LIMNOLOGY and OCEANOGRAPHY

Trophic plasticity of omnivorous fishes in natural and human-dominated landscapes

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Abstract

The persistence of diverse communities and functioning ecosystems under increasing anthropogenic pressure relies on food web rewiring and the ability of animals to expand or change their diet in disturbed ecosystems. We combined a suite of diet tracing techniques to study trophic plasticity in omnivorous fishes, ecomorphologically similar species with high competition potential, across different human land uses in subtropical streams. We found that the proportion of native forest cover, associated with intensive land use, altered the isotopic composition of fishes, which were more enriched in ^{13}C, without affecting the carbon isotope ratios of their prey and basal resources. There was also evidence for a nonlinear effect of native forest cover on the $\delta^{15}N$ values of basal resources, macroinvertebrates, and omnivorous fishes, indicating that nutrient pollution from agriculture propagated through stream food webs. The most widely distributed fish species shifted their diet from autochthonous resources to terrestrial invertebrates and sedimentary organic matter in disturbed streams. Moreover, the isotopic niche of this fish species was broader in streams with higher fish species richness, indicating the combined impacts of environmental change and competition on species coexistence. Therefore, our findings showed that the dominance and trophic niche breadth of dominant omnivores depend not only on the availability of resources but also on the interactions with their putative competitors.

Pervasive land use change is among the primary causes of biodiversity loss and food web simplification, altering ecosystem functioning worldwide (Etard et al. 2022; Kemp et al. 2023; Moi et al. 2023). The maintenance of healthy functioning ecosystems and high species diversity under increasing human pressure relies on food web rewiring and the ability of animals to

shift their diet in disturbed ecosystems with scarce resources (Lu et al. 2016; Kemp et al. 2023). In this context, omnivores play a functional role in enhancing food web stability as adaptive foraging allows them to adjust their diet (Kratina et al. 2012), facilitating their persistence in the face of human-induced disturbances (Carvalho et al. 2019). However, the ecological mechanisms underlying this trophic plasticity are not fully understood.

Omnivores have a broad diet and the ability to feed on resources from different trophic positions (Ingram et al. 2012; Gutgesell et al. 2022). Tropical environments contain high diversity and abundance of omnivorous species (Fricke et al. 2023), where generalism and opportunism are common strategies (Costa-Pereira et al. 2017; Garcia et al. 2017; Neves et al. 2021). For instance, common omnivorous tetra fishes exploit different aquatic microhabitats and consume many types of animal and plant resources (Delariva and Neves 2020), allowing them to respond to seasonal variability in resource availability (Costa-Pereira et al. 2017; Neves et al. 2021;

Additional Supporting Information may be found in the online version of this article.

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Gutgesell et al. 2022). Due to their trophic plasticity, omnivores are generally resilient to anthropogenic stressors and many omnivorous species even proliferate in highly degraded environments (Larentis et al. 2022).

Changes in environmental characteristics modify the diversity and availability of food resources for fish. Human disturbance, such as deforestation, can reduce allochthonous inputs, causing habitat homogenization, and increased consumer reliance on autochthonous carbon sources (Doi 2009). Such habitat homogenization can, in turn, reduce the trophic niche breadth of generalist animals, as predicted by MacArthur's habitat heterogeneity hypothesis (MacArthur 1972). However, there is currently no consensus on how human disturbances affect the trophic niches of omnivores, even across studies that use a consistent analytical approach. There is some empirical evidence that the trophic niches of mammals and birds exhibit a variable response to modified landscapes (Magioli et al. 2019). Similarly, the trophic niches of some neotropical birds became narrower in human-modified landscapes, but not for all trophic guilds (Navarro et al. 2021). In New Zealand, streams with high sedimentation and human disturbances were associated with compression of fish trophic niches (Burdon et al. 2019). By contrast, nitrogen pollution appears to expand the trophic niches of Brazilian fishes (Carvalho et al. 2019). Finally, trophic niche breaths of macroinvertebrates in Croatian streams (Price et al. 2019) or fish meso-predators in Sabah, Malaysian Borneo (Wilkinson et al. 2021) were not influenced by different types of land use.

Herein, we used a landscape disturbance gradient and combined stomach content and stable isotope analyses to quantify the diet and trophic niche of omnivorous fishes in a biodiversity hotspot in Southern Brazil. Despite its ecological relevance, the Atlantic Forest, a biome composed of the coastal forest or Atlantic rain forest and the tropical seasonal forest or semi-deciduous Atlantic Forest, has been dramatically reduced over the decades and replaced by agricultural and urban land use (Mohebalian et al. 2022). We tested the overarching hypothesis that, in response to the negative impacts of agriculture and urbanization expansion, and associated reduction of native riparian forest, the trophic ecology of a dominant omnivorous species should change. Specifically, we predicted that:

1. Human disturbances could promote changes in resource use by omnivorous fishes and, consequently, alter their stable isotope composition. However, human disturbances can also affect the isotopic composition of basal resources, which may reverberate to the isotopic composition of macroinvertebrate prey and their fish consumers. Lower native riparian forest cover can expose the streams to high solar incidence, and consequently increase algal productivity. Therefore, we expected that omnivorous fishes would have higher $\delta^{13}C$ and $\delta^{15}N$ values in streams with lower coverage of native forests and high inputs of nitrogen from agricultural practices.

2. As the proportion of native forest cover decreases, stream ecosystems are more strongly affected by leaching and silting events due to the greater exposure to torrential summer storms. Consequently, omnivorous fishes would be forced to switch their consumption and assimilation from abundant, high-quality autochthonous resources in forested areas to low nutritional resource (e.g., detritus) and allochthonous (terrestrial invertebrates) resources in areas with low coverage of native forest. Alternatively, omnivorous fishes in more open canopy streams would rely more on autochthonous resources, if these reaches have higher algal primary productivity.

3. The trophic niche of common omnivorous fish would become narrower in disturbed streams due to habitat homogeneity and low diversity of resources, but these effects could also be modulated by interactions with potential interspecific competitors. We addressed this hypothesis by applying niche theory, which predicts that in the absence of competitors, species can contract their trophic niches and consume their preferred food items. However, to reduce competitive pressure from potential competitors, species would expand their trophic niches by consuming alternative food items.

Methods

Study area and field sampling

Iguaçu and Piquiri rivers and their tributaries belong to the second largest basin in South America, the Paraná River (Abell et al. 2008). There is less than 4% of Atlantic Forest currently remaining in Paraná State and the native forest has been gradually replaced by monocultures, livestock farmland and other agroindustrial activities.

In the region between the Iguaçu and Piquiri river basins, we surveyed seven headwater streams (2nd and 3rd orders) across a gradient of native forest cover (5–75%; Supporting Information Fig. S1; Supporting Information Table S1) in the December of 2017 (wet season). We estimated human land uses in the areas encompassing each stream, by demarcating the catchment above each sampling site and inputting the geographical coordinates of the sampling sites into Quantum GIS software (QGIS version 2.18.10). Using the GRASS plugin in QGIS, we opened the MDE raster, and with the "r.watershed" and "r.water.outlet" tools, we delimited the catchment area for each sampling site (range: 6.6–18.2 km^2; Supporting Information Table S1). We used the 2017 land use cover data from the MapBiomas website (MapBiomas Project 2021) as a basis to calculate the different land use covers inside the polygon of each delimited catchment site. We calculated the area (km^2) for the following land uses: urbanized area—paved area, residential and industrial area; agricultural area—pastures, plantations of annual and perennial

crops and silviculture; and forested area—included areas of riparian forest and remnants of native forest. To estimate the proportion of native forest cover associated with each stream site, we calculated the proportions of the urbanized, agricultural, and forested areas from the total area (km^2) of each stream watershed. The native forest cover (%) was then used as a predictor in the subsequent analyses.

Physical and chemical habitat characteristics

We measured the key environmental variables that can be influenced by native forest cover (Supporting Information Table S1), as well as the mean stream width (m), depth (m), and flow velocity (m^3 s^{-1}) at five stream cross-sections. We used a Horiba U-50 multiparameter water quality probe for in situ measurements of water temperature (°C), pH, dissolved oxygen concentration (mg L^{-1}) and saturation (%), oxidation–reduction potential (ORPmv), specific electric conductivity (μS cm^{-1}), turbidity (NTU) and total solids (μS cm^{-1}). We replicated all these measurements three times across the stream reach in each stream. From each stream, we collected a 1-L water sample for laboratory analysis of chlorophyll *a* (μg L^{-1}), total phosphorus (μg L^{-1}), total nitrogen (mg L^{-1}), ammonium NH$_4$ (mg L^{-1}), soluble reactive phosphorus, SRP (μg L^{-1}), and nitrate NO$_3$ (mg L^{-1}) concentrations, following the approach described by Mackereth et al. (1978) and American Public Health Association (2005).

Fishes, their invertebrate prey, and basal resources

In each stream, we sampled the fish assemblages in a 50 m reach using electrofishing, making three passes of 40 min. The abundance of Characidae species comprised 50.9–75.5% of the total fish abundance in the sampled streams. Within this family, we focused our analysis on all omnivorous fish species (six species) of the genus *Astyanax*, *Bryconamericus*, and *Psalidodon*. These included *Psalidodon* aff. *paranae* (Eigenmann 1914) in sites S3 and S5, *Astyanax lacustris* (Lütken 1875) in S3 and S7, *Psalidodon* aff. *gymnodontus* (Eigenmann 1911) in S2, *Astyanax* aff. *fasciatus* Cuvier, 1819 in S7, and *Bryconamericus ikaa* (Casciotta, Almirón and Azpelicueta 2004) in S1. *Psalidodon bifasciatus* (Garavello and Sampaio 2010) was a dominant species and was collected from all sampled streams. Thus, the analysis of *P. bifasciatus* allowed us to quantify changes in the trophic ecology of a dominant species across a broad land use gradient and the potential effects of competition with species of close phylogenetic proximity and high morphological similarity. In addition, *P. bifasciatus* was less abundant in streams with co-occurrence of other characid species (S1, S2, S3, S5, and S7; mean numerical abundance: 33.5%) than in streams without the presence of another characid species (S4 and S5, mean numerical abundance: 71.4%).

For stomach content analysis, all specimens were anesthetized in eugenol, then fixed in 10% formaldehyde and later preserved in 70% alcohol. Subsequently, the specimens were identified, measured, and weighed in the laboratory. For the stable isotope analysis, during the sampling, adult specimens of each species were immediately euthanized via spinal section, identified, measured, and weighed in situ. The specimens were stored on ice for further processing in the laboratory. The fish samples were collected with authorization from the Instituto Chico Mendes de Conservação da Biodiversidade (license numbers 30182, 25039-1) and approved by the Ethics Committee on Animal Use of the Universidade Federal do Rio Grande do Sul (CEUA—32734), following the protocols in their ethical and methodological aspects for the use of fish. Voucher specimens were deposited in the ichthyology collection of the Departamento de Zoologia at the Universidade Federal do Rio Grande do Sul (Supporting Information Table S2).

We sampled larval aquatic insects (Ephemeroptera, Trichoptera, Plecoptera, Hemiptera, Coleoptera, Megaloptera, Odonata, Chironomidae, Simulidae) and other aquatic invertebrates (*Aegla* and Atyidae) using a kick net (0.04 m^2 and 200 μm mesh size) across the entire same stream reach. We sampled terrestrial invertebrates (Araneae, Coleoptera adult, Odonata adult, Auchenorrhyncha adult, Hemiptera adult, Hymenoptera, Orthoptera, Lepidoptera adult, Diptera adult) using an entomological net from riparian vegetation around each stream. We collected Oligochaeta manually in the soil around the streams.

Basal resources we sampled included riparian vegetation (terrestrial leaves of pteridophytes, monocotyledons, and seeds of dicotyledons), aquatic biofilm, particulate organic matter (POM) and sedimentary organic matter (SOM). We also sampled biofilm by scraping and washing rocks with distilled water. For POM, we collected a 1-L water sample per stream and filtered the water sample using a filtration apparatus attached to a vacuum pump using fiber filters (Macherey-Nagel® filters). We randomly sampled SOM from three sections of each stream. We froze all fish samples, prey invertebrates and basal resources at −20°C freezer until processing in the laboratory (Supporting Information Table S3).

Laboratory procedures

We analyzed the stomach contents of 309 fish specimens (Supporting Information Table S5). To reduce the variance caused by ontogenetic diet shifts, we inspected the gonads of all sampled fish and selected only adult specimens for further analysis. We removed fish stomachs and used optical and stereoscopic microscopes (Opton TIM-2B WF10X) to identify their contents to the lowest taxonomic resolution possible (usually family or genus). We quantified the diet items using the volumetric method, that is, the total volume of a food item taken by the fish population is given as a percentage of the total volume of all stomach contents (Hyslop 1980), using graduated test tubes and a glass counting plate (Hellawell and Abel 1971).

We analyzed a total of 266 samples of basal resources, prey, and fishes for nitrogen (δ^{15}N) and carbon (δ^{13}C) stable isotope ratios (Supporting Information Table S3). First, we washed all basal resources and prey with distilled water. For smaller taxa (e.g., Chironomidae and Simuliidae), we pooled at least 10 individuals into a single sample. For fish samples, we dissected dorsal muscle tissue and washed it with distilled water (Neves et al. 2021). Then, we lyophilized all samples, homogenized them using mortar and pestle and stored them in 2 mL Eppendorf tubes. Subsequently, we weighed 1.6 ± 0.2 mg for dry animal tissue, or 3.6 ± 4.2 mg for basal resources, into tin capsules and analyzed the samples at the Center for Nuclear Energy in Agriculture (CENA) at the University of São Paulo, Brazil. To determine the stable isotope ratios, we used a mass spectrometer system in the continuous flow (CF-IRMS) mode with a Carlo Erba elemental analyzer (CHN 1110) coupled to a Delta Plus mass spectrometer (Thermo Fisher Scientific). We present all values in delta notations, which represent the deviation of stable isotope ratios (^{13}C : ^{12}C and ^{15}N : ^{14}N) from universal standards: PDB limestone for carbon and atmospheric nitrogen for nitrogen. We did not correct the fish muscle δ^{13}C values for lipids because all C : N ratios were below 3.5, indicating negligible lipid content in the samples (Hoffman et al. 2015).

Statistical analyses

Effects of native forest cover on isotopic composition of omnivorous fishes, macroinvertebrate prey, and basal resources

To test our first hypothesis, we estimated the effects of native forest cover (%) on δ^{15}N and δ^{13}C values of basal resources, aquatic macroinvertebrates, and omnivorous fishes, using generalized additive models (GAMs) in the *mgcv* package (Wood and Scheipl 2017). We tested whether linear or polynomial relationships provided a better fit to the data by comparing models (Akaike's information criterion), RMSE values, and adjusted R^2. The regression lines and 95% confidence intervals predicted from GAMs were obtained using the *stat_smooth* function (Wickham 2016). To test the effects of the native forest cover (%) on diet consumption and assimilation, trophic niche, trophic position, and fish condition, we focused on *P. bifasciatus* due to its wide distribution (present in all streams: S1–S7). For this model species, we explored the main causes of the expansion or contraction of isotopic niches and their dominance in streams under different human disturbances. Thus, in the subsequent analyses, we focused on stomach content and stable isotope data of *P. bifasciatus* (derived from 10 to 16 individuals within each stream; Supporting Information Table S2).

Relationships between environmental variables, diet consumption, isotopic composition, and resource assimilation of a widely distributed omnivorous fish

To test our second hypothesis, we investigated changes in diet composition across a gradient of native forest cover. We also tested for the potential underlying environmental variables using the distance-based redundancy analysis (dbRDA) based on Bray–Curtis distance (Legendre and Anderson 1999) in the *vegan* package (Oksanen et al. 2020). We log-transformed (natural log) all the environmental variables due to the different measurement scales of each variable (i.e., oxygen concentration—mg L^{-1}; specific electric conductivity—μS cm^{-1}). The water temperature (°C) was converted to Kelvin, prior to the log-transformation. For the subsequent dbRDA analyses, we used native forest cover (%), water temperature (K), ammonium NH$_4$ (mg L^{-1}), SRP (μg NO$_3$-N L^{-1}), and nitrate NO$_3$ (mg L^{-1}) as the most relevant water characteristics (*see* Supporting Information for more details on variable selection). We performed a permutation test for dbRDA, using the *anova.cca* function, to assess the statistical significance (Oksanen et al. 2020). Similarly, to test the influence of environmental variables on the δ^{13}C and δ^{15}N of *P. bifasciatus*, we also applied a dbRDA based on Euclidean distance (Legendre and Anderson 1999) with the same environmental variables as used for diet composition.

As part of the second hypothesis, to investigate how native forest cover (%) is related to the assimilation of resources by *P. bifasciatus*, we applied Bayesian stable isotope mixing models in the *MixSIAR* package (Stock and Semmens 2016). Mixing models provide quantitative estimates of diet contributions when the number of diet sources is low (Phillips et al. 2014; Nielsen et al. 2018). We pooled potential diet sources into four isotopically homogeneous categories: (1) aquatic invertebrates, (2) terrestrial invertebrates, (3) aquatic biofilm and POM, and (4) SOM (*see* Supporting Information for more information about MixSIAR models and assumptions; Supporting Information Figs. S8, S9; Supporting Information Tables S9, S10). Fractionation is an important consideration when estimating a consumer's trophic position and resource assimilation (MixSIAR, Post 2002). For *P. bifasciatus*, we used trophic discrimination factors (TDF) of $1.3 \pm 0.3\%$ for C and $2.9 \pm 0.32\%$ for N (McCutchan et al. 2003). This enrichment is appropriate for muscle tissues of omnivorous fishes that consume mixtures of plant and animal diet (McCutchan et al. 2003). We also considered specific TDF values for plant resources (Bastos et al. 2017). Because this fish could assimilate bacteria and other microbes inhabiting basal plant resources, we followed the method of Neres-Lima et al. (2016) and doubled the mean discrimination factor and the variability estimate (SD) by the propagation of error ($\sqrt{(2 \cdot SD^2)}$), yielding the values $2.6 \pm 0.42\%$ for C and $5.8 \pm 0.45\%$ for N.

Effects of native forest cover on trophic niches of a widely distributed omnivorous fish

To test our third hypothesis, to understand the effects of native forest cover (%) on trophic niches of dominant omnivores, we calculated the trophic niche based on both stomach content and stable isotope analyses. We estimated the stomach contents niche breadth using the permutational analysis

of multivariate dispersions (PERMDISP; Anderson 2006) in the *vegan* package (Oksanen et al. 2020, for specific details, *see* Supporting Information Table S6). PERMDISP tests whether group means, or group dispersions differ, considering the site as a driver. To estimate the isotopic variance (isotopic niche) of omnivorous fishes, we calculated multivariate, ellipse-based metric (SEA$_c$, ‰) for each fish species (*P. bifasciatus* and other co-occurring Characidae species) in each stream using the *SIBER* package (Jackson et al. 2011).

Relationships among native forest cover, fish diversity, and trophic niche of a dominant omnivore fish

As part of the third hypothesis, to investigate the effects of both native forest cover (%) and co-occurring fish species on the trophic niche of the *P. bifasciatus*, we fitted generalized linear models (GLM) with the following structure: log(SEA$_c$) ~ native forest cover × fish richness. We used SEA$_c$ because stable isotopes provide a longer, time-integrated measure of resource use than stomach contents. We used a Gaussian family distribution in the *glm* function, assuring that the model assumptions were met. We then ran a simplified version (log(SEA$_c$) ~ native forest cover + fish richness) of the first model and compared both models using *anova* function. Because there was no significant interaction between the factors ($F_{[1,3]} = 0.68$, $p = 0.85$) or differences between the models with or without interaction ($F_{[1,4]} = 0.04$, $p = 0.86$), we fit the second simplified model.

Finally, to determine how both native forest cover (%) and co-occurring species were related to the dominance index (DI) of the *P. bifasciatus*, we also performed GLM with the following structure: DI ~ native forest cover × fish richness. A DI was calculated as the proportional abundance of *P. bifasciatus* within the fish assemblage in each stream (Perkins et al. 2018). We also tested the effects of native forest cover (%) on fish richness (fish richness ~ native forest cover) using GAM models due to the indication of nonlinear responses. All statistical analyses were performed in the language environment R, version 4.2.1 (R Core Team 2022).

Results

Isotopic composition of omnivorous fishes, macroinvertebrate prey, and basal resources

In agreement with our first hypothesis, human disturbances altered the stable isotope values of basal resources, macroinvertebrate prey, and omnivorous fishes. The streams with lower proportion of native forest cover were associated with an increase in $\delta^{13}C$ values of omnivorous fishes (GAM; $R^2 = 0.62$, $F_{[6,148]} = 58.6$, $p \leq 0.001$; Fig. 1A). There was also a nonlinear relationship between native forest cover and fish $\delta^{15}N$ values (GAM; $R^2 = 0.46$, $F_{[6,148]} = 30.8$, $p < 0.001$; Fig. 1B). There was no evidence that native forest cover affected $\delta^{13}C$ values of aquatic macroinvertebrates (GAM; $R^2 = 0.51$, $F_{[6,17]} = 2.93$, $p = 0.07$; Fig. 1C). However, there was strong evidence for the effects of the native forest cover on

$\delta^{15}N$ values of macroinvertebrates (GAM; $R^2 = 0.77$, $F_{[6,17]} = 11.8$, $p < 0.001$; Fig. 1D). Similarly, there was no evidence that the native forest cover influenced the $\delta^{13}C$ values of basal resources (GAM; $R^2 = 0.51$, $F_{[6,18]} = 1.41$, $p = 0.32$; Fig. 1E), but there was strong evidence of nonlinear effect on the $\delta^{15}N$ values of basal resources (dicotyledons; GAM; $R^2 = 0.85$, $F_{[6,18]} = 19.1$, $p < 0.001$; Fig. 1F). Aquatic macroinvertebrates and fishes were enriched in $\delta^{15}N$ (6.0 ± 1.9‰; 9.5 ± 1.1‰, respectively), especially in streams at intermediate values of the native forest cover (%) and where there were agricultural activities (S3, S4, and S5; Fig. 1; Supporting Information Fig. S4). For native vegetation (dicotyledons), the mean $\delta^{15}N$ value was 1.6 ± 2.2‰ and the highest values were in streams with the lowest coverage of forest cover.

Diet consumption and assimilation of a widely distributed omnivorous fish

In agreement with our second hypothesis, the proportion of native forest cover affected the trophic ecology of a dominant omnivorous species. The diet of *P. bifasciatus*, a widely distributed species across all focal streams, was different in each stream (Fig. 2A; Supporting Information Table S5). This species consumed a high proportion of terrestrial leaves, seeds, and aquatic insects (Ephemeroptera, Trichoptera, Plecoptera) in streams with higher native forest cover (Fig. 2A; Supporting Information Table S5). However, the diet shifted toward a higher consumption of terrestrial insects (Coleoptera, Hymenoptera, Diptera) and detritus in streams with low native forest cover (Supporting Information Table S5). Moreover, biofilm, POM, and aquatic invertebrates became less assimilated into the fish tissues in the most disturbed urban streams (Fig. 2B; Supporting Information Table S10). As hypothesized, in these disturbed streams, the most assimilated resources were terrestrial invertebrates and SOM (Supporting Information Fig. S10; Supporting Information Table S10).

The environmental characteristics associated with human disturbances affected both resource consumption (dbRDA, Fig. 3A) and isotopic composition (Fig. 3B) of the dominant omnivorous fish. There were strong patterns of associations between environmental variables and food items ingested by *P. bifasciatus* (dbRDA, $F_{[5,164]} = 4.64$, $p = 0.001$). In the CAP1 axis ($F_{[1,164]} = 12.22$, $p = 0.001$), higher consumption of plant resources was associated with higher proportions of native forest cover ($F_{[1,164]} = 7.80$, $p = 0.001$) while higher consumption of detritus and Diptera larvae was associated with higher concentrations of ammonium ($F_{[1,164]} = 3.00$, $p = 0.003$) and nitrate ($F_{[1,164]} = 3.30$, $p = 0.002$). In the CAP2 axis ($F_{[1,164]} = 6.61$, $p = 0.001$), negative scores suggested that the higher consumption of Coleoptera adult and other terrestrial insects was related to higher concentrations of SRP ($F_{[1,164]} = 2.21$, $p = 0.01$). Higher consumption of aquatic insects was positively associated with higher water temperature ($F_{[1,164]} = 6.91$, $p = 0.001$).
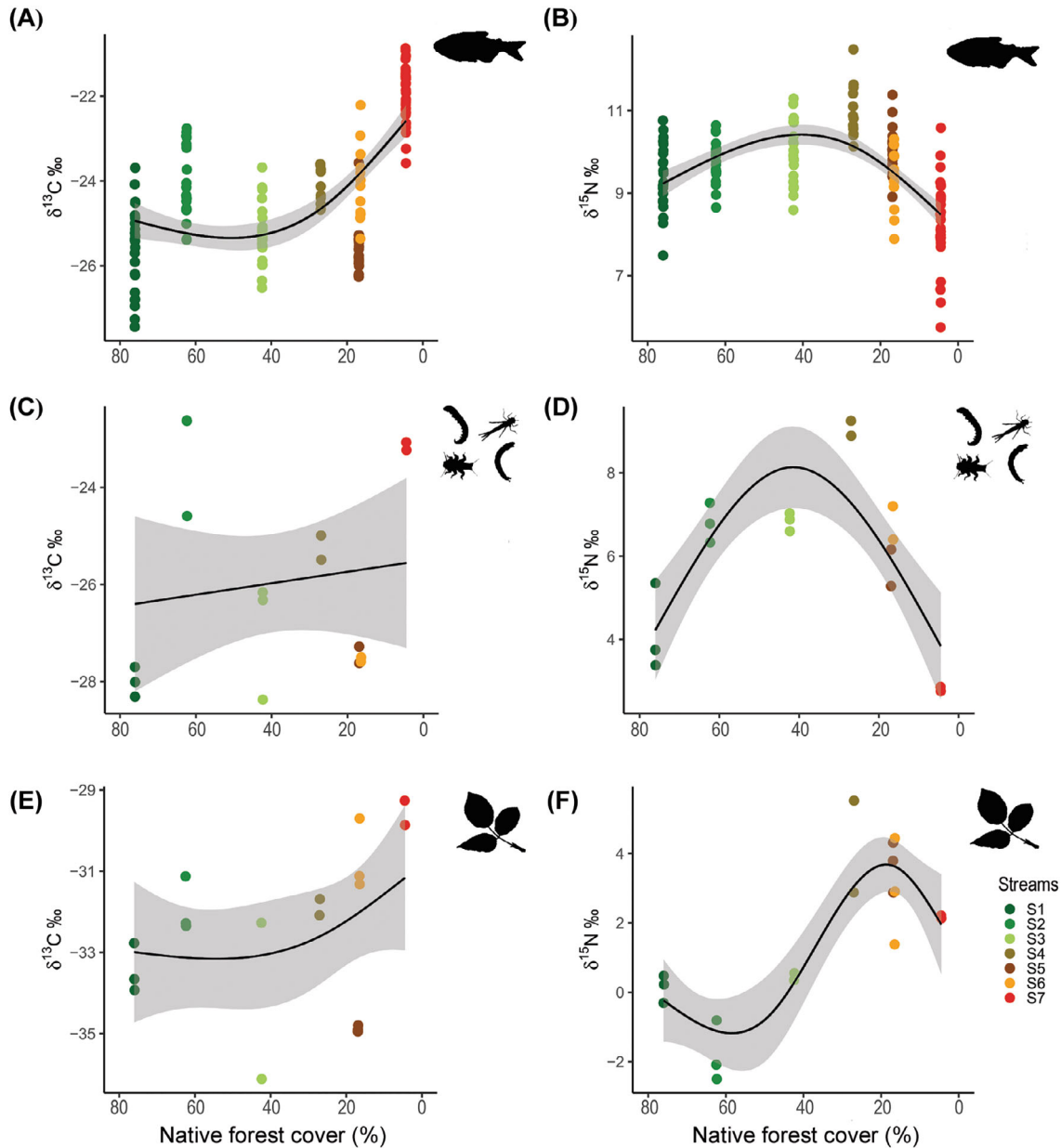
Fig. 1. The nonlinear effects of native forest cover (%) on $\delta^{13}C$ and $\delta^{15}N$ values of omnivorous fishes (**A**, **B**), aquatic macroinvertebrate prey (**C**, **D**) and basal resources (dicotyledons) (**E**, **F**). Black regression lines and shaded 95% confidence intervals predicted from GAMs. The GAM relationships were evaluated by the significance of the smooth terms.

There were also strong patterns of associations between environmental variables and the isotopic composition of *P. bifasciatus* (dbRDA, $F_{[5,83]} = 15.06$, $p = 0.001$; Fig. 3B). In the CAP1 ($F_{[1,86]} = 56.87$, $p = 0.001$), negative scores indicated that lower $\delta^{13}C$ values (-25.836 ± 0.9‰) were associated with streams characterized by higher proportions of native forest cover ($F_{[1,83]} = 35.43$, $p = 0.001$). In contrast, *P. bifasciatus* had higher $\delta^{13}C$ values (-22.051 ± 0.6‰) in urban streams with high nitrate concentrations ($F_{[1,86]} = 17.87$, $p = 0.001$). In the CAP2 ($F_{[1,86]} = 21.17$, $p = 0.001$), water temperature

($F_{[1,83]} = 9.37$, $p = 0.001$) was negatively associated with $\delta^{15}N$ values of *P. bifasciatus*. On this axis, *P. bifasciatus* had slightly elevated $\delta^{15}N$ values (11.0 ± 0.6‰) in streams with higher SRP concentrations ($F_{[1,83]} = 9.47$, $p = 0.001$) and with agricultural influence than in streams with higher native forest cover ($\delta^{15}N$ values, 9.4 ± 0.8‰).

Trophic niche of dominant omnivorous fish species

In agreement with our third hypothesis, the differences in the niche dispersion of *P. bifasciatus* among streams indicated
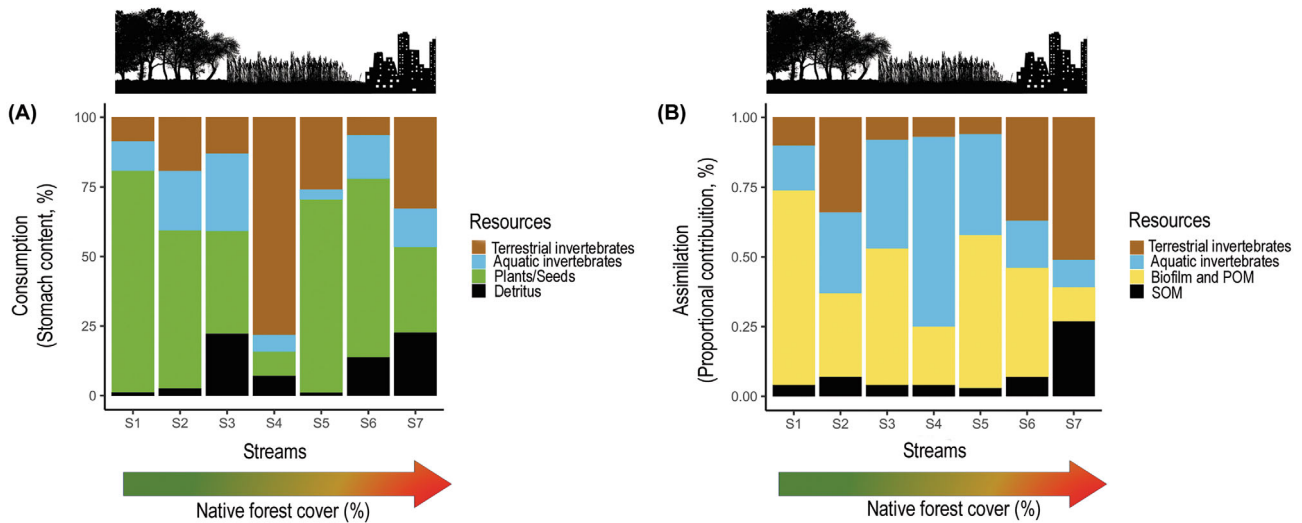
Fig. 2. The relative contribution (%) of main food resources consumed and assimilated by *P. bifasciatus* in seven streams along a gradient of native forest cover (%). (**A**) Proportions of consumed resources in diet were estimated by volume from stomach content analysis. (**B**) The assimilated diet contributions were estimated using a MixSIAR Bayesian mixing model. SOM denotes sedimentary organic matter and POM denotes particulate organic matter.
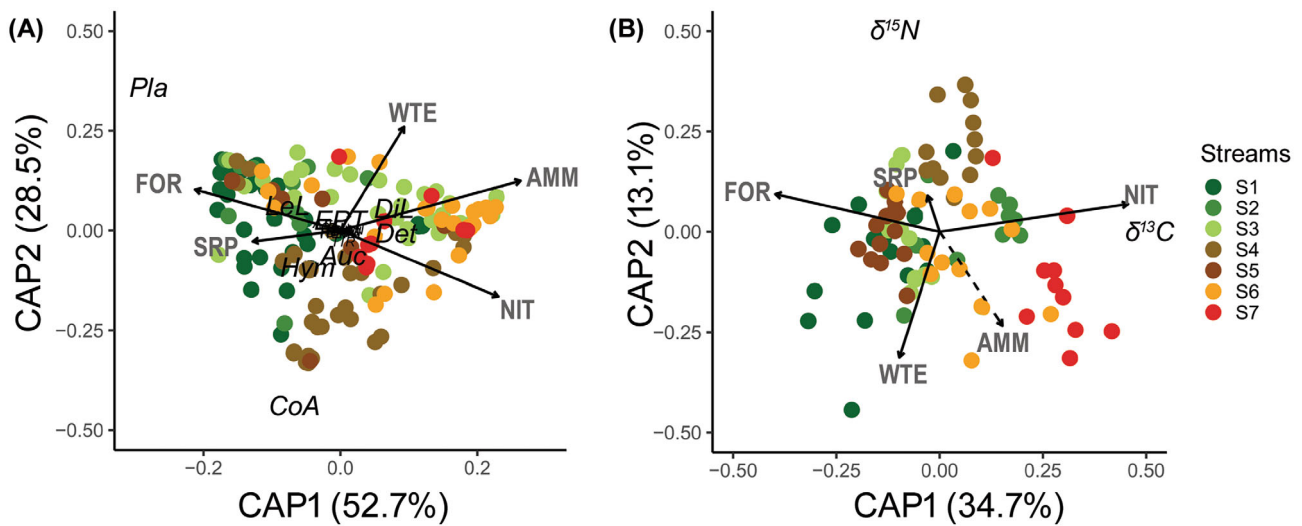

Fig. 3. Distance-based redundancy analysis (dbRDA) illustrating the association between (**A**) food items consumed and (**B**) isotopic composition (δ^{13}C and δ^{15}N) of *P. bifasciatus* and the key environmental variables for all streams (FOR: native forest cover, WTE: water temperature, AMM: ammonium, SRP: soluble reactive phosphorus, NIT: nitrate). Solid arrows indicate statistically significant associations. Food items code: Det: detritus, Pla: plants/seeds, AIR: aquatic insect remains, HemN: Hemiptera nymph, EPT: Ephemeroptera, Plecoptera, and Trichoptera larvae, OdoN: Odonata nymph, CoL: Coleoptera larvae, DiL: Diptera larvae, LeL: Lepidoptera larvae, TIR: terrestrial insect remains, Hym: Hymenoptera, Auc: Auchenorrhyncha, HemA: Hemiptera adult, CoA: Coleoptera adult, LepA: Lepidoptera adult, PleA: Plecoptera adult, Ara: Araneae, Cru: Crustacea, Oli: Oligochaeta.

that this species had more restricted diets in impacted streams than in streams with a higher proportion of native forest cover, suggesting intraspecific responses to different land use types (PERMDISP; $F_{[6,151]} = 2.50$, $p < 0.002$; Fig. 3A; Supporting Information Tables S6, S7). However, there was no evidence that these differences were related to the proportion of native forest cover (GAM; $R^2 = 0.21$, $F_{[1,6]} = 1.33$, $p = 0.30$).

There was moderate evidence suggesting that isotopic niche (measured as the size of the ellipse for each stream, SEA$_c$) of *P. bifasciatus* was influenced not only by the proportion of native forest cover (GLM; $R^2 = 0.62$, $F_{[1,5]} = 2.19$, $p = 0.03$; Figs. 4B, 5A), but also by the richness of the fish species (GLM; $R^2 = 0.73$, $F_{[1,4]} = 0.68$, $p = 0.003$; Fig. 5C). Variation in isotopic niche appeared to be related to the availability of resources
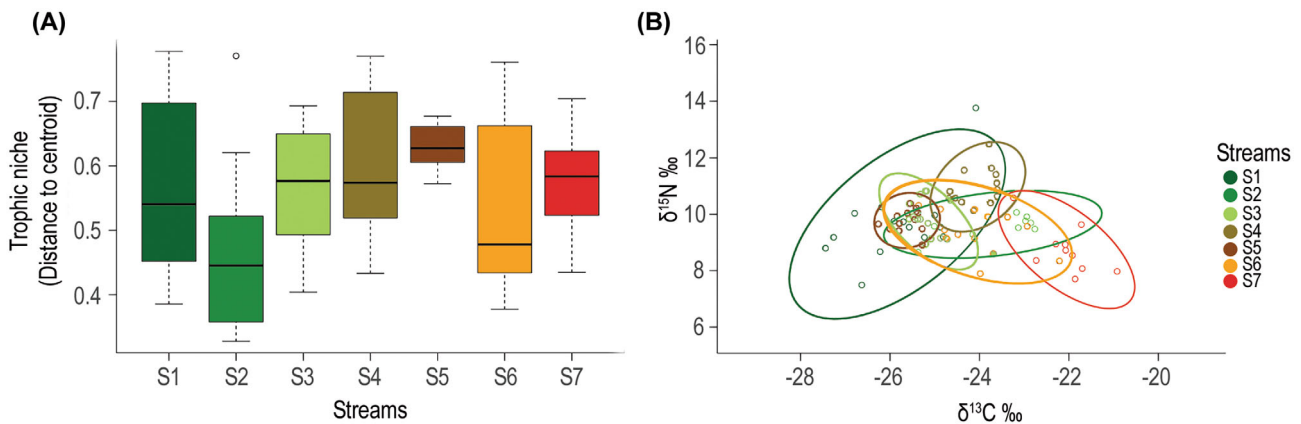
Fig. 4. Differences in the trophic niche (**A**) measured as a distance to the centroid (using PERMDISP) and (**B**) isotopic niches evaluated by the ellipse-based metric (SEA_c) of *P. bifasciatus* in seven streams along a gradient of native forest cover (S1–S7). Box lower and upper endpoints represent the 25th and 75th quartiles, respectively, and the horizontal bar inside each box represents the median trophic niche (for summary, *see* Supporting Information Tables S6, S7).

and to the co-occurrence of other tetra fish species. High isotopic niche variation of *P. bifasciatus* was observed when it co-occurred with *B. ikaa* and *P.* aff. *gymnodontus* (Fig. 6A,B), whereas lower isotopic variation was observed when it co-occurred with *P.* aff. *paranae* (Fig. 6C–E).

The isotopic niche of *P. bifasciatus* was broadest in low-impacted streams with a high proportion of native forest cover and a high richness of fish assemblages. Conversely, an isotopic niche was compressed in streams with agricultural influence and low fish richness (Figs. 4B, 5A), indicating a more selective diet. Although both native forest cover and fish richness were important factors influencing the isotopic niche of the dominant species, there was no evidence that native forest cover had an effect on fish richness (GAM; $R^2 = 0.36$, $F_{[1,4]} = 0.40$, $p = 0.71$; Fig. 5B), indicating that the effects of these variables were largely independent of each other.

Relationship among native forest cover, fish diversity, and trophic niche of dominant fish species

In agreement with our third hypothesis, there was strong evidence for the DI being negatively associated with the fish species richness indicating that *P. bifasciatus* dominance decreased with increasing richness of the fish assemblages (GLM; $R^2 = 0.66$, $F_{[1,5]} = 14.17$, $p < 0.001$; Fig. 5F). However, there was no evidence that the native forest cover affected either the *P. bifasciatus* dominance (GLM; $R^2 = 0.02$, $F_{[1,5]} = 0.10$, $p = 0.76$; Fig. 5D) or the breath of an isotopic niche (GLM; $R^2 = 0.001$, $F_{[1,5]} = 0.36$, $p = 0.87$; Fig. 5E).

Discussion

Here, we showed how differences in native forest cover, associated with human land use changes, altered the trophic ecology of omnivorous fishes. There was strong evidence for the nonlinear effects of the native forest cover on the δ^{15}N values of native vegetation, aquatic macroinvertebrates, and

omnivorous fishes, with the highest δ^{15}N values observed in streams with an intermediate cover of native forest, and agricultural influences with high concentrations of SRP and ammonium. Native forest cover affected δ^{13}C values of omnivorous fishes without changes to their prey, indicating the fishes modified their use of resources. As the native forest cover decreased, fishes reduced their consumption and assimilation of high-quality autochthonous resources and increased consumption of low-quality SOM and allochthonous terrestrial invertebrates with higher δ^{13}C values. Because deforestation can negatively influence species richness (in rural streams) or increase species richness through the introduction of exotic species (in urban streams), the isotopic niche of *P. bifasciatus* compressed with deforestation but expanded with the richness of other fish species (Supporting Information Table S11). In addition, deforestation tends to make the environment more homogeneous and reduce the diversity of food items and, consequently, result in more restricted niche breadths and greater competitive pressure for food resources. This scenario illustrates how species interactions can mediate changes in the isotopic niche of the dominant omnivorous consumer. These findings also indicate that the persistence of *P. bifasciatus* in disturbed habitats may be facilitated by plasticity in diet use and the trophic niche expansion in the presence of other competitors.

The impacts of riparian deforestation were related to the transference of solar energy to the aquatic ecosystems, the interception of nutrients and sediments that enter the streams, and the exchange of organic material between the terrestrial and aquatic realms (Casatti 2010). In addition to replacing the native forest composed mainly of C3 plants with C4 plants such as corn, wheat, and soybeans in agricultural areas, and grasses in urban areas (Magioli et al. 2019), the greater solar incidence in the exposed aquatic environment promotes increased productivity of algae, which can lead to eutrophication (Hill et al. 1995, 2008). In this study, the
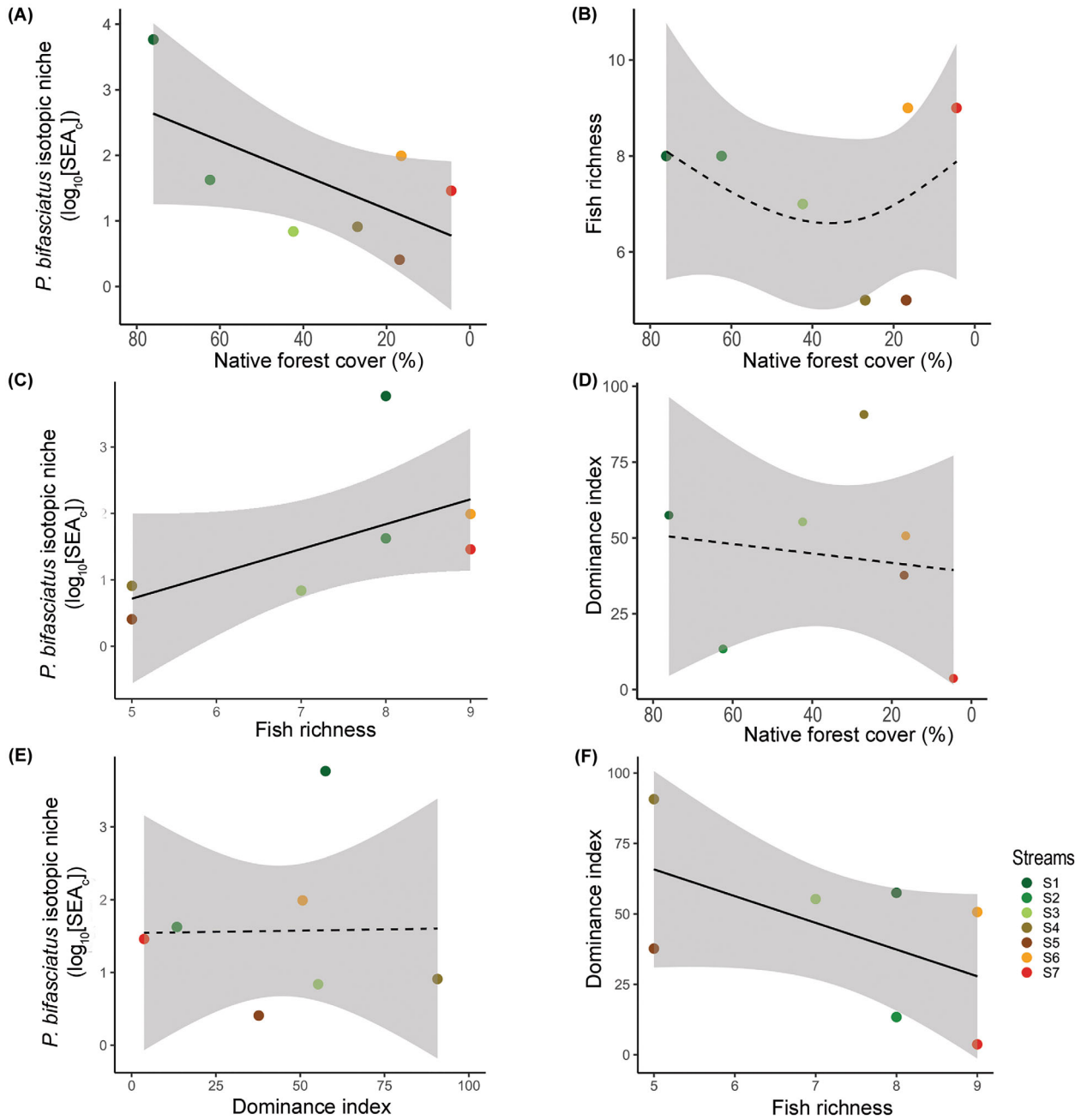
Fig. 5. The relationships between the native forest cover (%) and *P. bifasciatus* isotopic niche (log₁₀[SEAc]), fish community richness and *P. bifascistus* dominance index (**A**, **B**, **D**). Relationship among fish community richness, *P. bifasciatus* isotopic niche (log₁₀[SEAc]) and dominance index (**C**, **E**, **F**). Black lines and shaded areas represent predicted GAMs and GLMs fits and 95% confidence intervals. A solid black line indicates a significant relationship and a dotted black line indicates a nonsignificant relationship. The GAM relationships were evaluated by the significance of the smooth terms.

effects of land use changes surrounding streams were reflected in the isotopic composition of omnivorous fish tissues. Fishes had higher δ13C values in streams with a lower proportion of native forest cover, reflecting the changes in carbon sources due to land use changes. Shifts in algal productivity associated with land use changes for the same streams were previously reported by Larentis et al. (2022), suggesting bottom-up effects

on these food webs. In agricultural streams with high concentrations of ammonium (Supporting Information Table S1), fishes also had higher δ15N values. The fertilizers and other chemicals, such as heavy metals and animal sewage, are commonly used in agricultural activities and, in ecosystems with reduced riparian vegetation, can more easily enter aquatic ecosystems via runoff (Kautza and Sullivan 2015; Price
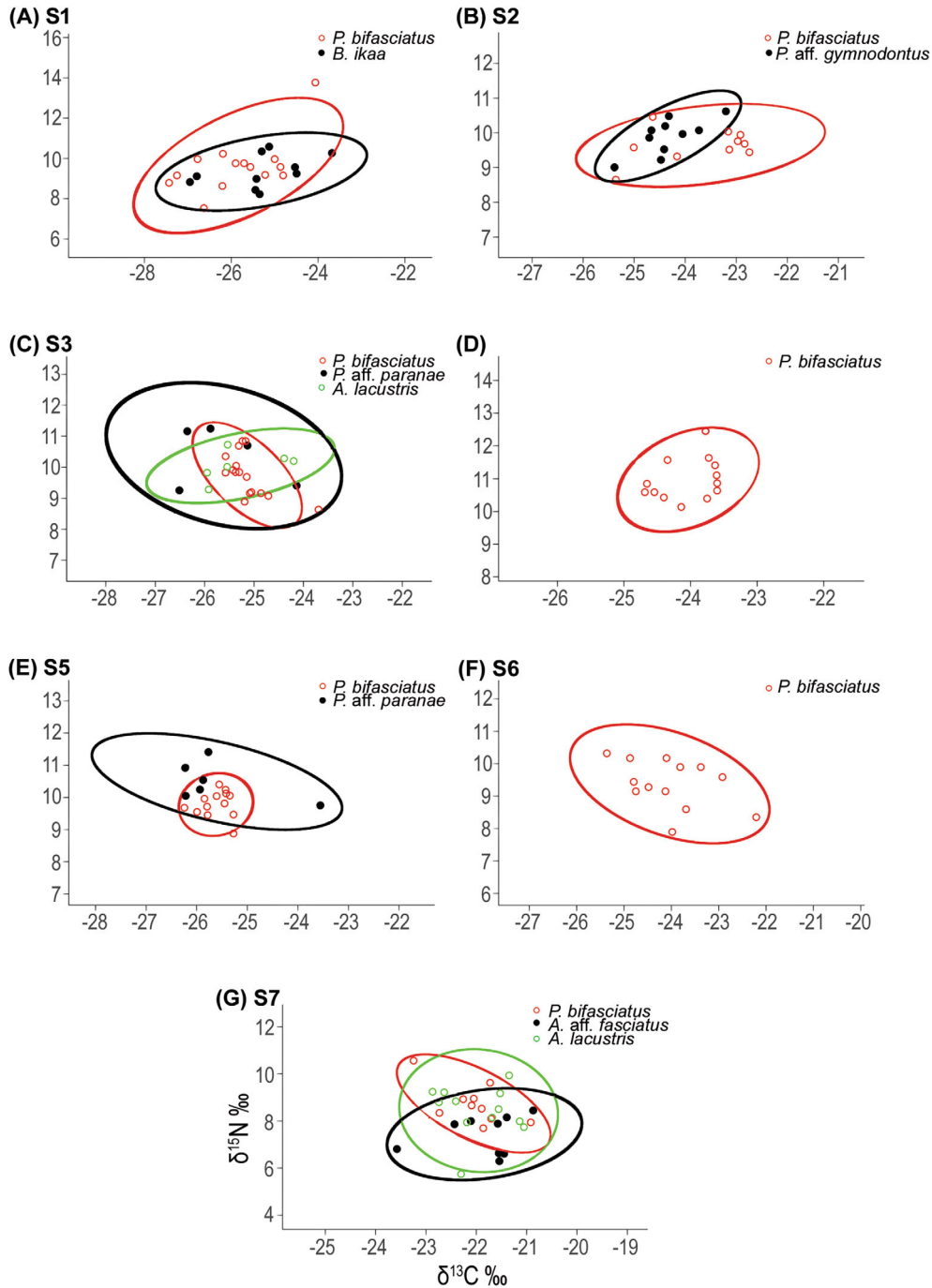
Fig. 6. Omnivorous tetra fish species coexisting in each of the seven streams and their isotopic niches, illustrated as the size of ellipses (SEA_c). The points represent the $\delta^{13}C$ and $\delta^{15}N$ isotopic values of each individual omnivorous species sampled in each stream. Colors illustrate different species in each stream.

et al. 2019). Studies have shown the effects of agriculture on the concentrations of nutrients in aquatic environments (Riseng et al. 2011; Carvalho et al. 2019) and suggested that these activities increase the $\delta^{15}N$ values. Artificial fertilizers have relatively low $\delta^{15}N$ values (-2 to $+2.5‰$, Rapisarda et al. 2010). However, the increased $\delta^{15}N$ values likely resulted from higher N-cycling and transformation (Anderson and Cabana 2005),

especially due to denitrification. Strong fractionation during the denitrification process often leaves the residual NO_3 pool highly enriched (Sigman and Casciotti 2001; Clément et al. 2003), which could explain the high $\delta^{15}N$ values observed in our study. Our findings highlighted how the changes in carbon source and input of nitrogen can reverberate through the food web up to omnivorous fishes.

Deforestation of riparian vegetation can alter the habitat complexity, primary productivity, and aquatic-terrestrial inputs (Sweeney et al. 2004; Wohl 2006; Price et al. 2019; Effert-Fanta et al. 2022). Aquatic habitats tend to become more homogeneous with reduced riparian cover and macroinvertebrate abundance and diversity tend to decline (Kautza and Sullivan 2015). In addition, these changes are often associated with higher sedimentation and silting loads. Thus, with the lower availability of autochthonous resources (i.e., macroinvertebrates), and greater input of sediments and terrestrial insects, particularly during the rainy season (the study area is rainy in summer), omnivorous fishes may be able to sustain their populations through shifting to these more abundant resources. Fishes can show spatiotemporal shifts in diet and trophic niche but not shifts in trophic position (Neves et al. 2021; Flood et al. 2023). Our analyses showed that tetra fish shifted from autochthonous to allochthonous resources across the forested-rural–urban gradient without changing their trophic position or condition factor (*see* details in Supporting Information Figs. S5–S7), indicating how feeding plasticity can promote their persistence.

It has been long recognized that riparian vegetation contributes large amounts of allochthonous detritus, especially to headwaters (Vannote et al. 1980). However, recent studies have suggested that food webs in many headwater streams, especially in the tropics, rely heavily on autochthonous within-stream derived resources (Brett et al. 2017; Ceneviva-Bastos et al. 2017; Reis et al. 2020; Wilkinson et al. 2021). Anthropogenic disturbances alter the relative contribution of aquatic and terrestrial invertebrate subsidies to tropical streams and can be used to determine ecosystem responses to disturbances with implications for conservation, management, and monitoring programs (Kautza and Sullivan 2015). It is also important to consider the effects of reduction of canopy cover on water temperature and, consequently, on the fish metabolism. Experimental work has suggested that warming can alter carbon incorporation into soft tissues, with increased values of $\delta^{13}C$ in muscle and liver at higher temperatures (Martino et al. 2019).

In agreement with Neves et al. (2021), we also observed that plants and seeds are consumed but not assimilated into the fish tissues. This incongruence between consumption and assimilation may be governed by several mechanisms. For instance, individual food items can differ in their digestibility and nutritional quality (Bowen et al. 1995). There may also be a lack of specialization in the digestive tract of tetra fishes to facilitate the breakdown, digestion, and assimilation of plant material (Pelster et al. 2015), or this incongruence can be caused by the higher nutritional quality of animal prey (Gerking 1994). Possible ecological and behavioral explanations, such as opportunistic feeding strategy and accidental consumption (Bastos et al. 2017; Bonato et al. 2018), have also been proposed. Alternatively, ingested plant material may include a biofilm, which is the main resource assimilated into fish tissues. Finally, we also need to consider the differences between the stomach content and stable isotope analysis, which focuses on trophic processes operating over different time scales (Nielsen et al. 2018). In addition to the incongruence between consumption and assimilation of plant resources, the disagreement between stomach contents and stable isotopes for stream S4 (high consumption of Coleoptera, but assimilation of aquatic invertebrates) may represent the sporadic supply of resources. During the sampling campaign, we observed animal carcasses on the banks of this stream, which could be related to the increased availability of decomposing beetles. This short-term coleopteran consumption close to the sampling campaign might not have been reflected yet in the stable isotope analyses.

The trophic niche of species can be influenced by the availability and diversity of resources but also by species interactions such as interspecific competition (Costa-Pereira et al. 2017; Perkins et al. 2018). Although there was no clear relationship between the breadth of the trophic niche and the proportion of native forest cover, we showed an intriguing positive association between the isotopic niche area of *P. bifasciatus* and the richness of other co-occurring fish species. In rural streams with a low richness of fish species, *P. bifacistus* had the most compressed isotopic niche, indicating more specialized resource exploitation. Similar results were observed by Perkins et al. (2018) for trout in temperate streams, who found trout, when dominant, had a contracted isotopic niche. By contrast, Carvalho et al. (2019) showed a narrower trophic niche for small and invasive characid fish in streams influenced by pasture activities. Our findings indicated that both deforestation and fish richness can alter the trophic niche of a widely distributed species.

The Niche variation hypothesis predicts that weaker competitive pressure leads to a niche expansion through greater between-individual variation while individual niche breaths remain constant (Van Valen 1965). In contrast to these predictions, in rural streams with low fish richness, we found a contracting isotopic niche of *P. bifasciatus*, while in forested and urban streams with high fish species richness, we found a niche expansion for this species. The mechanism that promotes the expansion of the trophic niche of widespread species, such as *P. bifasciatus*, in the presence of more competitor species needs to be further investigated. Although the richness of fish species was high in both forest and urban streams, it is important to highlight that the composition of fish fauna was different than in relatively unimpacted streams with high forest cover. Moreover, some native and endemic tetra fish species, such as *P.* aff *gymnodontus* and *B. ikaa*, only occurred in the relatively unimpacted streams with high forest cover.

Delariva et al. (2018) report lower fish richness in rural streams, suggesting that the physical–chemical alterations caused by agricultural activities play an important role in the environmental filtering of sensitive species. In urban streams, the richness of fish species increased due to the presence of species indicative of poor environmental quality, tolerant to hypoxia and anthropogenic stressors, such as *Synbrachus marmuratus* and

Hypostumus ancistroides (Supporting Information Table S11). These streams are also more susceptible to introduced fish species such as *Gymnotus sylvius* and *Oreochromius niloticus* (Larentis et al. 2022). The relationships among native forest cover, trophic niche, and fish richness rely strongly on the most pristine site, S1, the only stream in a Private Reserve of Natural Heritage (Salto Portão Park), reinforcing the role of protected areas for the conservation of biodiversity.

Our findings showed how anthropogenic disturbances alter the trophic ecology of omnivorous fish species and reinforce the fact that omnivory is not a static trait, but its magnitude changes across time and space (Kratina et al. 2012; Gutgesell et al. 2022). Through changes in habitat structure and the diversity of resources, deforestation can alter energy fluxes for consumers at high trophic levels. These findings also indicated that the wide distribution of dominant omnivores in streams with a gradient of native forest cover could be explained by shifts in diet from high-quality autochthonous resources to poor-quality and allochthonous resources, and, by expansion of the trophic niche in streams with high richness of fish species. Despite the challenging field work and financial resources in many tropical areas, more detailed insights into the mechanisms observed here would be gained in future studies by including more sites and species across other Neotropical biomes under increased human influence. Our findings are of particular importance in Brazil, where changes to the Forest Code in 2012 made regulations around minimum permanent preservation area size, such as riparian buffers, more flexible, with negative effects ignored or justified for economic advancement (Alves et al. 2020). This study showed that the effects of native forest cover on omnivorous fishes need to be investigated within a food web context to improve our understanding of wider effects on ecosystem functioning and to devise mitigation and conservation measures in highly threatened ecosystems.

Data availability statement

The datasey and R-scripts were archived in the DRYAD repository (https://doi.org/10.5061/dryad.xd2547dq2).

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Conflict of Interest

None declared.