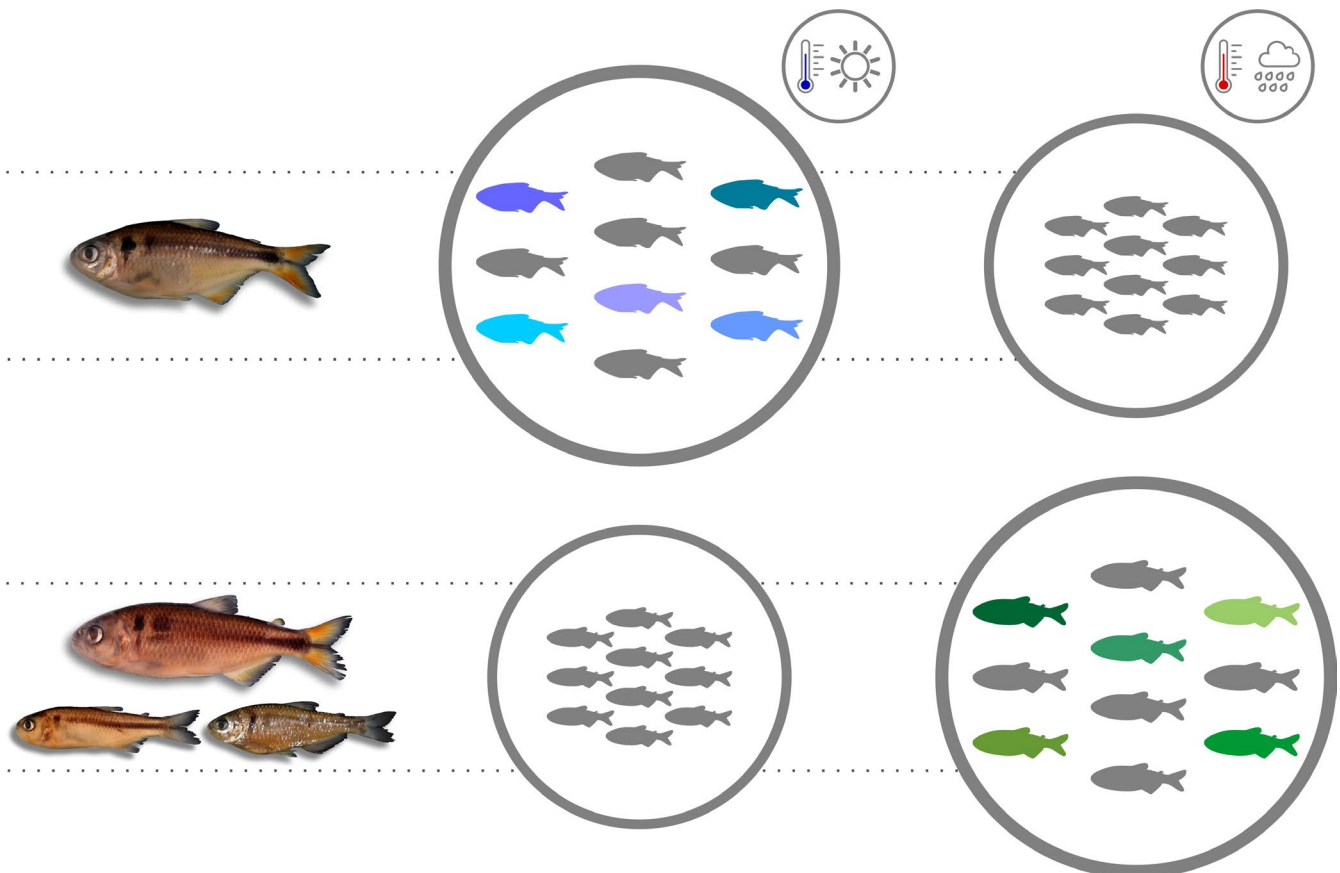


FIGURE 4 Schematic summary of the effects of seasonality in variation niche and individual specializations of the tetra fish in Neotropical headwater streams, southern Brazil. In the winter (dry season), *P. bifasciatus* tends to expand its population niche via increased between-individual variation (different colors). In the summer (wet season), *P. aff. gymnodontus*, *P. aff. paranae*, and *B. ikaa* tend to expand their population niches via increased between-individual variation (different colors). Small circles indicate niche contraction and homogenous diet among individuals

In addition, *P. aff. gymnodontus* has high morphological similarity (e.g., body size) with *P. bifasciatus* than another species (*P. aff. paranae* and *B. ikaa*). We acknowledge that this pattern emerged in only one stream and its potential explanations should be considered carefully. Future investigations should integrate species traits (e.g., body size) and their relative abundances to uncover whether *P. aff. gymnodontus* has the potential to exert greater competitive pressure on *P. bifasciatus*. Further, perhaps interspecific competition is alleviated by seasonal variations in resources and opposite patterns of trophic niche contraction between these two species. Our findings confirm the complex nature of the effects of interspecific competition, depending, for instance, on the identity of the competitor (Barros et al., 2017; Bolnick et al., 2010; Costa-Pereira et al., 2018).

The presence of interspecific, closely related potential competitors (i.e., family Characidae) had little explanatory power on the degree of individual specialization of *P. bifasciatus*. Thus, resource seasonality seems to be a more important driver of individual niche variation in this species. According to Bolnick et al. (2010), interspecific competition can increase or decrease individual specialization depending on the ecological context. Other factors like intraspecific competition can also affect and interact to determine the degree of individual specialization. Herein, the tendency toward greater individual specialization of *P. bifasciatus* in the winter may indicate a possible strategy that will give it success in periods of greater food shortages. Decreasing intraspecific competition via divergence in individual's foraging decisions can be important for this species when resources are scarce. In addition, a trophic generalist strategy in periods of greater ecological opportunity can increase the individual-level fitness (Costa-Pereira, Toscano et al., 2019). Thus, different combinations of these ecological drivers in a temporal context could lead to shifts in relative individual specialization and interaction between species, and consequently affect the coexistence of species and distribution patterns (Costa-Pereira et al., 2018). Seasonality has the potential to modulate the local maintenance of populations of species with highly competitive potential (Neves et al., 2018; Silva et al., 2017).

In conclusion, our results emphasize the importance of environmental seasonality on shaping niche variation within and across species. Importantly, these effects seem to be species-specific and context-dependent. While three of the studied species exhibit greater individual specialization in the rainy season, likely as a result of the increased diversity of available resources, *P. bifasciatus* presented greater individual specialization occurred in the dry season (Figure 4). These seasonal changes in the links between individual consumers and their prey can play an important role in altering temporally the magnitude of intra- and interspecific competition. Therefore, our results suggest that this temporal dimension of niche variation within populations has the potential to affect the coexistence of similar species, which is a promising avenue for future research. Herein, we conclude that the understanding of the dynamics of food webs within subtropical headwater streams can benefit from a perspective of intraspecific niche variation.

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CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.tqjq2bvx5> (Neves et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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