UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL

INSTITUTO DE BIOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

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PEIXES ONÍVOROS EM RIACHOS NEOTROPICAIS: RELAÇÕES ENTRE MORFOLOGIA, CONSUMO E ASSIMILAÇÃO E SUAS IMPLICAÇÕES NA COEXISTÊNCIA DE ESPÉCIES ECOMORFOLOGICAMENTE SIMILARES

PORTO ALEGRE, RS

2020

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Tese apresentada ao Programa de Pós-Graduação em Biologia Animal, Instituto de Biociências da Universidade Federal do Rio Grande do Sul, como requisito parcial à obtenção do título de Doutor em Biologia Animal.

Área de Concentração: Biologia Comparada

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Porto Alegre, RS

2020

Peixes onívoros em riachos neotropicais: relações entre morfologia, consumo e assimilação
e suas implicações na coexistência de espécies ecomorfologicamente similares

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Defesa: 11 de novembro de 2020.

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Á minha família

"Na vida, não existe nada a se temer, apenas a ser compreendido. "

Marie Curie

"But I still haven't found what I am looking for."

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AGRADECIMENTOS

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RESUMO GERAL

A coexistência de espécies é o cerne da Ecologia, especialmente em ambientes neotropicais com elevada riqueza de espécies ecomorfologicamente similares. Nesse sentido, o objetivo desse estudo foi verificar como espécies de lambaris - grupo mais diversificado da família Characidae - estão distribuídos em riachos subtropicais, utilizam recursos alimentares e coexistem localmente. Por serem classificadas como onívoras, buscou-se compreender o que elas consomem (análise de conteúdo estomacal) e assimilam (isótopos estáveis), bem como compreender como fatores extrínsecos (sazonalidade, uso e ocupação do solo da bacia hidrográfica) e intrínsecos (morfologia externa e interna) afetam o nicho trófico. As coletas foram realizadas por meio da técnica de pesca elétrica em dez riachos na região de cabeceira das bacias do Baixo Rio Iguaçu e Rio Piquiri, região oeste do Estado do Paraná. Foram coletadas seis espécies pertencentes aos gêneros *Astyanax*, *Bryconamericus* e *Psalidodon*, os quais ocorreram em alopatria ou em co-ocorrência (pares ou trio de espécies por riacho). Primariamente, *Psalidodon bifasciatus,* que era considerada endêmica da bacia do rio Iguaçu, teve sua distribuição geográfica ampliada por meio de evidências morfológicas e moleculares para a bacia do Rio Piquiri. Ademais, fatores extrínsecos, como sazonalidade e alterações do uso do solo, promoveram alterações na ingestão e assimilação de recursos pelas espécies, refletindo em variações do nicho trófico das mesmas. Além disso, fatores intrínsecos relacionados com as características morfológicas das espécies foram relevantes para partilha de recursos e baixa sobreposição alimentar. Ainda, as espécies exibiram distintos padrões de especialização individual de acordo com a sazonalidade. Especificamente, *P*. aff. *gymnodontus*, *P*. aff. *paranae* e *Bryconamericus ikaa* apresentaram maior especialização individual na estação chuvosa (verão), período de maior oportunidade ecológica. Por outro lado, *P. bifasciatus* exibiu maior especialização individual na estação seca (inverno), independente da presença de outro competidor. Consequentemente, o nicho isotópico das espécies foi afetado por variações sazonais, sendo mais contraído na estação seca (inverno) para *P. bifasciatus* e *P*. aff. *gymnodontus*. Além dos efeitos sazonais, a distribuição das espécies, bem como suas dietas e assimilações de recursos foram alteradas pelos diferentes usos do solo. Nesse aspecto, ao longo de um gradiente de redução de cobertura vegetal, o nicho isotópico de *P. bifasciatus* exibiu uma relação não-linear, sendo mais amplo nos riachos com maior riqueza de espécies e contraído nos riachos

com menor diversidade de peixes. Além de alterar a oferta e diversidade de recursos alimentares, a redução da cobertura vegetal no entorno dos riachos afetou indiretamente a interação de espécies. Destaca-se que a maior especialização individual de *P. bifasciatus* no período de maior escassez de recursos, juntamente com sua capacidade de ampliar seu nicho isotópico na presença de mais competidores em ambientes antropizados, pode ser a chave para compreender sua ampla distribuição e resiliência. Além dos fatores extrínsecos, verificou-se que a características morfológicas externas e internas das espécies também podem promover partição de recursos e diferentes usos do habitat. Dessa forma, espécies filogeneticamente mais próximas apresentaram tendência de divergência morfológica e trófica-. Em geral, espécies com corpo mais alongado, dentes pentacuspidados e intestino mais curtos (como *B. ikaa* e *P.* aff. *paranae*), assimilaram predominantemente invertebrados aquáticos. Por outro lado, espécies com corpo mais alto, dentes hepatcuspidados e intestino mais longos (a exemplo *P. bifasciatus* e *P.* aff. *gymnodontus*) assimilaram maiores proporções de invertebrados terrestres. Apesar das consideráveis proporções de material vegetal (folhas e sementes) ingeridos pelas espécies, nenhuma delas assimilou esse recurso. As espécies aqui estudadas não apresentaram características morfológicas a nível macro e microscópico que facilite a digestão e absorção de material vegetal. Assim, a partir do robusto aporte de dados sobre a ecologia trófica das espécies aqui avaliadas, conclui-se que a coexistência de pequenos caracídeos em riachos é facilitada por divergências morfológicas, que favorecem a partilha de recursos e baixa sobreposição, juntamente com as variações sazonais na oferta de recursos. Aponta-se que os impactos antrópicos afetam a interação de espécies, o que pode promover, por consequência, efeitos negativos nas redes tróficas e funcionamento dos ecossistemas.

Palavras chave: Characidae, dieta, isótopos estáveis, nicho trófico, ecomorfologia, sazonalidade, uso do solo

ABSTRACT

Species coexistence is the core of Ecology, especially in Neotropical environments with a high richness of ecomorphologically similar species. The main goal of this study was to verify how species of tetra fish species - the most diverse group of the family Characidae - are distributed in subtropical streams, use food resources and coexist locally. Because they are classified as omnivorous, we sought to understand what they consume (stomach content analysis) and assimilate (stable isotopes), as well as understanding how extrinsic (seasonality, land use) and intrinsic (external and internal morphology) factors affect their trophic niche. The field sampling campaigns were carried out using electrofishing in ten streams in the headwaters of the Lower Iguaçu and Piquiri river basins, in the western region of the State of Paraná. Six species belonging to the genera *Astyanax*, *Bryconamericus* and *Psalidodon* were collected, which occurred in allopathy or in co-occurrence (pairs or trio of species per stream). Primarily, *Psalidodon bifasciatus*, which was considered endemic to the Iguaçu River basin, had its geographic distribution expanded through morphological and molecular evidence for the Piquiri River basin. Extrinsic factors, such as seasonality and changes in land use, promoted changes in the consumption and assimilation of resources by species, reflecting variations in their trophic niche. In addition, intrinsic factors related to the morphological traits of the species were relevant for resource sharing and low food overlap. Furthermore, the species exhibited different patterns of individual specialization according to seasonality. Specifically, *P*. aff. *gymnodontus*, *P*. aff. *paranae* and *Bryconamericus ikaa* showed greater individual specialization in the rainy season (summer), a period of greater ecological opportunity. On the other hand, *P. bifasciatus* exhibited greater individual specialization in the dry season (winter), regardless of the presence of another competitor. Consequently, the isotopic niche of the species was affected by seasonal variations, being more contracted in the dry season (winter) for *P. bifasciatus* and *P*. aff. *gymnodontus*. In addition to seasonal effects, the distribution of species, as well as their diets and resource assimilations, have been altered by different land uses. In this respect, along a gradient of vegetation reduction, the isotopic niche of *P. bifasciatus* exhibited a non-linear feature, so that it was broader in streams with greater fish richness and contracted in streams with less richness. Therefore, in addition to changing the supply and diversity of food resources, the reduction of native vegetation cover around streams indirectly affects species interaction.

Both the greater individual specialization in the period of greatest resource scarcity ability to expand its isotopic niche in the presence of more competitors in anthropized environments, may be the key to understanding the wide distribution and resilience of *P. bifasciatus*. In addition to extrinsic factors, the external and internal morphological traits of the species can also promote resources partioning and different uses of the habitat. Phylogenetically closed species tend to diverge in morphology and diet. Species with elongated body, pentacuspid teeth and a shorter intestine (such as *B. ikaa* and *P.* aff. *paranae*), predominantly assimilated aquatic invertebrates. In contrast, species with deeper body, hepatcuspidated teeth and longer intestine (such as *P. bifasciatus* and *P.* aff. *gymnodontus*) assimilated higher proportions of terrestrial invertebrates. Despite the considerable proportions of plant material (leaves and seeds) ingested by the species, none of them assimilated this resource. Descriptively, the species studied here did not present morphological traits at the macro and microscopic level that facilitate the digestion and absorption of plant material. In conclusion, from the robust supply of data on the trophic ecology of the species evaluated here, the coexistence of small characids in streams can be facilitated by morphological divergences, which favor the resource partitioning and low overlap, along with seasonal variations in resource availability. Concerning the anthropic impacts affected the interaction of species, which can consequently promote negative effects on the food-webs and the functioning of ecosystems.

Key words: Characidae, diet, stable isotopes, trophic niche, morphological traits, seasonality, land use

INTRODUÇÃO GERAL

Compreender como as espécies coexistem localmente é ainda um dos principais desafios da Ecologia (Chesson, 2000), especialmente em ambientes altamente diversificados como a região Neotropical. Para isso, identificar diferenças ecológicas interespecíficas e como elas afetam a coexistência e o nicho das espécies é uma tarefa crucial (Ousterhout *et al.*, 2019). No caso de espécies similares que ocupam a mesma posição trófica, a Teoria de Nicho (Chesson, 2000; Chase & Leibold, 2003) prediz que tal coexistência ocorre somente quando as espécies diferem na força de interações bióticas e requerimentos ambientais, como temperatura, oportunidade ecológica, e recursos. Portanto, investigar os diversos eixos do nicho das espécies é o primeiro passo para inferir sobre essas relações.

Nos ambientes aquáticos tropicais, a coexistência de espécies pode ser facilitada pela elevada plasticidade trófica (Chase & Leibold, 2003). A onivoria é uma estratégia alimentar onde consumidores se alimentam de múltiplos níveis tróficos (Pimm & Lawton, 1978; Pimm, 1982; Pimm *et al.*, 1991; Kratina *et al.*, 2012). Embora, geralmente refira-se à alimentação de itens de origem animal e vegetal, onivoria também inclui casos onde um consumidor intermediário e seu predador competem por recursos compartilhados (Polis *et al.*, 1989; Holt & Polis, 1997; Ingram *et al.*, 2012). Especificamente em riachos neotropicais, a onivoria é representada por espécies de peixes de pequeno porte da família Characidae, popularmente conhecidos como lambaris. Entre esses, *Astyanax*, *Bryconamericus* e *Psalidodon* são os gêneros com maior riqueza de espécies e amplamente distribuídos (Eschmeyer *et al.*, 2020; Rossini *et al.*, 2016; Bonato *et al.*, 2017; Silva *et al.*, 2017; Terán *et al.*, 2020). Espécies desses gêneros são consideradas oportunistas devido a habilidade de mudarem sua dieta de acordo com variações espaço temporais na disponibilidade de recursos (Juncos *et al.*, 2015; Quirino *et al.*, 2015; Ruiz-Cooley *et al.*, 2017; Neves *et al.*, 2018). Ainda, embora haja vários estudos que relatam os recursos alimentares ingeridos (Delariva *et al.*, 2013; Silva *et al.*, 2017; Neves *et al.*, 2018; Pini *et al.*, 2019), pouco se sabe sobre o que essas espécies realmente assimilam, especialmente em relação a matéria vegetal consumida (Bonato *et al.*, 2017; Costa-Pereira *et al.*, 2017).

Lambaris também são reconhecidos pela elevada similaridade morfológica (Terán *et al.*, 2020). Essas espécies possuem um corpo comprimido lateralmente associada a grandes

nadadeiras anais que confere elevado potencial de manobrabilidade permitindo a exploração de vários compartimentos do habitat e a ocupação de vários nichos ecológicos diferentes (Ornelas-García *et al*., 2018; Portella *et al*., 2016; Delariva & Neves, 2018). A rápida radiação adaptativa deste grupo pode estar associada com as suas características morfológicas e elevada plasticidade trófica (Reis *et al*., 2016). Portanto, devido a essas características, é esperado que essas espécies possuam um elevado potencial competitivo e maior sobreposição de nicho (Gatz, 1979; Rocha *et al*., 2011). Contudo, estudos que investigaram a dieta de pequenas espécies de lambaris indicaram uma baixa sobreposição de nicho trófico (Portella *et al*., 2016; Silva *et al*., 2017; Bonato *et al*., 2018; Neves *et al*., 2018). Isso ressalta a necessidade de entender quais mecanismos estão associados a essa baixa sobreposição mesmo para espécies com elevada similaridade ecomorfológica. Nesse sentido, pesquisar como fatores extrínsecos (ex. sazonalidade, uso do solo, competição) e intrínsecos (ex. características morfológicas, alimentação, assimilação) alteram o nicho dessas espécies é essencial para elucidar como e quais mecanismos ecológicos estão atrelados a coexistência.

A Teoria de Forrageamento Ótimo e recentes evidências empíricas indicam que competição intra-interespecífica e oportunidade ecológica (ex. diversidade de recursos disponíveis, *sensu* Araújo *et al*., 2011) são os principais promotores de variação de nicho dentro de populações (Araújo *et al*., 2011; Costa-Pereira *et al*., 2018). Em relação à competição interespecífica, a Hipótese de Variação de Nicho afirma que a liberação ecológica ("*ecological release*") de espécies competidoras leva à expansão do nicho populacional em grande parte por meio do aumento da variação entre os indivíduos (Van Valen, 1965). Entretanto, há resultados conflitantes na literatura, como, por exemplo, se a competição interespecífica tem um efeito negativo ou positivo no grau de especialização individual (Bolnick *et al*., 2010; Araújo *et al*., 2011; Costa-Pereira *et al*., 2019). Por sua vez, a evidência empírica sugere fortemente que a competição intraespecífica favorece a variação de nicho individual (Svanback & Bolnick, 2007; Araújo *et al*., 2011). A Teoria de Forrageamento Ótimo pressupõe que os indivíduos tendem a consumir alimentos que permitam a maior conservação de energia possível, ou seja energeticamente favoráveis em relação ao custo-benefício (Stephens & Krebs, 1986). Como a competição intraespecífica tende a diminuir a disponibilidade de recursos preferenciais, espera-se que os indivíduos divirjam em seus nichos tróficos consumindo itens alternativos (Svanback & Bolnick, 2005).

Portanto, o esgotamento de recursos tanto por co-específicos quanto por heteroespecíficos pode afetar a variação de nicho (Svanbäck & Bolnick, 2005; Araújo *et al*., 2011), mas esse efeito também depende da disponibilidade ambiental de recursos alimentares.

Nesse sentindo, a sazonalidade pode ser uma fonte natural de variação na oferta de recursos e favorecer espécies oportunistas. Peixes onívoros em riachos neotropicais comumente vivenciam uma estação com elevada abundância de recursos alimentares, seguido por uma estação de escassez de recursos, correspondendo a estação chuvosa e seca, respectivamente (Pujarra *et al*., 2017; Quirino *et al*., 2017). A precipitação contínua durante a estação chuvosa aumenta o fluxo da água, o que por um lado dificulta o estabelecimento de macroinvertebrados aquáticos (Pujarra *et al*., 2017), mas aumenta o *input* de invertebrados terrestres e material vegetal (Lisboa *et al*., 2015; Tonin *et al*., 2017). Os subsídios alóctones são substancialmente reduzidos na estação seca, quando os peixes se alimentam predominantemente de recursos autóctones (Soares *et al*., 2013; Correa & Winemiller, 2014). Recentes trabalhos sugerem que variações sazonais relacionadas com a precipitação alteram a disponibilidade de recursos alimentares em diversos ambientes aquáticos, como planícies de inundação, lagos, rios e lagunas costeiras, e que promovem mudanças no nicho trófico de caracídeos (Quirino *et al*., 2015; Costa-Pereira *et al*., 2017; Garcia *et al*., 2017; Silva *et al*., 2017; Neves *et al*., 2018). Em riachos, os efeitos das mudanças temporais na dieta de onívoros em co-ocorrência e que utilizam recursos similares ainda são escassos. Portanto, entender as variações de nicho, especialmente em períodos de baixa disponibilidade de recursos e na presença de competidores, pode facilitar nossa compreensão sobre como elas coexistem localmente (Pereira *et al*., 2010; Igram *et al*., 2012; Wooton, 2017).

As variações sazonais naturais na oferta de recursos podem ser negativamente alteradas por mudanças no uso do solo no entorno de riachos. O desmatamento é uma das principais causas de perda de biodiversidade (Tofóli *et al*., 2017, Castro & Polaz, 2020). Especialmente em ambientes aquáticos, a redução da mata ciliar promove alterações físico-químicas, como maior sedimentação, aumento da temperatura devido a maior incidência solar acirrada pela redução da profundidade e maior aquecimento da massa de água, aporte de nitrogênio e outros componentes químicos oriundos de atividades agrícolas e urbanas (Casatti, 2010). Esses distúrbios antropogênicos, consequentemente, alteram a diversidade e

disponibilidade de recursos e afeta diretamente a dieta de espécies onívoras, como os lambaris (Ferreira *et al*. 2012; Carvalho *et al*., 2019a; Magioli *et al*., 2019; Zeni *et al*., 2019). Porém, o forrageamento adaptativo dessas espécies permite que eles ajustem sua aquisição de recursos (Kratina *et al*., 2012), o que facilitaria sua persistência em face a distúrbios antropogênicos (Tunney *et al*., 2012; Carvalho *et al*., 2019b). Nesse sentido, o nicho trófico das espécies pode refletir mudanças na oferta de recursos e também a competição com espécies invasoras, comumente registradas em ambientes impactados. Além disso, investigações sobre os efeitos do uso do solo no nicho trófico de espécies onívoras em riachos neotropicais ainda são incipientes para entender como algumas espécies conseguem sobreviver em ambientes drasticamente modificados.

Além da influência dos fatores extrínsecos mencionados, variações nas características morfológicas podem afetar a maneira como as espécies interagem entre si e, também, com o ambiente (Winemiller, 1991; Oliveira *et al*., 2010). Nesse sentido, a morfologia é capaz de predizer os padrões alimentares das espécies e seus usos do habitat (Gatz, 1979; Winemiller *et al*., 1995; Bonato *et al*., 2017; Baldasso *et al*., 2019). Especificamente para peixes, características morfológicas externas, como forma do corpo e posição da boca, são relacionadas com a habilidade locomotora e captura de presas (Motta *et al*., 1995; Russo *et al*., 2008; Barros *et al*., 2019; Keppeler & Winemiller, 2020). Já as características morfológicas internas, como dentes e comprimento de intestino, contribuem para a maceração, digestão e absorção do alimento (Delariva & Agostinho, 2001; Bonato *et al*., 2017; Garita-Alvarado *et al*., 2018). Adicionalmente, os estudos histológicos fornecem subsídios para a caracterização do trato digestivo, o que permite compreender a fisiologia e o hábito alimentar das espécies (Végaz-Velez, 1972, Fugi & Hahn, 1991; Albrecht *et al*., 2001).

As relações entre morfologia e dieta são mais evidentes em espécies especialistas, como detritívoras e piscívoras (Delariva & Agostinho, 2001; Burres *et al*., 2018; Bonato *et al*. 2017), cujas especializações morfológicas permitem a captura, ingestão e digestão bem-sucedida de recursos específicos (ex. detrito e peixes, respectivamente). Entretanto, a relação entre morfologia e dieta é menos evidente em espécies ecomorfologicamente similares (Burres *et al*., 2016b; Culumber & Tobler, 2016; Portella *et al*., 2016; Delariva & Neves,

2020). A investigação dessas variações morfológicas sutis nos permite determinar como elas compartilham recursos e coexistem em alta abundância e riqueza entre os ecossistemas tropicais.

A morfologia pode influenciar as interações ecológicas e o uso do habitat, e, portanto, moldar o nicho das espécies ao longo de suas trajetórias evolutivas (Ackermann & Doebeli, 2004). Nesse sentido, o conservacionismo de nicho filogenético (Harvey & Pagel, 1991) prevê que espécies proximamente relacionadas têm nichos ecológicos mais semelhantes e, portanto, maior potencial de competição do que espécies mais distantes filogeneticamente (Cachera & Le Loc'h, 2017). No entanto, em águas doces tropicais, a alta riqueza de espécies co-ocorrentes similares intriga os ecólogos, pois a divergência ecológica entre espécies intimamente relacionadas é mais comum do que o esperado (Sidlauskas, 2008, Pyron *et al*., 2015; Wang *et al*., 2017; Ornelas-García *et al*., 2018). Embora a similaridade filogenética ou morfológica tenha sido usada como proxy para similaridade ecológica (Morales-Castilla *et al*., 2015), poucos estudos testaram diretamente esta suposição para espécies de ecomorfologicamente similares de pequeno porte em riachos, como os lambaris (Keppeler & Winemiller, 2020). Portanto, uma abordagem que investigue os efeitos combinados de diferenças ecológicas e relações filogenéticas em nichos ecológicos é essencial para avançar nossa compreensão sobre a coexistência de espécies similares em diversos habitats tropicais.

Recentemente, as relações filogenéticas de Characidae foram reavaliadas por meio de inferências com dados morfológicos e moleculares, resultando na ressurreição do gênero *Psalidodon*, onde muitas espécies pertencentes ao gênero *Astyanax* foram realocadas para o gênero *Psalidodon* (Terán *et al*., 2020). Juntamente com os estudos taxonômicos, o conhecimento sobre a ecologia trófica dessas espécies tem crescido, mas uma investigação integrada sobre sua biologia evolutiva combinando relações filogenéticas e ecologia ainda não foi realizada (Mise *et al*., 2013; Portella *et al*., 2016; Bonato *et al*., 2017; Silva *et al*., 2017; Delariva & Neves, 2020; Nascimento *et al*., 2020). Atualmente não se sabe se as espécies filogeneticamente mais próximas também apresentam maior similaridade morfológica e trófica (conservacionismo de nicho), ou se divergem em seus traços (morfologia e dieta incongruentes com a filogenia). Essa é uma questão fundamental que pode elucidar como essas espécies evoluíram e são capazes de coexistir em seus habitats.

Nosso entendimento sobre a ecologia trófica de caracídeos vem principalmente das análises de conteúdo estomacal (Quirino *et al*., 2015, Silva *et al*., 2017; Neves *et al*., 2018; Pini *et al*., 2019), que indicam os recursos recentemente ingeridos (Hyslop, 1980; Di Beneditto *et al*., 2013; Park *et al*., 2015). Porém, dada a falta de especialização morfológica, principalmente interna, ainda não está claro se essas espécies podem assimilar a matéria vegetal ingerida (Clements *et al*., 2009; Pelster *et al*., 2015). Assim, a análise de isótopos estáveis pode ser útil para verificar se quais itens da dieta ingeridos são realmente assimilados aos tecidos em uma escala temporal mais ampla (por exemplo, ~ três meses; DeNiro & Epstein, 1981; Post, 2002; Fry, 2006; Boecklen *et al*., 2011; Bastos *et al*., 2017; Nielsen *et al*., 2018). O uso integrado dessas ferramentas permite uma melhor compreensão sobre as relações entre morfologia e a dieta dos peixes, bem como análise mais contundente dos seus nichos tróficos (Costa-Pereira *et al*., 2017; Bonato *et al*., 2018; Ornelas-García *et al*., 2018; Garita-Alvarado *et al*., 2018; Carvalho *et al*., 2019a)

Diante da incipiente base de dados sobre a biologia e ecologia básicas de peixes caracídeos de pequeno porte em riachos, cujas informações são fundamentais para compreender os mecanismos ecológicos que permeiam a coexistência, esse trabalho teve como principal objetivo investigar os efeitos dos fatores extrínsecos e intrínsecos na ecologia trófica de espécies onívoras e ecomorfologicamente similares. Para atingir esse objetivo, a área de estudo selecionada foi a região de divisa das bacias do Baixo rio Iguaçu e Piquiri. A bacia do baixo rio Iguaçu se destaca principalmente pela baixa diversidade de espécies (~ 6-15 espécies riachos; Abilhoa *et al*., 2008; Delariva *et al*., 2018) e elevado endemismo (Baumgartner *et al*., 2012). Já, a bacia do rio Piquiri exibe elevada diversidade (Graça & Pavanelli, 2007). Além da abundância e diversidade de espécies onívoras, estudos de ecologia trófica nesses ambientes foram realizados unicamente por análises de conteúdo estomacal. Juntamente com a presença de variações sazonais relacionadas a precipitação nessa região, essas características fornecem o cenário ideal para testar hipóteses e verificar padrões que permitam a melhor compreensão sobre a onivoria em riachos neotropicais. Assim, esse estudo foi dividido em seis capítulos (Figura 1):

- O primeiro capítulo foi oriundo de um minucioso processo de identificação das espécies de caracídeos coletados em riachos da bacia do Baixo Rio Iguaçu e Rio Piquiri. Por

meio de análises morfológicas e moleculares, a distribuição geográfica de *Psalidodon bifasciatus*, que até então era considerada endêmica da bacia do Rio Iguaçu, foi ampliada para riachos da bacia do Rio Piquiri.

- No segundo capítulo investigou-se como a oportunidade ecológica e a competição interespecífica afetam o grau de especialização individual e a amplitude de nicho populacional de lambaris em riachos subtropicais. Nós hipotetizámos que no verão os lambaris exibissem um nicho populacional trófico mais amplo e uma maior especialização trófica em nível individual, devido a uma maior diversidade de recursos alimentares disponíveis. Em seguida, focamos em uma espécie amplamente distribuída (Delariva et al., 2018), *Psalidodon bifasciatus*, encontrada em riachos com e sem outras espécies de caracídeos, para testar os efeitos da sazonalidade e da competição interespecífica na especialização individual. Então, com base na Hipótese de Variação de Nicho (Van Valen, 1965), esperávamos observar nichos populacionais estreitos e menor especialização de nicho individual em populações de *P. bifasciatus* co-ocorrendo com competidores interespecíficos potenciais.

- O terceiro capítulo combinou análises de conteúdos estomacais e isótopos estáveis para determinar como a variação sazonal na disponibilidade de recursos influencia o consumo e assimilação de recursos alimentares por duas espécies sintópicas do gênero *Psalidodon* na bacia do Baixo Rio Iguaçu. Nós hipotetizamos uma mudança no consumo de recursos e assimilação de principalmente recursos aquáticos na estação seca, para recursos principalmente terrestres durante a estação chuvosa. Com base nas previsões da teoria da competição (Pianka 1974; Schoner 1974), esperávamos nichos tróficos mais amplos, maior sobreposição de nicho e maior grau de onivoria na estação chuvosa devido à elevada abundância e diversidade de recursos alóctones. Em contraste, esperávamos nichos tróficos reduzidos na estação seca caracterizada pela diversidade de recursos reduzida e dominância de recursos autóctones. Também hipotetizamos que ambas as espécies se alimentariam em posições tróficas mais elevadas durante a estação seca, devido a uma dieta composta principalmente de recursos animais. Finalmente, esperávamos que ambas as espécies compartilhassem recursos alimentares durante os períodos de maior diversidade de recursos (estação chuvosa) e focassem sua dieta nos recursos preferidos durante os períodos de

escassez de recursos (estação seca). Essas informações melhorariam nossa compreensão dos mecanismos que facilitam a coexistência de onívoros ecomorfologicamente semelhantes em diversos ecossistemas neotropicais.

- O quarto capítulo teve como objetivo verificar como a redução de cobertura vegetal nativa afeta a dieta e nicho trófico de peixes onívoros (gêneros *Astyanax*, *Bryconamericus* e *Psalidodon*) em riachos das bacias do Baixo Rio Iguaçu e Rio Piquiri, usando análises de conteúdo estomacal e isótopos estáveis. Nós hipótetizamos que: i) como resultado da redução da cobertura vegetal, os peixes onívoros aumentam a ingestão de carbono C4 de monoculturas de grãos em áreas agrícolas e gramíneas em áreas urbanas; ii) aumento dos valores de $\delta^{15}N$ associados ao uso de fertilizantes em áreas agrícolas; iii) peixes onívoros têm variância isotópica reduzida com cobertura de vegetação nativa reduzida devido à diminuição da diversidade de recursos alimentares, mas pode depender do número de competidores; iv) peixes onívoros trocam seu consumo e assimilação de recursos autóctones com energia de alta qualidade em áreas florestais por recursos de baixo recurso nutricional (por exemplo, detritos) e recursos alóctones (invertebrados terrestres) em áreas com cobertura vegetal reduzida; v) como resultado da redução da diversidade de recursos, peixes onívoros diminuem na posição trófica indicando uma diminuição no grau de onivoria de acordo com a redução da cobertura vegetal no entorno dos riachos. Nesse contexto, esperava-se entender melhor sobre as características tróficas que facilitam a persistência de peixes onívoros em ambientes com diferentes graus e tipos de distúrbios antrópicos.

- O quinto capítulo analisou se as características morfológicas (forma corporal e aparato trófico interno) estão associadas com a dieta e nicho trófico (conteúdo estomacal e isótopos estáveis) e se essas características são congruentes com as relações filogenéticas de espécies de lambaris em riachos neotropicais. Além disso, verificar se a assimilação relativa dos recursos corresponde ao consumo relativo, como descrito pela análise convencional do conteúdo estomacal, bem como avaliar a existência de partição de recursos entre as espécies. Nós testamos a hipótese de que características morfológicas externas e internas estão associadas ao nicho trófico e que essas características são congruentes com a relação filogenética dos lambaris analisados. Esperávamos que espécies intimamente relacionadas fossem similares em seus traços morfológicos, e a coexistência entre eles fosse favorecida

pela partição de nicho resultando em baixa sobreposição de nicho. Considerando que essas espécies co-ocorrem em diferentes combinações de pares de espécies em riachos individuais, sua coexistência pode ser influenciada pela identidade de espécies co-ocorrentes. Os resultados desta análise integrada entre morfologia, dieta e filogenia podem ajudar a entender a biologia das espécies e suas interações ecológicas com implicações para a sua coexistência em riachos Neotropicais.

- O sexto capítulo teve como objetivo caracterizar a histomorfologia e histoquímica do trato digestivo de três espécies de caracídeos (*Psalidodon bifasciatus*, *P.* aff. *gymnodontus* e *Bryconamericus ikaa*), usando anatomia macroscópica e microscopia de luz, a fim de compreender as relações dessas características com o hábito alimentar. Assim, aumentar o conhecimento disponível a respeito dos aspectos morfofuncionais da digestão em peixes neotropicais onívoros e entender como essas características podem estar elacionados com a elevada plasticidade trófica reconhecida para essas espécies.
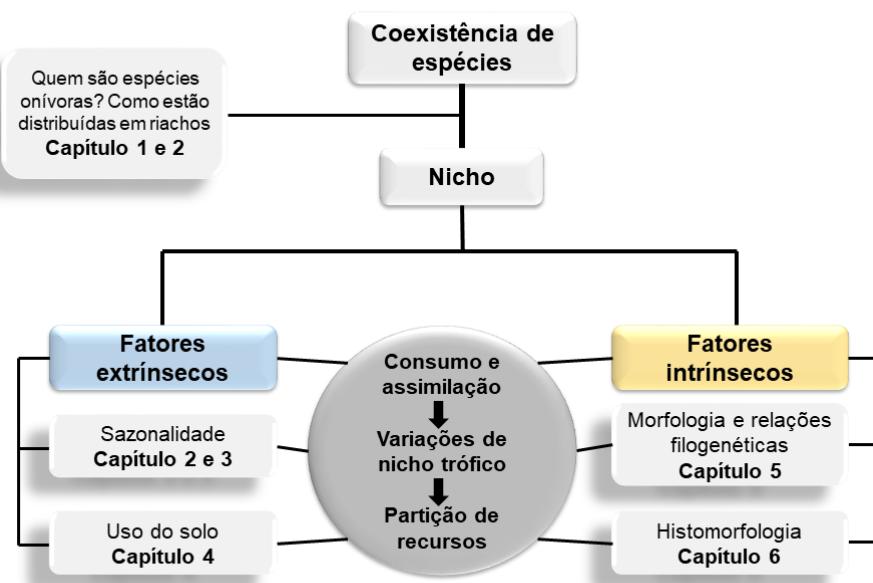
Figura 1. Organograma de estrutura de tese indicando os principais temas abordados em cada capítulo que visam compreender os fatores que facilitam a coexistência de peixes caracídeos (lambaris) em riachos neotropicais.

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Chapter 1

First record of *Astyanax bifasciatus* Garavello & Sampaio, 2010 (Teleostei, Ostariophysi, Characidae) in the Piquiri river basin, upper Paraná river basin

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First record of *Astyanax bifasciatus* Garavello & Sampaio, 2010 (Teleostei, Ostariophysi, Characidae) in the Piquiri river basin, upper Paraná river basin

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Abstract

Astyanax bifasciatus Garavelo & Sampaio, 2010 was originally described as endemic to the Iguaçu river basin. Between March 2017 and January 2018, specimens of *A. bifasciatus* were sampled during expeditions to headwater streams of the Piquiri river basin, upper Paraná river basin. The identification was confirmed both by morphological and molecular analyses, representing, therefore, the first record of the species outside of the basin of the Iguaçu River. In addition, the lack of structuring in the haplotype network confirms that the representatives of *A. bifasciatus* from both basins appear to comprise a single population.

Introduction

Astyanax Baird & Girard, 1854 is the richest genus of the Characidae with about 180 valid species (Fricke et al. 2019). Most species are highly morphologically similar and lack unique diagnostic characters making the process of accurately identifying species difficult (Rossini et al. 2016; Silva 2017). In the Iguaçu river basin, *Astyanax* is the most diverse and abundant group of fishes (Pavanelli and Oliveira 2009; Baumgartner et al. 2012; Pini et al. 2019). Among its representatives, *Astyanax bifasciatus* Garavello & Sampaio, 2010 is widely distributed throughout the basin (Garavello and Sampaio 2010; Baumgartner et al. 2012), where it is highly abundant both in the main channel (Delariva et al. 2013) and in smaller streams (Larentis et al. 2016; Delariva et al. 2018). According to Garavello and Sampaio (2010: 856), *A. bifasciatus* is diagnosed from other congeners by the following combination of characters: "infraorbital 3 deep, but not in contact with the preopercle, leaving a narrow, naked area between its border and the preopercle; the premaxillary outer series with 4 (rarely 5) pentacuspid teeth; the non-symphysial teeth in premaxillary inner series heptacuspid; the vertically elongate humeral blotch with the dorsal portion much wider than the ventral; the presence of a faint and diffuse 'post-humeral spot'; the presence of 36–40 perforated scales on the lateral line; the presence of 7–9, usually 8, gill-rakers on the first epibranchial and 10–13, usually 12, on the ceratobranchial".

The Iguaçu river basin is bordered by the Ribeira, Tibagi, Ivaí, Piquiri, and Paraná III basins (Parolin 2010). Among those, the Piquiri river basin has the third largest drainage area, also with extensive stretches free of damming in the upper Paraná river basin (Affonso et al. 2015; Cavalli et al. 2018). Recent ichthyofaunistic inventories in Piquiri river basin recorded a high diversity of fishes (152 species), mainly represented by small species belonging to the Loricaridae and Characidae (Gubiani et al. 2010; Delariva and Silva 2013; Dei Tos et al. 2014; Cavelli et al. 2018). However, those studies did not record *A. bifasciatus*. We report herein a geographic range extension for *A. bifasciatus* in the Piquiri river basin, representing the first record outside from the Iguaçu river basin. Additionally, we provide a brief description of these individuals, based on morphological characters and Cytochrome c oxidase subunit 1 (COI) gene sequences.

Methods

The Piquiri and Iguaçu rivers are direct tributaries of the Paraná River (Parolin et al. 2010). The Iguaçu basin is characterized by have a low diversity of species (Baumgartner et al. 2012). Piquiri basin, besides the high diversity, is one of the only rivers free of dams in Paraná state. Specifically, in western Paraná, both basins are mainly affected by agricultural activities, with monocultures of soybean, corn, and sugar cane (Parolin et al. 2010). At the border between these two basins, in the municipality of Cascavel, the fish fauna was sampled in nine headwater streams (Fig. 1).

The samplings were performed using electrofishing technique between March 2017 and January 2018. A collecting license was provided by the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio) (Process 30182) and approved by the Ethics Committee on Animal Use of the Universidade Federal do Rio Grande do Sul (CEUA; Permit number 32734) in accordance with protocols in their ethical and methodological aspects for the use of fish. Specimens were deposited at the ichthyological collection of the Universidade Federal do Rio Grande do Sul (UFRGS).

The identification of the specimens was based on Garavelo and Sampaio (2010). Measurements and counts followed Fink and Weitzman (1974), with the exception of the number of scale rows below the lateral line, which were counted from the scale row ventral to the lateral line to the scale row nearest to the origin of the first pelvicfin ray. The measurements were taken point to point with electronic calipers to the nearest 0.1 mm on the left side of specimens. Counts were taken under a stereomicroscope from the left side of specimens whenever possible.

Morphological variations were evaluated using a Principal Component Analysis (PCA) applied to meristic and morphometric data (based on percentage of standard length and percentage of head length). This analysis was run in R environment version 3.5.2 (R Core Team 2018) with 'vegan' package version 2.4-6 (Oksanen et al. 2019) and 'ggplot2' package version 3.1.0 (Wickham 2016).

Partial sequences of the COI gene were amplified for seven specimens from headwater streams of the lower Iguaçu River (4 specimens) and Piquiri River (3 specimens) basins. In addition, the COI gene of the four sintopic characidae species (*Astyanax* aff. *fasciatus* Cuvier, 1819; *Astyanax* aff. *paranae* Eigenmann, 1914; *Astyanax lacustris* (Lütken, 1875)

and *Bryconamericus ikaa* Casciotta, Almirón & Azpelicueta, 2004) was also amplified (Appendix Table A1). DNA was extracted from muscles fragments using CTAB methodology (Doyle and Doyle 1987). COI was amplified with primers cocktail FishF1t1 and FishR1t1 (Ivanova et al. 2007). PCR reactions were conducted in a reaction volume of 20 μL [10.3 μL of H2O, 2 μL of 10× reaction buffer (Platinum®Taq), 0.6 μL of MgCl2 (50 mM), 2 μL of dNTPs (2 mM), 2 μL of each primer (2 μM), 0.1 μL (5U) of Platinum® Taq (Invitrogen), and 100 ng of template DNA], under the following conditions: an initial DNA denaturation at 94 °C for 3 min followed by 35 cycles at 94°C for 30 s, 50 °C for 40 s, and 72°C for 1 min and a final extension at 72 °C for 10 min. The PCR products were purified using the Exosap enzymatic method (25% exonuclease, 25% Shrimp Alkaline Phosphatase and 50% deionized water), and the sequencing was performed by the company ACTGen (Porto Alegre, Rio Grande do Sul). The sequences were aligned using Clustal W in MEGA 6.0 software (Tamura et al. 2013) and the alignments were visually inspected for any obvious base miscall (e.g. base incorporated at the sequence different from the color pic in chromatograms). A Neighbor Joining dendogram and pairwise genetic distances between species were performed using Kimura-2-parameters model (K2P) (Kimura 1980) in the MEGA 6
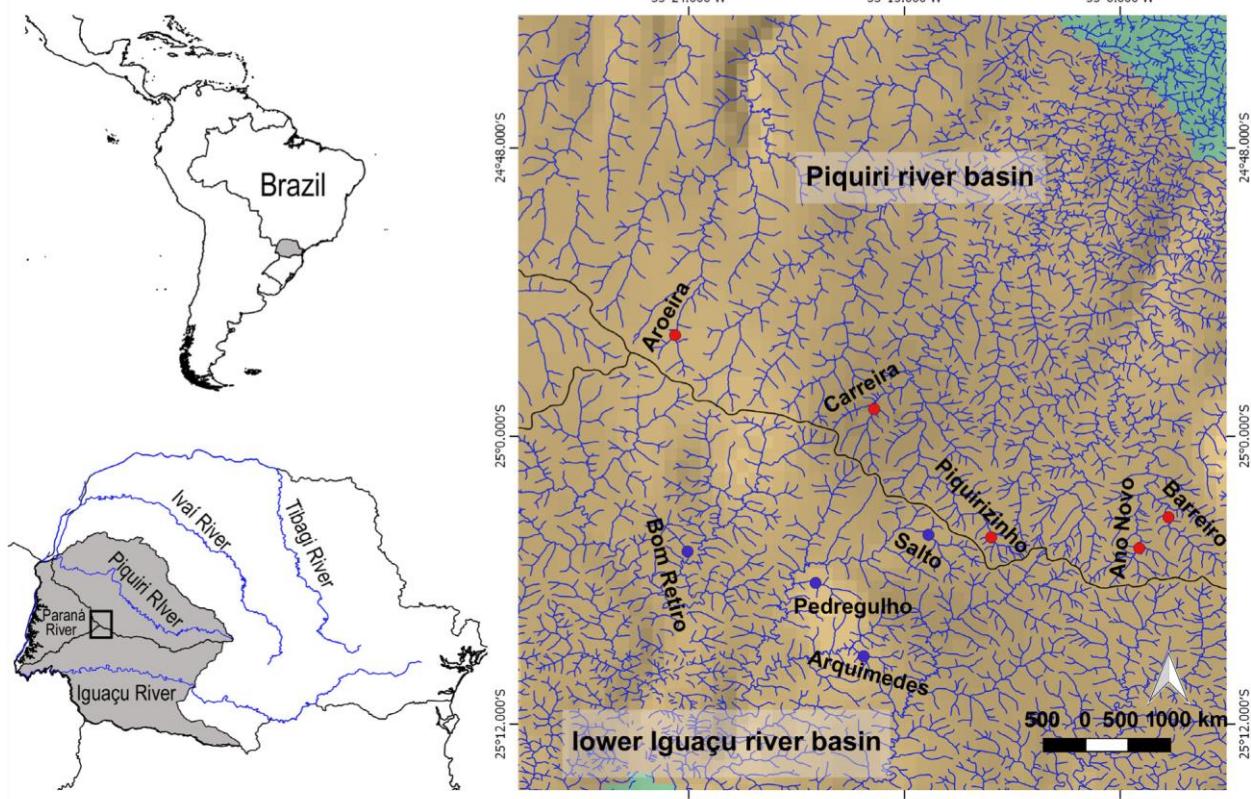
Figure 1. Distribution of *Astyanax bifasciatus*. Red circles are new records from the Piquiri river basin. Blue circles are records from the lower Iguaçu river basin. Black lines indicate the limits among Piquiri, lower Iguaçu, and Paraná III basins.

software (Tamura et al. 2013). Additionally, polymorphic sites were identified using DnaSP software (Librado and Rosas 2009), and haplotype networks were created from Median-Joining (Bandelt et al. 1999) with the use of PopArt 1.7 (Leigh and Bryant 2015) just for *A. bifasciatus* sequences. All generated sequences have been submitted to the GenBank database (Appendix Table A1).

Results

Astyanax bifasciatus Garavelo & Sampaio, 2010

Material examined (morphological data). BRAZIL • Piquiri river basin, upper Paraná river basin: Ano Novo stream (25°04′39.9″S, 053°5′11.9″W), collected by Neves M.P., Larentis C. and Delariva R.L., 12 April 2017 (UFRGS 26224, 5, 52.5–60.4 mm SL), 14 December 2017 (UFRGS 26225, 1, 58.2 mm SL) • Barreiro stream (25°03′22.7″S, 53°03′58.8″W) collected by Neves M.P., Larentis C. and Delariva R.L., 12 April 2017 (UFRGS 26227, 5, 69.6–79.4 mm SL), 14 December 2017 (UFRGS 26229, 4, 51.4–72.3 mm SL; UFRGS 26249, 1, 75.0 mm SL) • Carreira stream (24°58′52.1″S, 053°16′15.8″W), collected by Neves M.P., Larentis C. and Delariva R.L., 29 March 2017 (UFRGS 26231, 5, 74.4–91.3 mm SL), 4 August 2017 (UFRGS 26231, 2, 56.4–65.5 mm SL), 3

January 2018 (UFRGS 26253, 2, 74.0–80.2 mm SL) • Piquirizinho stream (25°04′12.7″S, 053°11′22.6″W), collected by Neves M.P., Larentis C. and Delariva R.L., 29 March 2017 (UFRGS 26237, 8, 59.9–70.2 mm SL), 19 December 2017 (UFRGS 26239, 4, 55.0–60.3 mm SL) • Aroeira stream (24°55′47.4″S, 053°24′33.9″W), collected by Neves M.P., Larentis C. and Delariva R.L., 20 March 2017 (UFRGS 26240, 5, 77.9–63.7 mm SL) • Iguaçu river basin: Arquimedes stream (25°09′10.2″S, 053°16′41.9″W), collected by Neves M.P., Larentis C. and Delariva R.L., 27 July 2017 (UFRGS 26235, 10, 69.4– 93.1 mm SL), 18 December 2017 (UFRGS 26258, 1 73.5 mm SL) • Salto stream (25°04′06.9″S, 053°13′59.6″W), collected by Neves M.P., Larentis C. and Delariva R.L., 14 March 2017 (UFRGS 26242, 5, 50.1–77.9 mm SL), 25 July 2017 (UFRGS 26243, 5, 45.1–51.4 mm SL) • Bom Retiro stream (25°04′48.4″S, 053°24′02.9″W), collected by Neves M.P., Larentis C. and Delariva R.L., 28 July 2017 (UFRGS 26244, 10, 77.9–100.1 mm SL) • Pedregulho stream

(25°6′7.2″S, 53°18′42.2″W), collected by Neves M.P., Larentis C. and Delariva R.L., 27 July 2017 (UFRGS 26247, 5, 56.1–82.0 mm SL), 18 December 2017 (UFRGS 26248, 5, 62.1–74.4 mm SL; UFRGS 26251, 3, 46.5–80.5 mm SL).

Comparative material examined. BRAZIL • Piquiri river basin, upper Paraná river basin: *Astyanax* aff. *fasciatus*: Aroeira stream (24°55′47.4″S, 053°24′33.9″W), collected by Neves M.P., Larentis C. and Delariva R.L., 11 January 2018 (UFRGS 26256, 1, 62.0 mm SL) • *Astyanax* aff. *paranae*: Carreira stream (24°58′52.1″S, 053°16′15.8″W), collected by Neves M.P., Larentis C. and Delariva R.L., 3 January 2018 (UFRGS 26252, 2, 50.1–54.5 mm SL) • *Astyanax lacustris*: Aroeira stream (24°55′47.4″S, 053°24′33.9″W), collected by Neves M.P., Larentis C. and Delariva R.L., 11 January 2018 (UFRGS 26255, 1, 84.2 mm SL) • *Astyanax bifasci atus*: rio Iguaçu basin: stream in Palmas PPBIO (26° 30′33″S, 51°36′50″W), collected by Dala-Corte R., Ca mana M., Dalmolin M. and Jacob C., 20 January 2016 (UFRGS 22090, 2 of 3, 70.0– 75.5 mm SL) • Municipality of Foz do Iguaçu: Tamanduazinho river (25.55°S, 054.52°W), collected by Oliveira, C. and Roxo F. F., 13 September 2012 (LBP 16180, 4, 68.3– 78.1 mm SL) • *Astyanax gymnodontus*: rio Iguaçu basin: rio Iguaçu, municipality of Laranjeiras, collected by Garavello J. C., Soares A. S., Rodrigues R. J., Veber M. J. and Paschoa M. M., 10 November 1990 (UFRGS 11923, 3, 84.7–118.9 mm SL). • *Astyanax gymnogenys*: rio Timbó basin: rio dos Pardos (26.43°S, 050.96°W), collected by Geuster C. J. and Spier E. F., 27 November 2010 (UFRGS 14070, 1, 150.6 mm SL). • *Astyanax minor:* rio Iguaçu basin: Reservatório Vossoro, tributary of rio São João (25.82°S, 049.07°W), collected by GERPEL team, June 2007 (UFRGS 14780, 10, 72.1–82.0 mm SL). • *Astyanax serratus*: rio Iguaçu basin: rio Lageado, municipality of Porto Amazonas (25.54°S, 049.89°W), collected by Bertaco V. A., Artioli L, Wingert J. M., 15 October 2009 (UFRGS 11435, 3,47.4–72.1 mm SL) • *Astyanax troya*: arroyo Cuña Pirú basin: Misiones, collected by Azpelicueta M., Aichino D. and Méndez D., 29 October 2004 (UFRGS 10079, 5, 44.1–61.1 mm SL). • *Astyanax ribeirae*: rio Iguape basin: stream on the road between Iguape and Icapara (24.08°S, 047.53°W), collected by Bertaco V. A., Carvalho F. R., Jerep, F. C. and Thomaz A., 27 November 2010 (UFRGS 13689, 3, 36.0– 42.6 mm SL).

Identification. Two hundred and twenty-two representatives of *Astyanax bifasciatus* were sampled from five headwater streams of the Piquiri river basin. Most diagnostic characters proposed for those species were confirmed in representatives of both basins, with the only exception being the number of teeth cusps on the inner premaxillary series, which were pentacuspid in all sampled specimens. Garavello and Sampaio (2010) stated that *A. bifasciatus* have heptacuspid teeth; however, in their description contradicts that information by stating that the inner premaxillary teeth have five "pentacuspid teeth, rarely 4" (p. 856), similar to the conditions observed in all the specimens examined herein (39 from the Piquiri River and 40 from the Iguaçu River). In addition, the specimens share other meristic (Table 1) and coloration characters (i.e. fins red in life; the presence of two humeral blotches; Fig. 2) consistent with the original description of *A. bifasciatus*.

The comparisons between specimens from the Iguaçu and Piquiri rivers employing morphological (PCA; Fig. 3) and molecular tools (COI gene; Fig. 4, Appendix Table A2) showed homogeneity between representatives of both basins, confirming those samples represented a single species. Molecular results indicate a low genetic divergence between the specimens sampled from streams in the Iguaçu and the Piquiri basins (≤0.008). In addition, no structure for each basin (Piquiri and Iguaçu) was observed in haplotype distributions in the network (Fig. 4). The BLAST comparison of the sequences obtained here with available sequences in GenBank resulted in a 100% match with *A. bifasciatus* from the Iguaçu river basin. However, similar matches were also observed in samples attributed to *Astyanax minor* Garavello & Sampaio, 2010 (99.7%), also from the Iguaçu River, and *Astyanax* aff. *intermedius* Eigenmann, 1908 (99.8%) from the Jordão River, a tributary from the Iguaçu River.

Ecological notes. The specimens of *A. bifasciatus* were captured synoptically with other species of the genus reported for the Piquiri river basin, such as *A.* aff. *fasciatus*, *A. lacustris*, and *A.* aff. *paranae* in third-order streams 4.5 m (mean) wide, 50 cm deep, and moderate with marginal vegetation (Fig. 5). Several microhabitats were observed including with backwaters, large pools, and rapids. The substrates were composed of rocks, gravel, and pebbles, and

Table 1. Morphometric data of *Astyanax bifasciatus* specimens originating from the lower Iguaçu and Piquiri river basins.

Basin	Lower Iguaçu River				Piquiri River			
	N	Range	Mean	SD	N	Range	Mean	SD
Standard length (mm)	40	45.1—100.2	72.2	—	39	51.4—91.3	67.4	—
Percentage of standard length								
Predorsal distance	40	48.5—52.8	51.3	1.0	39	49.1—53.9	51.7	1.2
Prepelvic distance	40	43.7—49.4	46.6	1.3	39	41.6—49.3	45.8	1.6
Prepectoral distance	40	22.3—26.4	24.2	1.0	39	20.7—26.0	23.3	1.1
Preanal distance	40	61.6—68.2	65.2	1.9	39	59.3—68.9	64.0	2.0
Depth at dorsal-fin origin	40	30.1—36.9	33.5	1.6	39	30.3—35.4	32.8	1.5
Caudal peduncle depth	40	10.1—12.2	11.0	0.5	39	10.2—12.1	11.2	0.4
Caudal peduncle length	40	11.5—14.3	12.6	0.6	39	10.9—13.9	12.6	0.7
Anal-fin base	40	20.9—28.3	24.2	1.5	39	21.8—27.0	23.8	1.5
Dorsal fin length	40	20.1—26.8	24.0	1.4	39	21.0—26.2	23.5	1.1
Pelvic fin length	40	13.8—18.6	16.2	1.2	39	13.7—17.1	15.6	0.8
Pectoral fin length	40	18.1—23.5	21.4	1.3	39	18.1—23.8	20.9	1.0
Head length	40	22.8—27.0	24.5	1.1	39	23.2—26.2	24.6	0.6
Percentage of head length								
Snout length	40	23.6—31.8	29.0	1.3	39	26.8—31.8	29.4	1.4
Upper jaw length	40	33.3—44.0	37.1	2.1	39	32.6—42.1	36.4	1.9
Orbital diameter	40	31.0 — 39.3	34.7	2.0	39	30.0 — 37.7	34.4	1.7
Interorbital width	40	29.2 — 35.6	31.6	1.4	39	26.4 — 34.8	31.8	1.5

Figure 2. *Astyanax bifasciatus*. **A.** UFRGS 26235, 85.0 mm SL, Arquimedes stream, lower Iguaçu river basin, Paraná, Brazil. **B.** UFRGS 26231, 91.3 mm SL, Carreira stream, Piquiri river basin, upper Paraná river basin, Paraná, Brazil.
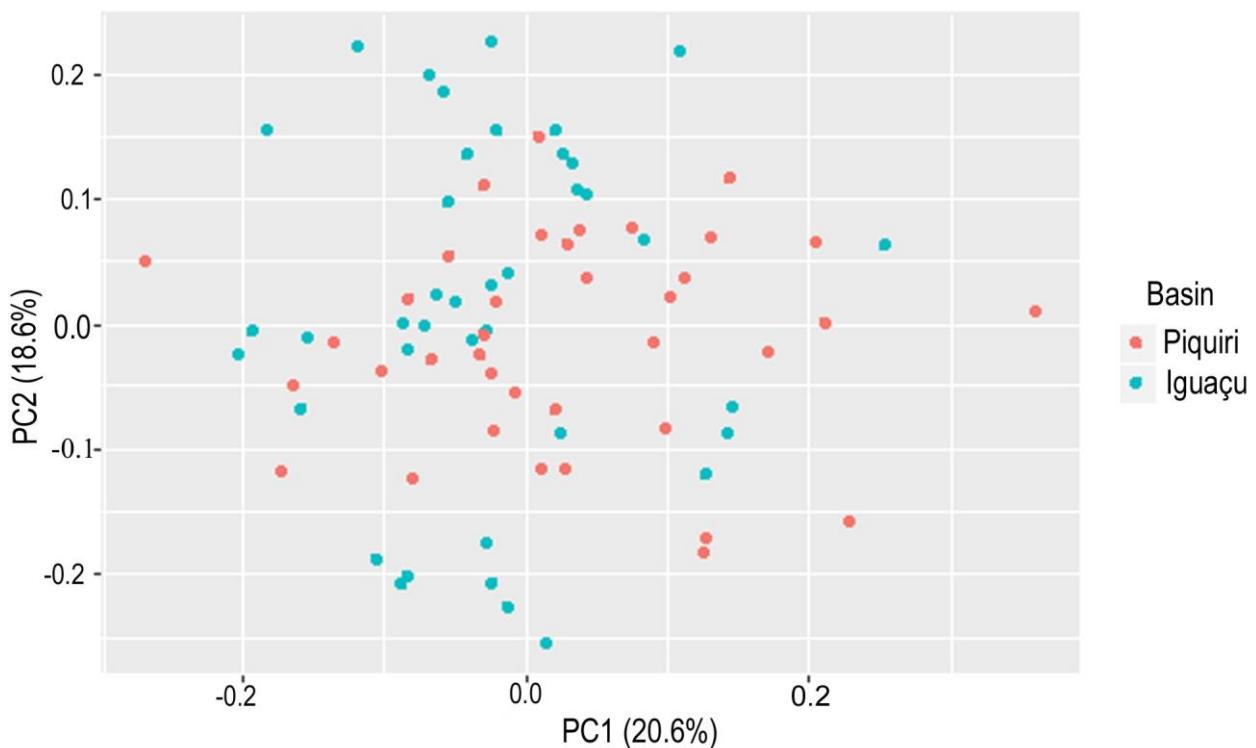
Figure 3. Ordination of populations of *Astyanax bifasciatus* in lower Iguaçu and Piquiri river basins, Paraná, Brazil, produced by the first two axes of the principal component's analysis (PCA 1 and PCA 2) applied to the correlation of 16 morphometric and meristic data of the specimens (based on percentage of standard length and percentage of head length).
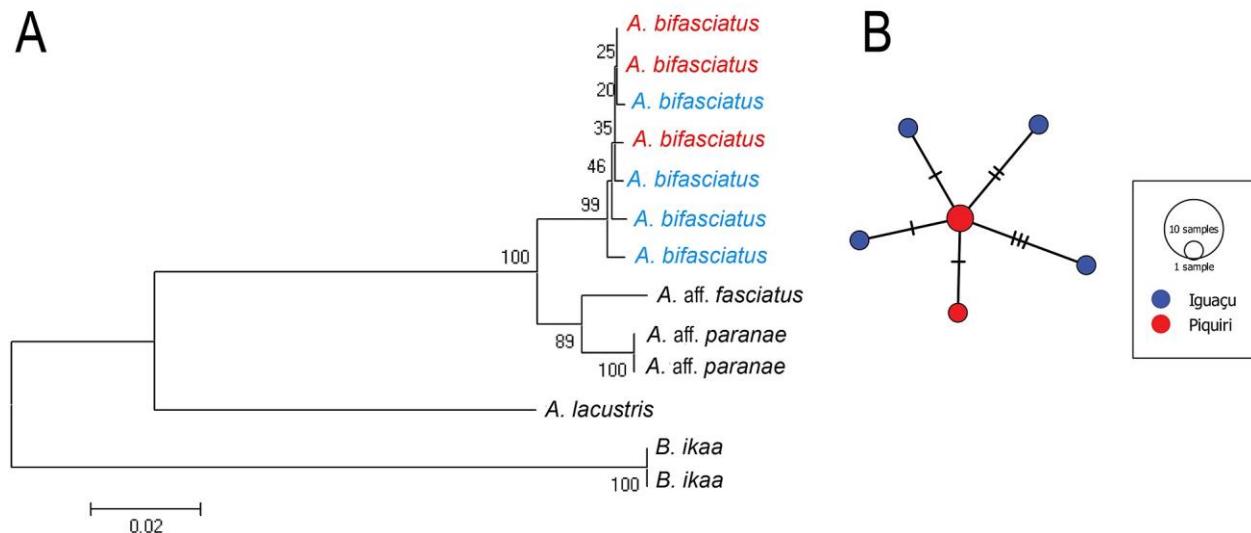
Figure 4. Genetic analyses of *Astyanax bifasciatus* in streams of lower Iguaçu and Piquiri river basins based on COI gene. **A.** Neighborjoining tree of 13 sequences (Table A1) using genetic distances, with the branch lengths equivalent to the number of base substitutions per site. Bootstrap values (1000 replications) are indicated next to the branches. Blue: specimens from Iguaçu River basin. Red: specimens from Piquiri river basin, upper Paraná River basin. **B.** Haplotype network of *A. bifasciatus*. Traces in each branch refer to number of mutational steps between haplotypes.

the water flow was moderate. The areas around the Ano Novo, Barreiro, and Piquirizinho streams are deforested, whereas the Carreira stream has its headwaters within a conservation unit (Centro de Educação Ambiental Suely Marcondes de Moura Festugatto, Cascavel city). The Aroeira stream is within the city of Cascavel and is impacted by pollution and urbanization.

Preliminary results from stomach content analysis of 130 specimens corroborate the omnivorous habit of *A. bifasciatus*, as suggested by Neves et al. (2015); the diet consists mainly of aquatic (Ephemeroptera) and terrestrial insects (Coleoptera and Hymnoptera), seeds, and detritus.

Discussion

Astyanax bifasciatus is the most abundant species in the Iguaçu river basin (Baumgartner et al. 2012). It is omnivorous and easily found in several streams (Neves et al. 2015; Delariva et al. 2018). The species is recognized as highly resilient to many stressors caused by human activities, such urbanization and agriculture (Nimet et al. 2020). Herein, the morphological, meristic, and morphometric characters obtained from the specimens collected in the streams of the Piquiri River are largely congruent with those provided by Garavello and Sampaio (2010) and observed for the Iguaçu River specimens examined herein, despite the imprecise diagnosis of that species. In addition, the molecular tools also

confirm that both samples represent a single species, justifying their identification as *A. bifasciatus.*

The absence of structure between the two basins in the haplotype network points to a single population, although the present data is unable to determine the presence of gene flow between representatives of both basins neither other biogeographic processes behind each possible scenario. On the other hand, considering the small genetic distance between the samples of *A. bifasciatus* examined herein, the isolation of the Iguaçu river basin (~22 mya, Oligo-Miocene period) with the uplift of the Iguaçu Falls (Severi and Cordeiro 1994), does not explain the current distribution pattern of the species. A similar scenario was observed by MoraisSilva et al. (2018) with *Trichomycterus davisi* (Haseman 1911) and *T. stawiarski* (Miranda Ribeiro 1968), species that were initially considered endemic to the Iguaçu river basin, but are also present in the Piquiri and the Ivaí river basins, and consist of a single population.

Considering yet the efficiency of the COI marker to elucidate taxonomic problems (Kwong et al. 2013; Rossini et al. 2016), the similarity between the sequences and those identified as "*A. minor*" (99.7%), from the Iguaçu River, and "*A.* aff. *intermedius*" (99.8%), from the Jordão River (Iguaçu river basin), seem indicative of a single species being mistakenly identified under at least three different names. Although the present results indicate a broader distribution for *A. bifasciatus* and refutes the

endemism of the species for the Iguaçu river basin, other studies did not detect the species in river basins adjacent to the Iguaçu River, such as the survey on the main channel and tributaries of the Piquiri river basin (Cavalli et al. 2018). The absence of *A. bifasciatus* in Cavalli et al.'s checklist may be due to both the difficulty in the identification of *Astyanax* species, but also in the assumption that *A. bifasciatus* of Garavello and Sampaio (2010) was endemic to the Iguaçu river basin. Similarly, it is possible that *A. bifasciatus* might be present in adjacent drainages such as the Ivaí and the Tibagi river basins (Viana et al. 2013; Claro-García et al. 2018). In addition, it is

necessary to investigate the border regions between those basins to better understand the processes that lead to the sharing of this species and possibly other species currently considered endemic of the Iguaçu River. Finally, a robust and integrative taxonomic review of *Astyanax* in the Iguaçu and adjacent river basins would elucidate the distribution pattern of the species and provide accurate tools for the identification of *Astyanax* samples in those basins.
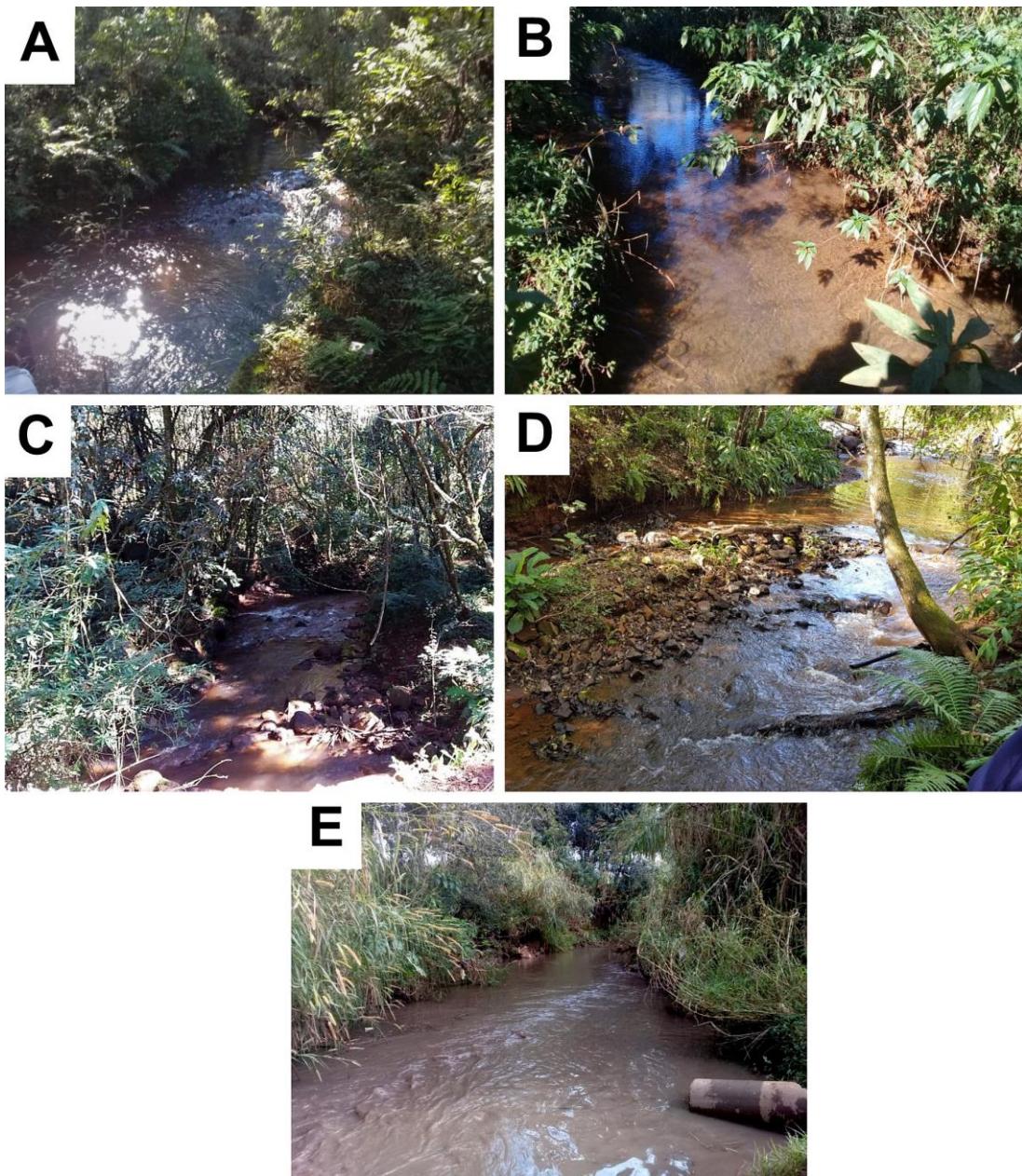
Figure 5. Localities where *Astyanax bifasciatus* specimens were recorded in Piquiri river basin, upper Paraná river basin. **A.** Ano Novo. **B.** Barreiro, both from sub-basin of the Tourinho River. **C.** Piquirizinho. **D.** Carreira, both from sub-basin of the Piquirizinho River. **E.** Aroeira, from sub-basin of the Melissa River.

Acknowledgements

Authors' Contributions

MPN and RLD collected the specimens; MPN, PCS, and ALN-F identified the specimens, MPN conducted morphological, molecular procedures, and statistical analysis; MPN, PCS, and ALN-F interpreted the data; MPN and ALN-F wrote the text; and PSC, RLD and CBF improved and reviewed the manuscript.

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Appendix

Table A1. Voucher number and genetic sequences accession numbers (GenBank) of *Astyanax bifasciatus* specimens and other syntopic Characidae species from the basins of the lower Iguaçu River and Piquiri River (upper Paraná river basin) generated in this study.

Specimen voucher	Accession number	Species	Basin
UFRGS 26251(TEC 8953A)	MK557882	*A. bifasciatus*	Iguaçu
UFRGS 26251(TEC 8953B)	MK557883	*A. bifasciatus*	Iguaçu
UFRGS 26251 (TEC 8953C)	MK557884	*A. bifasciatus*	Iguaçu
UFRGS 26258 (TEC 8960)	MK557881	*A. bifasciatus*	Iguaçu
UFRGS 26253 (TEC 8955A)	MK557885	*A. bifasciatus*	Piquiri
UFRGS 26253 (TEC 8955B)	MK557886	*A. bifasciatus*	Piquiri
UFRGS 26249 (TEC 8951)	MK557880	*A. bifasciatus*	Piquiri
UFRGS 26256 (TEC 8958)	MN053307	*A.* aff. *fasciatus*	Piquiri
UFRGS 26252 (TEC 8954A)	MN053305	*A.* aff. *paranae*	Piquiri
UFRGS 26252 (TEC 8954B)	MN053306	*A.* aff. *paranae*	Piquiri
UFRGS 26255 (TEC 8957)	MN053308	*A. lacustris*	Piquiri
UFRGS 26250 (TEC 8952A)	MN053303	*B. ikaa* (I)	Iguaçu
UFRGS 26250 (TEC 8952B)	MN053304	*B. ikaa* (I)	Iguaçu

Table A2. Pairwise distance between of the *Astyanax bifasciatus* specimens and other syntopic Characidae species from the basins of the lower Iguaçu River and Piquiri River (upper Paraná river basin) generated in this study. I = Iguaçu river basin, P = Piquiri river basin.

		1	2	3	4	5	6	7	8	9	10	11	12	13
1. TEC 8960	*A. bifasciatus* (I)	—												
2. TEC 8953A	*A. bifasciatus* (I)	0.006	—											
3. TEC 8953B	*A. bifasciatus* (I)	0.005	0.008	—										
4. TEC 8953C	*A. bifasciatus* (I)	0.003	0.006	0.005	—									
5. TEC 8955A	*A. bifasciatus* (P)	0.002	0.005	0.003	0.002	—								
6. TEC 8955B	*A. bifasciatus* (P)	0.002	0.005	0.003	0.002	0.000	—							
7. TEC 8951	*A. bifasciatus* (P)	0.003	0.006	0.005	0.003	0.002	0.002	—						
8. TEC 8954A	*A.* aff. *paranae* (P)	0.034	0.034	0.032	0.034	0.032	0.032	0.034	—					
9. TEC 8954B	*A.* aff. *paranae* (P)	0.034	0.034	0.032	0.034	0.032	0.032	0.034	0.000	—				
10. TEC 8958	*A.* aff. *fasciatus* (P)	0.036	0.039	0.034	0.036	0.034	0.034	0.036	0.022	0.022	—			
11. TEC 8957	*A. lacustris* (P)	0.153	0.157	0.155	0.155	0.155	0.155	0.153	0.156	0.156	0.162	—		
12. TEC 8952A	*B. ikaa* (I)	0.227	0.223	0.229	0.229	0.229	0.229	0.227	0.227	0.227	0.233	0.212	—	
13. TEC 8952B	*B. ikaa* (I)	0.227	0.223	0.229	0.229	0.229	0.229	0.227	0.227	0.227	0.233	0.212	0.000	—

Chapter 2

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

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ORIGINAL ARTICLE

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

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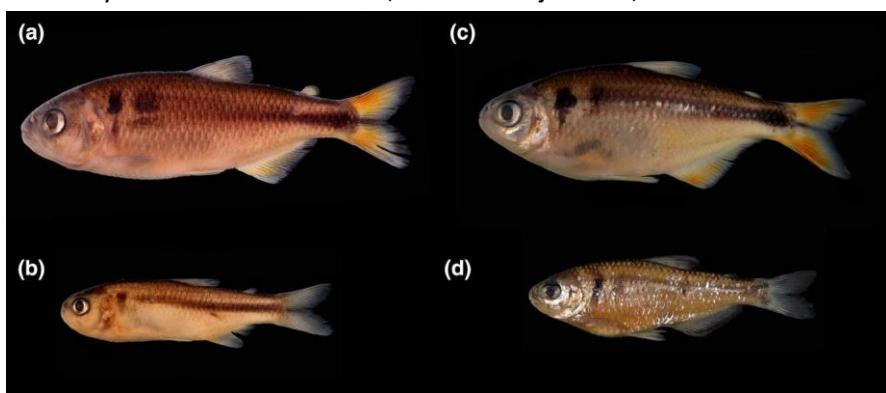
FIGURE 1 Species studied: (a) *Psalidodon* aff. *gymnodontus* (UFRGS 25,725, 95.4 mm SL); (b) *Psalidodon* aff. *paranae* (UFRGS 26,232, 48.0 mm LS); (c) *Psalidodon bifasciatus* (UFRGS 26,235, 85.0 mm SL); and (d) *Bryconamericus ikaa* (UFRGS 26,246, 49.0 mm SL)

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.

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. *parane* (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 breath, 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_{ij} describing the proportion of the jth all resources category in individual i's diet, q_j, is the proportion of the jth 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,

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.*

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.

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
Season	0.01 (0.09)	0.15	.88	−0.99 (0.16)	−6.06	**<.001**
Number of cooccurring 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

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

Intercept	0.29
(0.06)	4.65
	<.001
	−1.07
(0.19)	−5.58
	<.001

Neotropical headwater streams, southern Brazil, in the winter and summer seasons

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

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$_i$

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

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 (Pap)	−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: PSi ~ 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; LoweMcConnell, 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.
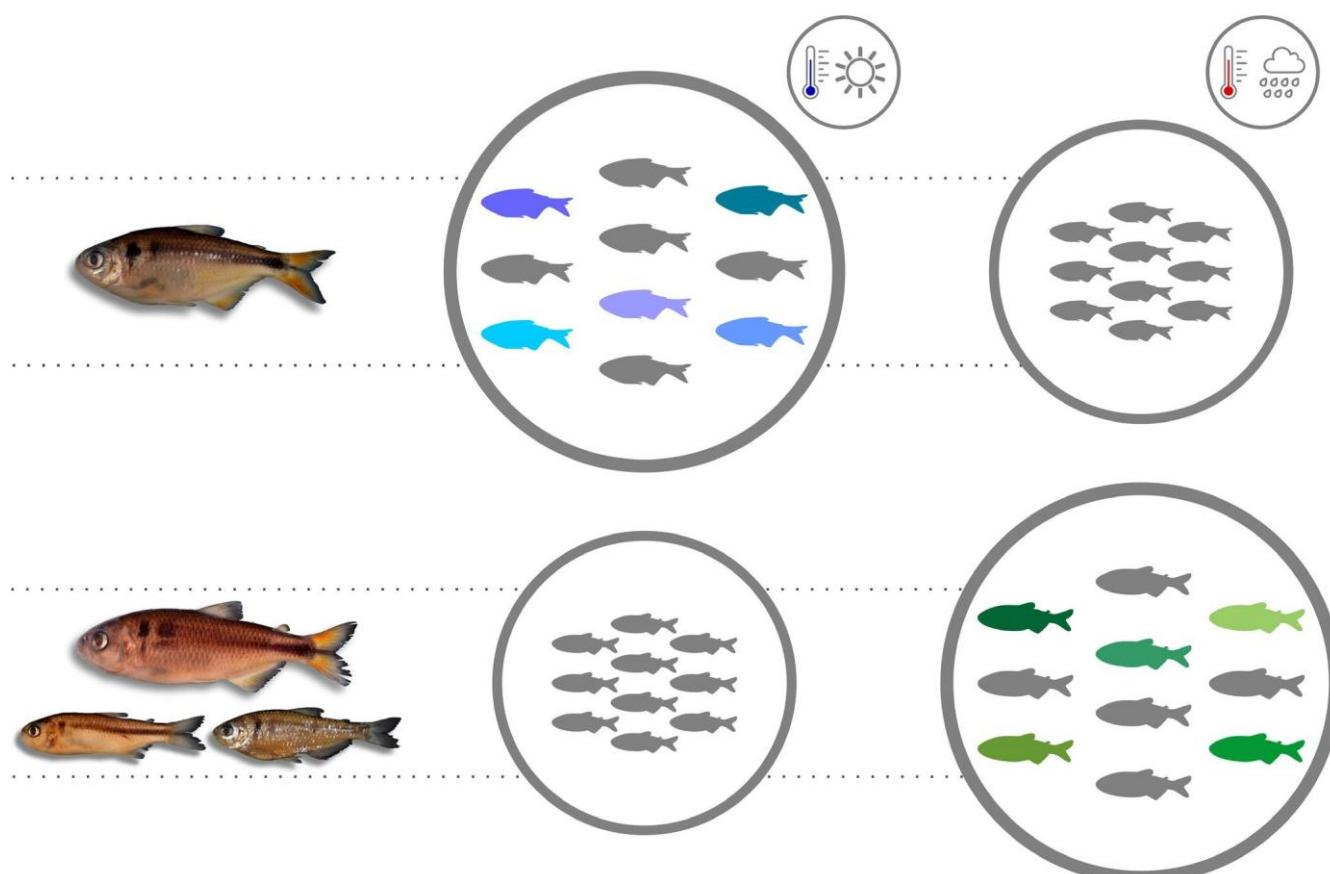
FIGURE 4 Schematic summary of the effects of seasonality in variation niche and individual specializations of the tetra fish in Neotropical headwater streams, southern Brazil. In the winter (dry season), *P. bifasciatus* tends to expand its population niche via increased between-individual variation (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.

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.tqjq2 bvx5 (Neves et al., 2020).

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SUPPORTING INFORMATION

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

1   **Supporting information**

2

3   Seasonality and interspecific competition shape individual

4   niche variation in co-occurring tetra fishes in Neotropical streams

5

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20 **SUPPORTING INFORMATION**
21

22
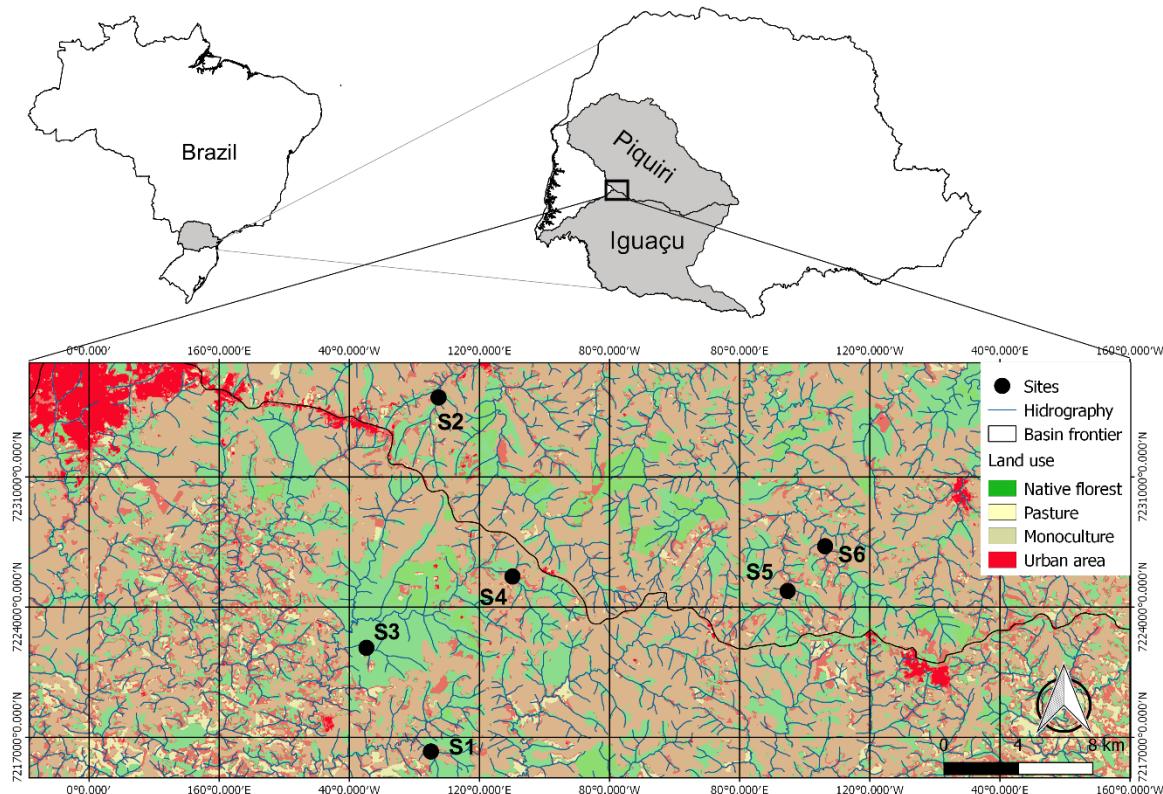
24 **FIGURE S1** Study area highlighted from the hydrographic map of the Paraná State,

25 southern Brazil. Lower Iguaçu River basin: S1, S3 and S4. Piquiri River basin: S2, S5 and

26 S6.
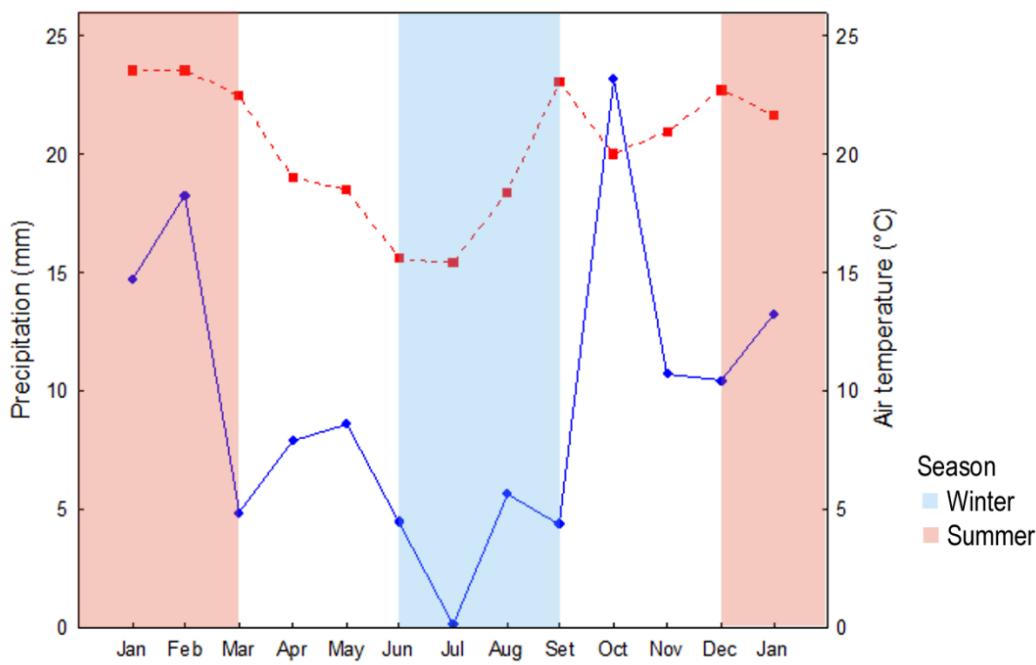
27

28   **FIGURE S2** Average monthly precipitation (blue circle) and air temperature (red

29   square) in the city of Cascavel, western region of the state of Paraná, southern Brazil,

30   between January 2017 and January 2018. (data were provided by the Paraná Weather

31   System [Simepar] from the Cascavel weather station).

32   **TABLE S1** Description of the water abiotic parameters and percentages of land uses in in neotropical headwater streams, Lower

33   Iguaçu river and Piquiri river basins, southern Brazil, in the winter (W) and summer (S) of 2017. Lower Iguaçu River basin: S1, S3 and

34   S4. Piquiri River basin: S2, S5 and S6.

Sites	S1		S2		S3		S4		S5		S6	
Stream	Arquimedes		Carreira		Pedregulho		Rio do Salto		Ano Novo		Barreiro	
Basin	Iguaçu		Piquiri		Iguaçu		Iguaçu		Piquiri		Piquiri	
Vegetal cover (%)	66		42		75		50		57		49	
Variable/Season	W	S	W	S	W	S	W	S	W	S	W	S
Width (m)	4.5	4.5	4.9	5.6	3.8	4.0	3.7	3.9	4.4	5.4	3.7	3.9
Depth (m)	0.2	0.2	0.3	0.4	0.2	0.2	0.2	0.4	0.3	0.5	0.4	0.3
Flow rate (m³/s)	0.2	0.3	0.6	1.1	0.3	0.3	0.4	0.4	0.4	0.7	0.6	0.5
Water temperature (ºC)	14.6	21.6	16.5	23.9	16.8	23.5	16.4	18.8	14.4	20.9	14.9	21.9
pH	7.3	7.5	7.7	6.8	6.9	7.3	7.2	6.7	7.4	7.3	7.4	6.8
ORPmV	149.3	111.0	186.7	272.3	134.0	110.3	120.0	207.3	73.6	127.7	60.6	67.3
Eletric conductivity(Ms/cm)	0.031	0.011	0.021	0.007	0.022	0.020	0.017	0.015	0.041	0.030	0.020	0.022
Trubidity NTU	9.0	28.8	8.5	6.0	0.0	10.9	0.0	7.2	0.0	3.6	8.1	5.5
Dissolvid oxygen (mg/L)	9.4	9.5	10.9	8.8	9.4	10.2	9.2	8.6	10.2	14.3	10.2	10.2
Dissolvid oxygen %	98.5	110.4	114.9	107.0	99.4	123.0	96.2	95.0	75.3	166.2	104.9	119.9
Total solids	0.020	0.007	0.014	0.004	0.020	0.013	0.011	0.010	0.027	0.020	0.048	0.015
Chlorophyll-α (µg/L)	0.03	0.00	0.00	0.27	0.05	0.00	0.00	0.05	0.03	0.00	0.08	0.00

35

36

37   **TABLE S2** Feeding items (%) according to their origin consumed by the tetra fish in

38   neotropical headwater streams, Lower Iguaçu river and Piquiri river basins, southern Brazil,

39   in the winter (W) and summer (S) of 2017.Values based on volume data as a percentage of

40   feeding items. Codes: SD = Standard deviation; cm = centimeters, g = grams. Asterisk

41   indicates values below 0.1%. The most consumed feeding items are in bold.

Species	*Psalidodon* aff. *gymnodontus*		*P.* aff. *parane*		*P. bifasciatus*		*B. ikaa*	
Standard length (cm, Mean±SD)	8.8±1.2		4.7±0.6		6.2±1.6		4.2±0.7	
Weight (g, Mean±SD)	19.5±8.2		2.1±0.9		6.8±5.3		1.5±0.6	
Season	W	S	W	S	W	S	W	S
Stomach analysed	56	32	5	5	116	153	16	15
Autochthonous	19.6	18.4	61.4	33.8	41.5	18	86.6	53.1
Testate Amoebae						*		0.3
Nematoda	*			0.1	*	0.1		
Bivalvia								0.8
Acarina	*					*		
Conchostracoda						*		
Atyidae	0.4				7.8	0.2		
Aegla sp.	0.9	5.5			0.3			
Ephemeroptera	0.1	2.1	10.5	1.3	2.5	1.3	**44.7**	**18.2**
Odonata	2.1				2.3	0.3		4
Plecoptera	*	0.5			0.1	*		
Hemiptera					0.1			
Coleoptera	0.3	0.3	1.8	1.3	0.8	0.6	4.3	1.1
Trichoptera	5.9	*		8	2.8	0.6	**19.6**	**16**
Diptera (larvae and pupae)	1.2	1.2			1.3	*	0.4	0.3
Ceratopogonidae	*			0.1	0.1	*	0.3	0.2
Chironomidae	0.5	0.3	1.8	2.8	0.6	0.1	0.2	5.1
Simuliidae	0.2	0.1	1.8	9.4	0.4	1.1	1.5	1.6
Lepidoptera (larvae and pupae)	0.5	5.1			1.9	9.1	6.9	1.6
Aquatic insect remains	5.4	3.2	**45.6**	**10.7**	**14.3**	3.9	8.8	4

Scales	2.1	*			0.3	*	*	0.1
Diatoms	*	*					*	
Filamentous algae					*			
Aquatic plant		0.2			6.1	0.7		
Allochthonous	73.6	70.2	38.6	55.5	37.2	75.7	10.4	20.3
Oligochaeta					0.1		3.3	4.8
Aranae		1.7			0.7	0.4		1.9
Oniscidae					2.3			
Plecoptera					0.4	0.1		
Auchenorrhyncha	1			**13.4**	2	0.3		
Coleoptera	8.2	**22.2**	1.8	**34.1**	5	4.2	0.4	0.3
Diptera	3.8			2.7	0.2		1.6	
Lepidoptera	0.3	3.1			0.8	0.1		
Hymenoptera	2.2	**12.1**	**29.8**	2.7	**10.5**	3.7	2.2	2.9
Terrestrial insect remains	1.4	2.5		2.7	1.1	1.5	2.9	
Leaves	**29.9**	**12.2**	7		9.1	4.1		
Seeds	**26.7**	**16.4**			5	**61.3**		**10.4**
Undetermined	**6.7**	**11.3**		**10.7**	**20.5**	**6.2**	**2.9**	**26.6**
Sediment/Detritus	6.7	11.3		10.7	20.5	6.2	2.9	26.6

42

43   **TABLE S3** Summary of PERMDISP – p-value of comparisons of diet breadth of the tetra fish in neotropical headwater streams, Lower Iguaçu

44   river and Piquiri river basins, southern Brazil, in the winter (W) and summer (S) of 2017. Observed p-value below diagonal, permuted p-value

45   above diagonal. Values in italics are adjusted p-values for within-season pairwise species comparisons. Non-italicized values are adjusted p-values

46   for between-season comparisons of all of the possible pairwise species comparisons. Significant p-values are in bold. $p < 0.01$ represent p-values

47   under 0.00. Species codes: Pag= *P.* aff. *gymnodontus*; Pap= *P.*aff. *paranae*; Pbi= *P. bifasciatus*; Bik= *B. ikaa.*

Site	S1				S2				S3				S4		S5		S6	
Species/Season	Pag W	Pag S	Pbi W	Pbi S	Pap W	Pap S	Pbi W	Pbi S	Pbi W	Pbi S	Bik W	Bik S	Pbi W	Pbi S	Pbi W	Pbi S	Pbi W	Pbi S
Pag W		**0.02**	0.29	0.09	*<0.01*	0.61	0.66	0.99	*0.02*	0.94	0.07	0.94	0.27	0.42	0.96	0.56	0.50	0.32
Pag S	**0.02**		0.20	*<0.01*	**<0.01**	0.35	0.14	*0.01*	<0.01	*0.04*	<0.01	0.06	**0.01**	*0.01*	0.10	*0.01*	0.18	0.20
Pbi W	0.30	0.21		**0.03**	*<0.01*	0.98	0.75	0.33	*0.01*	0.36	*0.03*	0.48	0.11	0.18	0.57	0.16	0.95	0.98
Pbi S	0.08	*<0.01*	**0.02**		**0.04**	0.14	0.11	0.08	0.93	0.17	0.97	0.16	0.57	0.61	0.37	0.26	0.07	*0.03*
Pap W	*<0.01*	<0.01	<0.01	0.04		**0.01**	*<0.01*	<0.01	*0.01*	<0.01	0.05	**<0.01**	*0.01*	0.03	*0.04*	<0.01	*<0.01*	*<0.01*
Pap S	0.60	0.36	0.99	0.15	**0.01**		0.83	0.58	0.15	0.67	0.26	0.62	0.42	0.37	0.59	0.46	0.93	0.98
Pbi W	0.65	0.14	0.76	0.11	*<0.01*	0.82		0.65	0.08	0.67	0.15	0.74	0.33	0.34	0.77	0.48	0.84	0.78
Pbi S	0.99	*0.02*	0.33	0.09	*<0.01*	0.58	0.66		**0.03**	0.95	0.08	0.94	0.31	0.40	0.97	0.61	0.48	0.34
Pbi W	*0.02*	*<0.01*	*0.01*	0.93	*0.01*	0.15	0.07	**0.03**		0.07	0.89	0.11	0.44	0.61	0.33	0.11	0.05	**0.01**
Pbi S	0.93	*0.04*	0.36	0.17	<0.01	0.65	0.68	0.94	0.06		0.13	0.91	0.38	0.53	1.00	0.71	0.57	0.39
Bik W	0.05	*<0.01*	*0.02*	0.96	0.05	0.25	0.13	0.08	0.87	0.12		0.17	0.52	0.64	0.43	0.20	0.11	**0.02**
Bik S	0.94	0.05	0.49	0.16	**<0.01**	0.65	0.76	0.94	0.11	0.91	0.18		0.43	0.48	0.95	0.64	0.57	0.52
Pbi W	0.25	**0.01**	0.10	0.56	*0.01*	0.41	0.32	0.31	0.46	0.37	0.49	0.43		0.99	0.65	0.60	0.26	0.10
Pbi S	0.43	*0.01*	0.18	0.64	**0.04**	0.36	0.36	0.43	0.63	0.55	0.65	0.49	0.98		0.66	0.69	0.22	0.19
Pbi W	0.97	0.10	0.58	0.35	*0.03*	0.59	0.76	0.96	0.34	1.00	0.42	0.94	0.67	0.66		0.85	0.56	0.59
Pbi S	0.58	*0.01*	0.18	0.25	<0.01	0.49	0.46	0.61	0.14	0.70	0.21	0.66	0.59	0.69	0.84		0.35	0.20
Pbi W	0.50	0.18	0.95	0.06	*<0.01*	0.93	0.82	0.49	0.05	0.56	0.11	0.58	0.26	0.24	0.56	0.35		0.96
Pbi S	0.31	0.21	0.98	*0.03*	**<0.01**	0.98	0.78	0.35	**0.01**	0.37	**0.03**	0.51	0.10	0.20	0.60	0.20	0.96	

48

49 **TABLE S4** Values obtained through the SIMPER analysis based in the diet of the tetra fish

50 in neotropical headwater streams, Lower Iguaçu river and Piquiri river basins, southern

51 Brazil, in the winter (W) and summer (S) of 2017. Codes: SD= Standard deviation. Most

52 average groups are highlighted in bold.

Site	Species	Feeding items	Average	SD	Ratio	Average W	Average S	Cumulative contribution
S1	*Psalidodon* aff. *gymnodontus*	Seeds	0.18	0.22	0.84	**0.025**	0.016	0.21
		Leaves	0.17	0.2	0.87	**0.028**	0.012	0.41
		Coleoptera adult	0.12	0.21	0.57	0.008	**0.021**	0.54
	P. bifasciatus	Seeds	0.19	0.22	0.87	0.009	**0.019**	0.22
		Leaves	0.17	0.19	0.91	**0.014**	0.01	0.41
		Sediment/Detritus	0.12	0.17	0.68	**0.016**	0.001	0.55
S2	*P.* aff *paranae*	Aquatic insects remains	0.26	0.24	1.08	**0.005**	0.001	0.29
		Hymnoptera	0.14	0.12	1.16	**0.003**	0	0.45
		Coleoptera adult	0.11	0.23	0.49	0	**0.004**	0.58
	P. bifasciatus	Sediment/Detritus	0.16	0.23	0.7	**0.015**	0.005	0.18
		Ephemeroptera	0.09	0.17	0.57	**0.009**	0.002	0.28
		Aquatic insects remains	0.08	0.09	0.86	**0.006**	0.003	0.37
		Aquatic plant	0.06	0.22	0.29	**0.023**	0	0.44
		Seeds	0.06	0.14	0.45	0	**0.011**	0.51
S3	*B. ikaa*	Ephemeroptera	0.26	0.23	1.13	**0.014**	0.005	0.3
		Trichoptera larvae	0.14	0.18	0.77	**0.006**	0.004	0.46
		Sediment/Detritus	0.08	0.13	0.63	0	**0.004**	0.55
	P. bifasciatus	Seeds	0.31	0.32	0.99	0.001	**0.156**	0.35
		Aquatic insects remains	0.12	0.15	0.84	**0.019**	0.004	0.49
		Hymnoptera	0.12	0.15	0.82	**0.016**	0.007	0.62
S4	*P. bifasciatus*	Sediment/Detritus	0.19	0.21	0.91	0.006	0.006	0.22
		Seeds	0.18	0.31	0.57	0	**0.018**	0.43
		Ephemeroptera	0.08	0.21	0.4	0.001	**0.005**	0.53
S5	*P. bifasciatus*	Seeds	0.18	0.3	0.61	0.001	**0.014**	0.2
		Sediment/Detritus	0.17	0.22	0.77	0.002	**0.008**	0.39
		Aquatic insects remains	0.16	0.19	0.82	0.004	**0.005**	0.57
S6	*P. bifasciatus*	Seeds	0.31	0.36	0.86	0.001	**0.107**	0.33
		Aquatic insects remains	0.1	0.13	0.78	**0.008**	0.005	0.43
		Hymnoptera	0.09	0.18	0.51	0.006	**0.007**	0.53

53

Chapter 3

Seasonal feeding plasticity can facilitate coexistence of dominant omnivores in tropical streams

Mayara P. Neves, Pavel Kratina, Rosilene L. Delariva, J. Iwan Jones and Clarice B. Fialho

Seasonal feeding plasticity can facilitate coexistence of dominant omnivores in tropical streams

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60

1   **Abstract**

2   Coexistence of ecomorphologically similar species in diverse tropical ecosystems has been

3   a focus of long-term debate among ecologists and evolutionary biologists. Such coexistence

4   can be promoted by trophic plasticity and seasonal changes in omnivorous feeding. We

5   combined stomach content and stable isotope analyses to determine how seasonal variation

6   in resource availability influences the consumption and assimilation of resources by two

7   syntopic fish of the genus *Psalidodon* in the Lower Iguaçu basin. We also tested the impact

8   of seasonality on trophic niche breadth and diet overlap of these two dominant omnivores.

9   Seasonal changes in resource availability strongly influenced the consumption and

10   assimilation of resources by the two fish species. Both species exhibited high levels of

11   omnivory, characterized by high diversity of allochthonous resources in the wet season.

12   Terrestrial invertebrates were the main source of diet during this season. However, in the

13   dry season, both species reduced their isotopic niches, indicating diet specialization. High

14   diet overlap was observed in both seasons, but the isotopic niche overlap was smaller in the

15   dry season. Substantial reduction in *P. bifascistus* isotopic niche and a shift toward aquatic

16   invertebrates can facilitate coexistence during this season of resource shortage. Feeding

17   plasticity allows omnivorous fish to adjust their trophic niches according to seasonality,

18   promoting the exploitation of different resources during periods of greater resource

19   diversity. This seasonal variation could be an important mechanism that contributes to the

20   resource partitioning and coexistence of dominant omnivores in neotropical streams.

21

22   **Keywords:** neotropical fish, omnivory, species coexistence, stable isotope analysis, trophic

23   niche.

Chapter 4

Land use changes alter trophic ecology of neotropical omnivorous fish

Artigo a ser submetido na revista Ecology

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Mayara P. Neves, Rosilene L. Delariva, Daniel M. Perkins, Clarice B. Fialho and Pavel Kratina

1   **Land use changes alter trophic ecology of neotropical omnivorous fish**

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16

17   **Running head**: Land use changes alter the trophic ecology fish

18 **Abstract**

19 Negative effects of deforestation on ecosystem functioning has been reported across the

20 world. However, the mechanisms behind of the persistence of omnivorous species under

21 anthropogenic disturbances are still unclear. Herein, we combined the gut content and

22 stable isotope analyses to verify the effects of the reduced native forest gradient in diet and

23 trophic niche of omnivorous fish (genus *Astyanax* and *Bryconamericus*) in streams from

24 lower Iguaçu and Piquiri river basins, southern Brazil. As land use changed, fish became

25 more enriched in ^{13}C and more slightly enriched in ^{15}N, in a non-linear fashion. Coupled

26 with changes in consumption, there were also differences in the proportions of resources

27 assimilated by omnivorous fish. Specifically, fish assimilated high proportion of

28 autochthonous resources with high energy (aquatic insects) in streams with high native

29 forest cover. However, in streams with drastic reduced native forest cover and urban

30 influence, sedimentary organic matter (low quality) and allochthonous (terrestrial

31 invertebrates) resources with greater enrichment in ^{13}C were most assimilated by

32 omnivorous fish. In streams with agricultural influences, fish were more enriched in ^{15}N.

33 There was a decline in the trophic position of fish, indicating a decrease in the degree of

34 omnivory. Isotopic niches of *Psalidodon bifasciatus*, a widespread species, were broadest

35 in unaffected streams with high native forest cover, reduced in streams with agricultural

36 influence and become wider again in streams with urban influence. However, this variation

37 was related to the richness of fish species, but not by deforestation. Thus, our findings

38 suggest that the persistence of dominant omnivorous under different anthropogenic

39 disturbances may be explained by high plasticity in diet and expansion of the niche in

40 presence of other competitors.

41   **Keywords:** Anthropogenic disturbance, environmental gradients, gut content, stable

42   isotopes, freshwater

43

Chapter 5

Morphological divergence and partitioning among tetra fish in subtropical streams

Artigo a ser submetido na revista Freshwater Biology

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Mayara P. Neves, Pavel Kratina, Clarice B. Fialho and Rosilene L. Delariva

Morphological divergence and niche partitioning of tetra fish in subtropical streams

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Running head: Morphology divergence and diet of tetra fish species

Keywords: body shape, internal trophic apparatus, stomach content, stable isotopes, trophic niche, phylogeny

ABSTRACT

22

23 **1.** Morphological differences among species may be related to their trophic ecology

24 (ecological divergence-convergence) or reflect their phylogenetic relationships (niche

25 conservationism) with implications for coexistence.

26 **2.** Herein we investigated whether external and internal morphology traits (body shape and

27 internal trophic apparatus) were associated with trophic niche (stomach contents and stable

28 isotopes) and if these traits were congruent with phylogenetic relationship of tetra fish in

29 neotropical streams.

30 **3.** Tetra fish species showed several complex examples of convergence and divergence in

31 morphology, consume and assimilation; refuting the hypothesis phylogenetic niche

32 conservationism. Species with elongated bodies, such as *B. ikaa* and *P.* aff. *paranae*

33 distantly related, tend to have teeth with fewer cusps, few and shorter gill rakers, and also

34 shorter intestine and fewer pyloric caeca associated with greater assimilation of aquatic

35 invertebrates. Species with teeth with a higher number of cusps, such as *P. bifasciatus* and

36 *P.* aff. *gymnodontus*, had gill rakers in greater number and more elongated, as well as

37 greater intestinal length and greater number of pyloric caeca associated with greater

38 proportions of assimilation of terrestrial invertebrates. External and internal morphology

39 was significantly related to stable isotopes ratios, but not to stomach content analysis. Only

40 *B. ikaa* had congruent diet and assimilation, reinforcing the aquatic insectivore diet. The

41 three species of *Psalidodon* and *A. lacustris* ingested similar proportions of plant material,

42 terrestrial and aquatic invertebrates. However, the plant material was not assimilated by any

43 of the species.

44 **4.** There was intermediate and high overlap between both close (*P. bifasciatus* x *P.* aff.

45 *gymnodontus*) and distant (*P. bifasciatus* x *A. lacustris*; *P. bifasciatus* x *B. ikaa*) related

46 species. Specially in relation to *P. bifasciatus*, the niche contraction or expansion seems to

47 be related to the species in co-occurrence.

48 **5.** Morphological divergences of the tetra fish species might reflect on ecological

49 differences, related to the capture, ingestion and assimilation of food resources which

50 facilitate niche partitioning, and consequently, their coexistence.

Chapter 6

Histomorphology of digestive tract of three small characid fish from Iguaçu River basin

Artigo a ser submetido na revista Journal of Fish Biology

Mayara P. Neves, João Paulo de A. Amorim, Rosilene L. Delariva and Clarice B. Fialho

1 **Histomorphology of digestive tract of three small characid fish from Iguaçu**
2 **River basin**

3

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17

18 **Running head**: Digestive tract of small characid fish

19   **Abstract**

20   The aim of this study was to characterize the morphology and histochemistry of the

21   digestive tract of three small characid fish (*Psalidodon bifasciatus*, *P.* aff. *gymnodontus* and

22   *Bryconamericus ikaa*), freshwater omnivorous species found in streams from Iguaçu River

23   basin, using gross anatomy and light microscopy. Characid fish species had some

24   differences in their anatomical digestive traits, but with histological structure similarities.

25   Species had a short and tubular esophagus that opens in a stomach, a J-shaped saccular

26   organ, with a thick wall and consisted of cardiac, fundic and pyloric regions. There were

27   four main intestinal loops and presence of pyloric caeca in the anterior region.

28   *Bryconamericus ikaa* presented lower number of pyloric caeca and shorter intestine length.

29   In contrast, *P. bifasciatus* had great number of pyloric caeca and longer intestine. All

30   species presented similar histological structure of wall of the digestive tract composed of

31   four layers: mucosa, submucosa, muscular, and serosa. In general, mucosa was composed

32   of columnar epithelium with presence of goblet cell in esophagus and intestine.

33   Specifically, goblet cells seem more abundant in the posterior region of the intestine. In all

34   portions of the intestine, enterocytes were columnar cells with a PAS-positive brush border.

35   Submucosa layer was think in esophagus and decreased in stomach and intestine. Gastric

36   glands were abundant in cardiac and fundic region of stomach. Muscularis, mainly circular

37   layer, was well developed in esophagus and stomach (pyloric region) in comparison with

38   intestine. Such both anatomical and histological traits can be associated with omnivory

39   recognized for these species. These first results about digestive trait of these species could

40   be useful to answer further questions about ingestion, digestion, absorption and assimilation

41   of food.

42

43   **Keywords:** morphology, histology, digestive tract, feeding ecology, Characidae

CONCLUSÕES GERAIS

- Foram amostradas seis espécies de caracídeos nos riachos das bacias do Baixo Rio Iguaçu e Rio Piquiri, as quais ocorreram com distintos padrões de distribuição. Especificamente, *Psalidodon* aff. *gymnodontus* e *Bryconamericus ikaa* ocorrem somente em riachos com elevada cobertura vegetal na microbacia. Por outro lado, *Astyanax lacustris* e *A.* aff. *fasciatus* foram registrados em elevada abundância em riachos urbanos. *Psalidodon bifasciatus* foi a única espécie amplamente distribuída e co-ocorreu em sintopia com outras espécies de caracídeos ou em alopatria. Embora fosse considerada endêmica da bacia do Rio Iguaçu, *P. bifasciatus* teve sua distribuição geográfica ampliada para a bacia do Rio Piquiri. Nesse sentido, uma revisão taxonômica robusta e integrativa de *Psalidodon* e *Astyanax* na bacia do Rio Iguaçu e bacias adjacentes poderá elucidar o padrão de distribuição dessas espécies e fornecer ferramentas acuradas para a identificação dessas espécies.

- Os resultados aqui obtidos enfatizam a importância da sazonalidade ambiental na modelagem da variação de nicho dentro e entre as espécies. É importante ressaltar que esses efeitos parecem ser específicos da espécie e dependentes do contexto. Enquanto três das espécies estudadas (*P.* aff. *gymnodontus*, *P.* aff. *paranae* e *B. ikaa*) apresentam maior especialização individual no período chuvoso, provavelmente em decorrência do aumento da diversidade de recursos disponíveis, *P. bifasciatus* apresentou maior especialização individual no período de seca. Essas mudanças sazonais nas ligações entre consumidores individuais e suas presas podem desempenhar um papel importante na alteração temporal da magnitude da competição intra e interespecífica. Portanto, isso sugere que essa dimensão temporal da variação de nicho dentro das populações tem o potencial de afetar a coexistência de espécies similares, o que é uma via promissora para pesquisas futuras. Aqui, conclui-se que a compreensão da dinâmica das teias alimentares em riachos de cabeceira subtropicais pode se beneficiar de uma perspectiva de variação de nicho intraespecífico.

- A variação sazonal nas condições ambientais também influenciou a amplitude do nicho trófico e a sobreposição de recursos de espécies de peixes onívoros sintópicos. A plasticidade trófica permite que explorem recursos alternativos durante períodos de maior disponibilidade. Para compreender completamente esta plasticidade trófica, pesquisas futuras devem investigar como as preferências alimentares de cada espécie aliviam a competição interespecífica por recursos compartilhados. Então, poderá inferir se tais mudanças no fornecimento de recursos podem favorecer melhores competidores por recursos aquáticos durante a estação seca, ou melhores competidores por recursos terrestres durante a estação

chuvosa. Este estudo mostra como a onivoria e a plasticidade trófica podem ser importantes para a coexistência de espécies filogeneticamente relacionadas em diversos ecossistemas tropicais. Considerando as previsões climáticas futuras para a América do Sul, que indicam um clima mais seco e quente, essas descobertas destacam a necessidade de melhor compreensão mecanicista da coexistência em mudanças nos ecossistemas de água doce.

- Os distúrbios antropogênicos podem afetar os peixes onívoros, uma chave importante na estrutura da teia alimentar, o que pode ter efeitos significativos no funcionamento do ecossistema. As espécies onívoras mudaram sua dieta em um gradiente reduzido de vegetação nativa, bem como suas relações nicho trófico frente a alterações nas variáveis abióticas e bióticas. O desmatamento pode alterar a estrutura do habitat e a diversidade de recursos alimentares em riachos, refletindo em mudanças na fonte de carbono (autóctone para alóctone) para peixes onívoros. A persistência de onívoros dominantes pode ser explicada por mudanças na dieta de recursos de alta qualidade de origem autóctone para recursos de baixa qualidade (matéria orgânica sedimentar) e alóctones, e também, pela expansão do nicho trófico em riachos com alta riqueza de espécies de peixes. Isso é essencial tendo em vista que, no Brasil, as últimas mudanças no Código Florestal tornaram mais flexíveis as reduções de áreas de preservação permanente, como a mata ciliar, e os efeitos negativos foram ignorados para a justificativa do avanço econômico. Além disso, os efeitos da redução da cobertura florestal nativa em peixes onívoros precisam ser expandidos para uma abordagem de teias alimentares para uma melhor compreensão desses efeitos no funcionamento do ecossistema, a fim de fornecer medidas de mitigação e conservação para ecossistemas altamente ameaçados.

- A divergência morfológica das espécies de lambaris aqui estudas repercutiu em diferenças ecológicas, como captura, ingestão e assimilação de recursos. Diferenças ecomorfológicas e plasticidade trófica podem ser a raiz dos processos de especiação. Conforme previsto pela Teoria do Nicho, essas diferenças sutis podem favorecer a coexistência dessas espécies similares com alto potencial de competição em riachos neotropicais. A morfologia interna e externa foi capaz de predizer a assimilação de recursos mesmo para espécies com alta similaridade ecomorfológica. O uso de isótopos estáveis juntamente com a análise do conteúdo estomacal provou ser uma ferramenta valiosa no entendimento da ecologia trófica das espécies avaliadas. Para maior poder de inferência sobre os processos de divergência, conservacionismo de nicho e interações entre espécies, futuras investigações sobre as outras espécies dos gêneros aqui estudados são necessárias. Ainda assim, é necessário compreender

a plasticidade trófica dessas espécies em outros ambientes neotropicais, como rios, lagos e lagunas costeiras, considerando as variações de características intra e interespecíficas.

- Em conclusão, as características anatômicas e histológicas do trato digestivo são consistentes com o hábito onívoro das espécies de peixes caracídeos avaliadas aqui. Esse estudo fornece a primeira descrição da histologia e da histoquímica do trato digestivo desses pequenos caracídeos na bacia do Rio Iguaçu. As espécies apresentaram um esôfago curto, estômago em formato de J com a presença das regiões cardíaca, fúndica e pilórica. O intestino tem três alças com cecos pilóricos. A estrutura histológica do trato digestivo foi composta por mucosa, submucosa, muscular e serosa. Essas camadas e tipos de células foram diferentes ao longo do trato digestivo. As células caliciformes foram abundantes principalmente no esôfago e na região posterior do intestino. Análises futuras, como morfometria e contagem dos tipos de celulares, ainda são necessárias para verificar as diferenças entre regiões de traço digestivo e também entre espécies. Essas investigações podem ser úteis para responder perguntas sobre ingestão alimentar, digestão, absorção e assimilação de alimentos e tempos de digestão.

ANEXOS

VÍDEOS DE DIVULGAÇÃO CIENTÍFICA

- **https://www.youtube.com/watch?v=4QA_6wfx1nA&t=56s**

- **https://www.youtube.com/watch?v=IdbkczFmmiE**

RESUMOS PUBLICADOS EM EVENTOS

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SEASONAL FLUCTUATIONS IN USE OF RESOURCES BY FIVE SMALL ENDEMIC FISHES (CHARACIDAE) IN SUBTROPICAL ENVIRONMENTS

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Tema/Meio de apresentação: Ecologia de Comunidades/pôster

Seasonality is characterized by environmental changes derived from the annual cycles of temperature and water levels, with consequent changes in the availability of food resources In this study, we hypothesized that seasonal changes in the use of resources by species promotes trophic niche segregation. Samplings were performed quarterly between August 2013 and May 2014 at 14 sites in the Pelotas River basin, using gill nets of different mesh sizes, seining, casting nets and electrofishing. We analyzed 1,253 stomach contents belonging to *Astyanax dissensus*, *Astyanax paris*, *Astyanax saguazu*, *Astyanax xiru* and *Bryconamericus patriciae* according to the volumetric method. Allochthonous resources were clearly the most consumed by the species especially in periods of higher temperatures. *A. xiru*, *A. saguazu* and *B. patriciae*, presented a more constant diet during the sampling period (herbivore, aquatic insectivorous and detritivore/aquatic insectivorous, respectively). The diet of *A. dissensus* and *A. paris*, more drastic changes were observed in the proportions of allochthonous and autochthonous resources. For these species, the consumption of allochthonous resources increased during November, February and May. The differences observed in the proportions of consumption of allochthonous and autochthonous items were significant (Chi-square, $x^2 > 5.99$, $p < 0.05$). The trophic niche breadth evaluated by Permutational Analysis of Multivariate Dispersions (PERMIDISP) was significantly different between the species, being that in August, the species presented lower values of diet breadth. In the other periods, the highest values of niche breadth were related to the increase in the consumption of allochthonous items. Thus, the variations observed in the proportions of the resources against the seasonal oscillations seem to be important factors for the trophic segregation, species interactions and coexistence.

Coexistência de peixes de pequeno porte em ambientes lóticos neotropicais: evidência de diferenciação de nicho trófico

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A competição por alimento é um fator direcionador na diversificação das espécies, uma vez que para mitigar seus efeitos, as espécies coexistentes tendem a divergir no uso dos recursos. Nesse sentido, entender os processos que norteiam a partilha de recursos entre organismos morfologicamente semelhantes e co-ocorrentes, é fundamental para o embasamento de estudos biológicos, bem como, ações de conservação e manejo de ecossistemas Sendo assim, utilizou-se neste estudo um conjunto de sete espécies de caracídeos de pequeno porte simpátricas, com morfologia e estratégias alimentares semelhantes, e que co-ocorrem em ambientes aquáticos lóticos sazonais, afim de testar a hipótese de que a coexistência de espécies de peixes de pequeno porte em rios neotropicais, é facilitada pelo uso diferencial do nicho. As coletas dos peixes foram realizadas em seis pontos distribuídos nos rios Verde e São Domingos, Bacia do alto rio Paraná, Brasil, em dois períodos hidrológicos (chuvoso e seco). Foram utilizadas redes de arrasto, tarrafa e redes de emalhar. Através da análise de 2.143 conteúdos estomacais, pelo método volumétrico, observou-se que a dieta das espécies diferiram entre si (PERMANOVA, pseudo-F = 215,25; p < 0,01) e que consumiram uma ampla variedade de itens, principalmente de origem alóctone, como sementes, vegetais terrestres e insetos terrestres. Além disso, as mesmas apresentaram diferenças inter e intraespecíficas na composição alimentar entre os períodos hidrológicos, sendo possível identificar, através da análise SIMPER, os itens que particularizam cada espécie e que contribuíram para segregação trófica entre elas. Apesar da variedade de recursos utilizados pelas espécies, não foi possível observar por meio da análise PERMDISP, um padrão consistente e significativo de expansão ou contração do espectro alimentar entre os períodos hidrológicos, como era previsto. A sobreposição de nicho alimentar, calculada a partir do índice de Pianka, apresentou valores intermediários e baixos (<0,60), para os pares de espécies em ambos períodos hidrológicos, embora o período chuvoso tenha apresentado uma leve tendência de aumento (ANOVA, F = 12,1; p < 0,001). Neste sentido, ficou evidente a existência de partilha de recursos entre as espécies de caracídeos de pequeno porte, facilitada pela exploração de recursos preferenciais distintos, bem como, pelas variações intraespecíficas em resposta disponibilidade sazonal de recursos. A alternância de itens e proporções desses na dieta, bem como, mudanças no comportamento de forrageio, em momentos propícios, provavelmente, seja o ponto chave da coexistência destas espécies.

Palavras chaves: Characidae, partição de recursos, rios tropicais

DIET-ASSOCIATED MORPHOLOGICAL DIVERGENCE IN CHARACID FISH IN A SUBTROPICAL RIVER

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Abstract: Diet and morphology are instruments that reveal the dynamics and interactions among species. Herein we investigate the body morphology through geometric morphometry and to relate to the diet of five sympatric characins. Samplings were performed quarterly between August 2013 and May 2014 at 14 sites in Pelotas River basin. The contents of 1,253 stomachs from *Astyanax dissensus*, *Astyanax paris*, *Astyanax saguazu*, *Astyanax xiru* and *Bryconamericus patriciae* were analyzed under optical and stereoscopic microscopes according to the volumetric method. In order to test differences in diet composition among of the species was applied Permutational Multivariate Analysis of Variance. The left sides of preserved fish were photographed. Photographs were digitized and landmarked using tpsUTIL and tpsDIG2, respectively. Landmarks were superimposed and aligned to correct for size, rotation and translation. Principal components were then used to describe major axes of shape variation among species. All analyzes were run in R Programming Environment. There was a significant difference in the diet composition among species (Permanova, Pseudo-F= 58.1; *p*<0.001). In relation to body morphology, principal component 1 explained 43.3% and principal component 2 24.5% of the variation in shape among individuals. Negative PC1 values segregated species of higher body, snout and short caudal peduncle, whose diet was based mainly on aquatic insects, such as *A. saguazu*. In positive PC1, species of more elongated body, with herbivorous habit (*A. xiru*) and diet based on detritus and aquatic insects (*B. patriciae*). In PC2, negatively segregated species with large insect consumption, while positively, species that consumed mainly leaves and seeds. The species with more generalist diet, such as *A. dissensus* and *A. paris*, exhibited a morphological overlap and did not form a welldefined group like the other species. These results indicate that the shape differentiation play a critical role in coexistence of similar species.

Key-words: stomach contents, resource feeding, geometric morphometrics, niche

VARIAÇÕES SAZONAIS INTRAESPECÍFICAS NA DIETA DE PEQUENOS CARACÍDEOS EM RIACHOS NEOTROPICAIS

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Palavras-chave: ecologia trófica; amplitude de nicho; coexistência; sazonalidade

Riachos são extremamente dinâmicos e diversos, sendo afetados de modo marcante por variações sazonais. Esses ambientes exibem uma fauna de peixes peculiar, muitas vezes endêmica, constituída por espécies de pequeno porte, com potencial de dispersão limitado e interações ecológicas complexas. Diante disso, o presente estudo teve como objetivo investigar as variações sazonais intraespecíficas na dieta de lambaris, cuja similaridade morfológica as tornam potenciais competidoras e, portanto, bons modelos em investigações sobre coexistência. Amostragens foram realizadas em cinco riachos (baixo Iguaçu= S1, S2 e S4; Piquiri= S3) em julho/2017 (inverno) e dezembro/2018 (verão) por meio da técnica de pesca elétrica. Os conteúdos estomacais foram analisados por meio do método volumétrico. Para testar diferenças na composição da dieta entre os riachos e estações foi utilizada a Análise de Variância Multivariada Permutacional (PERMANOVA two way). A variabilidade da dieta das espécies (riacho/estação) foi avaliada pela Análise de Dispersões Multivariadas Permutacional (PERMIDISP). Todas as análises foram realizadas no programa R Programming Environment. Foram analisados 327 estômagos de Astyanax bifasciatus, Astyanax cf. bifasciatus, *Astyanax* aff. *paranae*, Astyanax sp. e Bryconamericus ikaa. Os caracídeos aqui avaliados consumiram uma ampla gama de itens alimentares, como folhas/sementes (48,2%), insetos aquáticos (21,7%), insetos terrestres (19,4%) e detrito (7,6%). Foram observadas diferenças significativas na dieta das espécies (PERMANOVA, Estações: Pseudo-F=5,6, p=0,001; Riachos: Pseudo-F=8,3, p=0,001; Estações*Riachos Pseudo-F=2,9, p=0,001). Em S1, A. bifasciatus e Astyanax sp. exibiram diferenças significativas na variabilidade individual intraespecífica entre estações (inverno: 0,63; 0,59; verão: 0,52; 0,65; respectivamente. F3,126=6,3; p=0,0005). Já em S2, *A. bifasciatus* e *B. ikaa* exibiram maiores amplitudes no verão (inverno: 0,53; 0,52; verão: 0,58; 0,61; respectivamente. F3,103=2,7; p=0,004). Em S3, *A.* cf. *bifasciatus* exibiu variabilidade similar em ambas estações (0,62; F3,53=20,9; p=0,89), enquanto que *A.* aff. *paranae* exibiu maior variabilidade no verão (inverno:0,35; verão:0,62; F3,53=20,9; p=0,04). Em S4 foi registrado a ocorrência apenas de um caracídeo, *A. bifasciatus*, o qual não apresentou diferenças significativas na variabilidade individual intraespecífica entre as estações (inverno/verão: 0,59; F1,31=6,3; p=0,99). Maior variabilidade para a maioria das espécies no verão parece estar relacionada com maior consumo de itens de origem alóctone, principalmente sementes. O hábito onívoro, juntamente com a ampla plasticidade trófica observada indicam partilha de recursos. Assim, esses resultados enfatizam os fatores que favorecem a coexistência, os quais estão relacionados com variações sazonais intra e interespecíficas. Além disso, o número de espécies, bem como o grau de parentesco entre elas (congêneres) devem ser investigados para melhor compreensão da diversidade de onívoros em riachos neotropicais.

VARIABILIDADE INTRAESPECÍFICA NA DIETA DE UM PEIXE ONÍVORO EM RIACHOS SOB INFLUÊNCIA DE DIFERENTES USOS DO SOLO

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Palavras-chave: Characidae; ecologia trófica; amplitude alimentar; antropização

Lambaris são espécies generalistas com elevada plasticidade trófica. São conhecidos pela capacidade de enfrentar mudanças abruptas no ambiente aquático relacionadas principalmente com a oferta de recursos alimentares e, consideradas resistentes. Atualmente, além das variações sazonais relacionadas com o regime hidrológico, os riachos têm sido severamente alterados pelas atividades humanas. Diante disso, o presente estudo investigou a variabilidade intraespecífica na dieta de Astyanax bifasciatus em riachos da bacia do Baixo rio Iguaçu sob influência de diferentes usos do solo, na região de Cascavel, Paraná. As coletas foram realizadas em dezembro/2017 com a técnica de pesca elétrica em três riachos: florestado (n=44), rural (n=24) e urbano (n=13). Essa classificação foi obtida a partir do cálculo da porcentagem de cobertura vegetal, bem como, áreas agrícolas e urbanas com auxílio do programa Google Earth Pro para delimitação da área da microbacia (km²). Os conteúdos estomacais foram analisados por meio do método volumétrico. Para testar diferenças na composição da dieta entre os riachos foi utilizada a Análise de Variância Multivariada Permutacional (PERMANOVA). Para analisar a variabilidade da dieta entre os indivíduos em cada riacho foi aplicado a Análise de Dispersões Multivariadas Permutacional (PERMIDISP) baseado na distância das amostras (indivíduos) da média do grupo (população/riachos). Adicionalmente, foi utilizado a Análise de Similaridade Percentual (SIMPER) para avaliar os itens alimentares que mais contribuíram para a dissimilaridade intraespecífica entre os riachos avaliados, usando a dissimilaridade de Bray-Curtis. Indivíduos inseridos no riacho florestado exibiram elevado consumo de sementes (79%) e insetos aquáticos e terrestres em menores proporções. Já nos riachos rurais os principais itens consumidos foram insetos terrestres como Coleoptera (56%), Hymnoptera (16%) e Homoptera (11%). Sementes (78%), detrito (11%) e larvas de Diptera (Chironomidade e Simulidae) foram consumidos por indivíduos coletados no riacho urbano. As dietas das populações foram significativamente diferentes entre os riachos (PERMANOVA, Pseudo-F=7,59; p=0.001). Além disso, resultados da PERMIDISP indicaram diferenças significativas na variabilidade individual intraespecífica entre os riachos amostrados (PERMIDISP, F2,78= 6,95; p= 0,002). No riacho urbano, A. bifasciatus apresentou menor variabilidade individual (0,45) quando comparado com riacho rural (0,59) e florestado (0,58). De acordo com SIMPER, sementes e Coleoptera (adulto), sementes e detrito, Coleoptera (adulto) e detrito foram os itens que mais contribuíram para a diferenciação intraespecífica entre os riachos florestado x rural, florestado x urbano e urbano x rural, respectivamente. Assim, esses resultados indicam que alterações no uso do solo (agricultura e/ou urbanização) promovem mudanças na disponibilidade e oferta de recursos. Espécies generalistas, como A. bifasciatus, conseguem se manter em ambientes com diferentes graus de antropização. Suas características morfológicas externas e internas permitem a exploração de diferentes compartimentos do habitat e consumo de recursos alimentares diversos. Contudo, a exposição crônica a contaminantes podem acarretar em diminuição da abundância e biodiversidade local.

Coexistence of characid fishes in Neotropical headwater streams mediated by intraspecific seasonal variations

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Coexistence of species is the primordial core of many ecological issues. Here we studied four small characid species of headwater streams, belonging to the genera *Astyanax* and *Bryconamericus*, to investigate the effects of co-occurrence and seasonality on population and individual trophic niche amplitude. Samplings were performed in winter (July 2017) and summer (December 2017) at six headwater streams in the lower Iguaçu River and Piquiri River basins, using electrofishing. We quantified trophic niche from the analysis of 403 gut contents belonging to *Astyanax* aff. *gymnodontus*, *Astyanax* aff. *paranae*, *Astyanax bifasciatus* and *Bryconamericus ikaa*. Characid species here consumed a wide diversity of feeding resources, which differed significantly between the seasons. Individual specialization was significantly different among species and seasons (GLMM, Anova, Chisq = 8.13; $p<0.00$). For most species, there was a greater degree of individual specialization and the population niche became broader in the summer (hot/rainy) related to the higher intake of allochthonous items (terrestrial insects and leaves/seeds). *Astyanax bifasciatus* was the exception and had greater individual specialization in winter. In addition, the individual specialization of *A. bifasciatus* was significantly influenced by seasonality (GLMM, Anova, Chisq = 54.37; $p<0.00$), but not by co-occurrence species (GLMM, Anova, Chisq = 3.11; $p<0.08$). Therefore, seasonality was the mainly factor that influences the dynamics of population niche. Thus, we infer that the coexistence of the species analyzed here is favored by intraspecific variations and resource partitioning, together with seasonal effects on the supply and availability of food. Herein, we conclude that the understanding of the dynamics of the trophic niche in headwater streams is extremely complex and should be studied from the perspective of intraspecific variation, taking into account the seasonality and the presence of species with competitive potential. Thus, individual specialization may both alter and be altered by community ecology interactions.

Palavras-Chave: Co-occurrence, Freshwater, Individual specialization, Seasonality, Tetra fishes, Trophic niche

Seasonal shifts in feeding and assimilation of *Astyanax* fishes (Characidae) from Lower Iguaçu River basin, Brazil

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We investigate the effect of seasonality on the consumption and assimilation of feeding resources of two omnivorous fishes. Fish, basal resources and potential prey items were collected from a stream in the Lower Iguaçu River basin in dry (July/17) and wet (December/17) season by electric fishing. For gut content analysis, 60 specimens of *Astyanax* aff. *gymnodontus* (D = 60; W = 36) and 47 *A. bifasciatus* specimens (D = 32; W = 15) were analyzed. For isotopic analysis, ten specimens of each species were selected in each season. Significant differences in diet were observed among species and seasons (PERMANOVA, Pseud-F= 2.27; *p*=0.003). In dry season *A.* aff *gymnodontus* consumed mainly leaves/seeds (56.7%) and terrestrial insects (17%), and *A. bifasciatus,* leaves/seeds (40.4%) and detritus (39.7%). In wet season, *A.* aff *gymnodontus* consumed terrestrial insects (45.9%) and leaves/seeds (22.7%); and *A. bifasciatus*, leaves/seeds (57.3%) and aquatic (20.6%) and terrestrial (19.5%) insects. In dry season, highest values of diet breadth were observed for *A. bifascitus* (0.57), while in wet season, for *A.* aff. *gymnodontus* (0.60). The Pianka's index indicated high overlap in both dry (0.74) and wet (0.81) seasons. In addition, in the wet condition, we observed major Isotopic similarity (0.36) and isotopic overlap percentage (64.2%), compared with dry condition (*ISim*= 0.17; %Overlap= 37.1%). Based on estimates using a dual-isotope MixSIAR Bayesian mixing model, *A.* aff. *gymnodontus* assimilated mainly aquatic (67%) and terrestrial (24%) invertebrates in dry condition, and large fractions of terrestrial invertebrates (68%) with similar proportions of the aquatic invertebrates (17%) and SOM (15%) in wet condition. Similarly, in dry condition, *A. bifasciatus* also assimilated mainly aquatic invertebrates (79%), whereas in the wet condition, terrestrial (59%) and aquatic (27%) invertebrates, and SOM (14%). Thus, the coexistence among species are favored by seasonal variations in the supply and availability of resources.

Palavras-Chave: Coexistence, Food overlap, Gut content, Seasonality, Stable isotopes, Trophic niche