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# Anthropogenic nutrient loading affects both individual species and the trophic structure of river fish communities

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Although the concept of trophic interactions has been used for a long time, there are still considerable gaps in our understanding of the effect of various environmental factors on trophic interactions within river fish assemblages. Carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios of 20 species of fish belonging to both eurytopic and rheophilic ecological groups from a large temperate rivers were used to evaluate overall trophic niche use and trophic position of species, and to find out how environmental variability associated with nutrient loading affects individual and community-wide aspects of trophic structure. The study was carried out at 11 sites along the European rivers Vltava and Elbe, representing a continuous gradient of pollution and habitat degradation. Corrected Standard Ellipse Area (SEAc) was significantly larger for the group of eurytopic ecological species than for rheophilic species. Despite narrower isotopic niche space, rheophilic fish species occupied a higher trophic position, suggesting that these species use resources more enriched in  $^{15}\text{N}$ . Of the 11 environmental variables tested, nutrients had a significant effect on trophic niche area of species (SEAc), indicating that eutrophication is of critical importance for fish assemblages. Isotopic niche area of species was found to be positively influenced by total phosphorus, and negatively affected by concentrations of nitrate ( $\text{N-NO}_3^-$ ) and ammonia ( $\text{N-NH}_4^+$ ). A negative association between oxygen demand and a measure of trophic diversity - mean distance to centroid (CD) - and a measure of density and clustering of species - mean nearest neighbor distance (MNND) - were found, indicating that the oxygen demand is a key factor influencing community trophic structure. An observed pattern where nutrient loading influenced both individual species and trophic structure of the fish assemblage provides strong support for an anthropogenic influence on riverine food webs.

## KEYWORDS

food webs, freshwater fish, nutrient loading, rivers, stable isotope analysis, trophic niches

## 1. Introduction

Human induced habitat alterations such as river regulation, flow adjustments, eutrophication, and pollution generally lead to degradation of riverine environments, resulting in a worldwide reduction in the ecological quality of fish assemblages (Duncan and Lockwood, 2001; Freeman et al., 2003; Aarts et al., 2004; Musil et al., 2012). As such, freshwaters are among the habitats most endangered by loss of biodiversity (Xie et al., 2003; Dudgeon et al., 2006; Erős et al., 2019). In anthropogenically impacted rivers, fish species with generalist requirements are expected to have an advantage over more specialized ones. Generalist species often exhibit limited migration behavior (Baras et al., 1994; Winter and Fredrich, 2003), lower habitat preference (Capra et al., 2018), or more general use of trophic resources (Guinan et al., 2015). As a result, guilds of specialist rheophilic species, that are highly adapted to specific riverine conditions, have declined more than generalist eurytopic species (Valová et al., 2006; Latli et al., 2018; Bierschenk et al., 2019; Maire et al., 2019).

From the trophic perspective, eurytopic fish species may pose potential threats to rheophilic species in anthropogenically degraded freshwater ecosystems (Aarts and Nienhuis, 2003; Aarts et al., 2004) as they can shift diet and resources therefore leading to more competition with specialized taxa. However, the outcome of feeding interactions may also be shaped by various environmental factors associated with nutrient loading. An assessment of trophic interactions of river fish assemblages affected by increased nutrient supply is of considerable importance (Yates and Bailey, 2010; de Carvalho et al., 2020; Wang et al., 2021).

When evaluating the impact of nutrient loading, fish become one of the most important indicators of community responses as they typically occupy higher trophic levels and reflect long-term changes in ecosystems (Bierschenk et al., 2019). Understanding the implications of nutrient loading for isotopic niche characteristics of riverine fishes is a therefore a key question as it may allow prediction of functional shifts in river ecosystems (Olin et al., 2002; Warry et al., 2016; Bierschenk et al., 2019). Nutrient addition is assumed to alter ecosystem function with a bell shaped response (Heiskary and Bouchard, 2015; Schmutz and Sendzimir, 2018). Nutrients alter resource quantity and quality, and *via* influence on primary producers alter the density and species composition of herbivores, and are further transferred to higher trophic levels. Although a slight increase in nutrients may have a positive effect on communities, excessive nutrient loading may induce deterioration of basal resource diversity (Hilton et al., 2006) with subsequent cascading effects (Kratina and Winder, 2015; De Castro et al., 2016; Price et al., 2019).

Such changes associated with intensive land use can result in increased omnivorous feeding in generalist species of fish (Champagne et al., 2022). For example, in the study of Champagne et al. (2022), it has been shown that in an ecosystem with high agricultural intensity, generalist fish may become more omnivorous and occupy lower trophic positions owing to greater consumption of algae and less energy derived from terrestrial

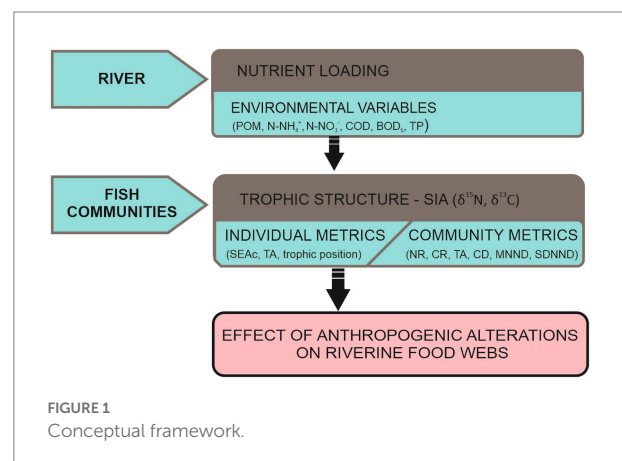
pathways. On the contrary, in streams with reduced aquatic secondary production, the reliance of fish on terrestrial resources could increase as they compensate for the loss of aquatic resources (Kraus et al., 2016). Based on these findings, it can be suggested that the generalist fish species increase their trophic niche size but could have lower trophic position in river fish assemblages affected by increased nutrients inputs. On the contrary, rheophilic species (e.g., benthivores) are known to consume mostly terrestrial and benthic macroinvertebrates (Kottelat and Freyhof, 2007), which may result in higher trophic position demonstrated in these specialist fish species.

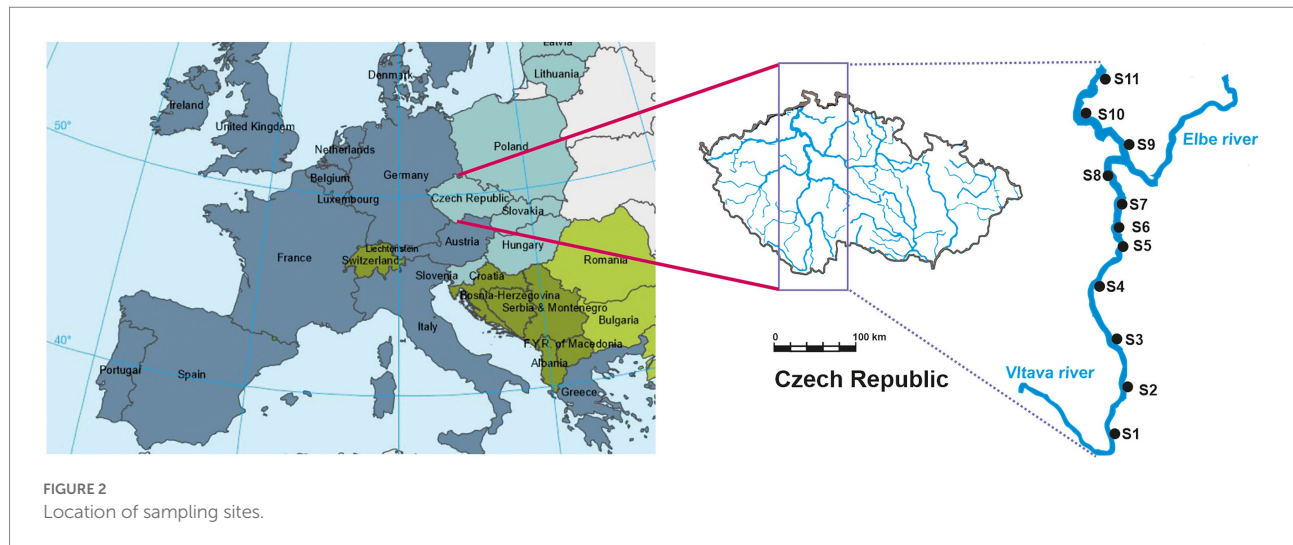
In this study we used stable isotope analysis to examine how environmental factors associated with increased nutrient inputs affects both individual and community trophic structure (Figure 1). The study was carried out at 11 sites along the Vltava and Labe rivers, Czech rivers representing a continuous gradient of pollution and habitat degradation due to anthropogenic activities. The objectives of this study were to (1) identify the isotopic niche (TA, SEAc) and trophic position of rheophilic and eurytopic group of species, and (2) to evaluate the effect of environmental variables on the trophic structure of fish assemblages. We predict that eutrophication would be the major factor that would influence trophic niche area and trophic position of fish in the food chain. To evaluate the influence of nutrient loading on trophic niche of fish assemblages, we related in-stream chemical variables to observed trophic patterns.

## 2. Materials and methods

### 2.1. Sample preparation and measurement

Data were collected from the rivers Vltava and Elbe in the Czech Republic, central Europe (Figure 2; EEA Map of Europe. European Environment Agency, 2022). A total of 11 sites were explored to obtain a gradient of anthropogenic stressors (Figure 2), eight (S1–S8) on the Vltava and three on the Elbe (S9–S11). The Vltava is the longest river within the





Czech Republic, with a basin area of 28,090 km<sup>2</sup> and 43 km length. The Vltava is one of the main tributaries of the Elbe. The eight sites were located from the headwaters to near the confluence with the Elbe at Mělník, 837 km from the source of the Elbe. The Elbe is one of the major rivers of Europe. It rises in the Giant Mountains of northern Czech Republic, flows through Germany and discharges into the North Sea near Hamburg. Samples were collected from the Elbe at three sampling sites 818, 767 and 738 km from the source and downstream of the confluence with the Vltava, with the most downstream at Děčín on the German border. All surveys of fish and invertebrates were performed May to June 2019. Sampling sites S1, S2, S3, S6, S8 were natural or near natural river habitats surrounded by naturally heterogeneous habitats, and characterized by a combination of shallow fast-flowing reaches interspersed with deeper and slower flowing sections, enabling the development of aquatic vegetation. Sites S4, S5, S6, S7, S8, S9, S10, S11 were characterized by a higher degree of anthropogenic degradation of habitats, either channelized for navigation and influenced by the presence of weirs and dredging of the riverbed, or impacted by fortification of banks by concrete and stones which considerably reduces the development of aquatic and riverine vegetation, leading to reduced habitat heterogeneity (Figure 2).

Samples of fish were collected by electric fishing, with an output voltage of 300–600 V (50 Hz) powered by a Honda engine and a LENA generator (Bednář, Czech Republic<sup>1</sup>). Fish were caught by electrofishing using a two-pass depletion method (Seber and Le Cren, 1967) to ensure representative estimates of fish abundance at each site. Fish were collected using both qualitative and quantitative methods to survey the whole community. Overall, 754 individuals of 20 fish species were used for determination of isotopic ratios and samples were kept frozen until laboratory processing. At the same time, benthic

invertebrates were collected from each site, all samples were held on ice for later analyses. Invertebrates were sampled by the kick-sampling method (Frost, 1971), using a net with a 500 μm mesh size and the same sampling effort. Various type of substrate were sampled at eight different points at each study site, to ensure that individuals from various habitats were present in each sample. Collected invertebrates were identified, mainly to genus. All samples were held on ice for later analyses. Isotopic ratios of aquatic invertebrate consumers were used as a baseline to calculate trophic position of fish species (Post, 2002). In the laboratory, all fish were identified to species, measured (Standard Length, mm), weighed (Total Weight, g) and samples of dorsal muscle tissue dissected from a minimum of 3–12 adult individuals per species for stable isotope analysis according to availability (Table 1; Supplementary Table S1). All institutional and national animal welfare guidelines were followed (law no. 246/1992), and approved by the ethical committee of the Faculty of Science, Charles University, Prague. Fish species were classified into eurytopic and rheophilic ecological guilds according Aarts et al. (2004).

To evaluate the influence of nutrient loading on trophic niche of fish assemblages, we related in-stream chemical variables to observed trophic patterns. Water quality data for each sampling sites was derived from long-term nutrient concentration monitoring by the Czech Hydrometeorological Institute, CHMI<sup>2</sup>, which conducts monthly monitoring at the sampling sites. Environmental parameters included pH, dissolved oxygen (DO, mg l<sup>-1</sup>), total nitrogen (TN, mg l<sup>-1</sup>), nitrate (N-NO<sub>3</sub><sup>-</sup>, mg l<sup>-1</sup>), ammonium (N-NH<sub>4</sub><sup>+</sup>, mg l<sup>-1</sup>), phosphate (P-PO<sub>4</sub><sup>3-</sup>, mg l<sup>-1</sup>), total phosphorus (TP, mg l<sup>-1</sup>), BOD<sub>5</sub> (biological oxygen demand), COD (chemical oxygen demand), POM (particulate organic matter), DOM (dissolved organic matter, conductivity and chlorophyll-*a*). The frequency of

1 <https://www.r-bednar.cz/>

2 <http://www.chmi.cz>

TABLE 1 Number of samples and size of individuals (Total Length: TL) used for each fish species, together with species level Bayesian trophic niche metrics measured, including the total area of convex hull (TA), Standard Ellipse Area (SEA), ellipse area corrected for small sample size (SEAc), species-specific variance in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

Species	English name	<i>n</i>	TL (mm)	TA (‰ <sup>2</sup> ) mean $\pm$ s.d.	SEAc (‰ <sup>2</sup> ) mean $\pm$ s.d.	$\delta^{13}\text{C}$ (‰) mean $\pm$ s.d.	$\delta^{15}\text{N}$ (‰) mean $\pm$ s.d.
<b>Rheophilic</b>							
<i>Barbatula barbatula</i>	Stoneloach	6	96.8 $\pm$ 12.7	0.02 $\pm$ 0.0	0.08 $\pm$ 0.0	-22.14 $\pm$ 0.7	12.6 $\pm$ 0.9
<i>Barbus barbus</i>	Barbel	43	201.7 $\pm$ 79.8	1.99 $\pm$ 1.6	1.0 $\pm$ 0.4	-21.95 $\pm$ 1.5	12.97 $\pm$ 0.8
<i>Cottus gobio</i>	Bullhead	27	77.0 $\pm$ 13.3	1.79 $\pm$ 2.3	1.38 $\pm$ 0.8	-22.95 $\pm$ 1.7	13.37 $\pm$ 1.1
<i>Gobio gobio</i>	Gudgeon	56	111.0 $\pm$ 22.9	1.41 $\pm$ 1.3	1.42 $\pm$ 1.6	-23.63 $\pm$ 1.8	14.48 $\pm$ 1.8
<i>Chondrostoma nasus</i>	Nase	54	283.2 $\pm$ 115.4	2.20 $\pm$ 2.2	1.71 $\pm$ 1.1	-22.95 $\pm$ 1.9	13.78 $\pm$ 1.3
<i>Leuciscus idus</i>	Ide	15	179.3 $\pm$ 63.9	2.43 $\pm$ 3.6	2.78 $\pm$ 2.7	-25.62 $\pm$ 1.3	14.3 $\pm$ 1.3
<i>Leuciscus leuciscus</i>	Dace	49	163.9 $\pm$ 37.1	3.04 $\pm$ 3.1	2.72 $\pm$ 3.2	-23.07 $\pm$ 2.0	13.87 $\pm$ 1.3
<i>Salmo trutta</i>	Brown trout	6	145.8 $\pm$ 21.7	1.02 $\pm$ 0.0	2.02 $\pm$ 0.0	-23.34 $\pm$ 0.6	13.23 $\pm$ 1.2
<i>Thymallus thymallus</i>	Grayling	3	247.3 $\pm$ 16.3	0.47 $\pm$ 0.0	1.71 $\pm$ 0.0	-23.04 $\pm$ 0.5	10.07 $\pm$ 0.5
<i>Vimba vimba</i>	Vimba	2	113.0 $\pm$ 1.4	0.06 $\pm$ 0.0	0.21 $\pm$ 0.0	-25.12 $\pm$ 0.3	16.47 $\pm$ 0.6
<b>Eurytopic</b>							
<i>Abramis brama</i>	Common bream	10	215.3 $\pm$ 111.8	5.78 $\pm$ 5.4	7.7 $\pm$ 7.5	-25.54 $\pm$ 2.2	15.51 $\pm$ 1.6
<i>Alburnus alburnus</i>	Bleak	106	124.8 $\pm$ 24.2	3.02 $\pm$ 2.9	1.38 $\pm$ 1.0	-25.72 $\pm$ 1.5	14.06 $\pm$ 1.3
<i>Anguilla Anguilla</i>	Eel	3	359.0 $\pm$ 264.6	1.72 $\pm$ 0.0	6.24 $\pm$ 0.0	-27.22 $\pm$ 1.7	14.9 $\pm$ 0.8
<i>Blicca bjoerkna</i>	Silver Bream	6	225.7 $\pm$ 92.1	3.88 $\pm$ 0.0	4.49 $\pm$ 0.0	-27.79 $\pm$ 1.2	15.97 $\pm$ 1.2
<i>Carassius auratus gibelio</i>	Gibel carp	3	193.7 $\pm$ 39.4	13.16 $\pm$ 0.0	47.72 $\pm$ 0.0	-30.33 $\pm$ 2.0	14.54 $\pm$ 3.7
<i>Gymnocephalus cernua</i>	Ruffe	13	92.50 $\pm$ 13.7	0.31 $\pm$ 0.2	0.34 $\pm$ 0.1	-27.11 $\pm$ 0.5	16.79 $\pm$ 1.1
<i>Neogobius melanostomus</i>	Round goby	31	83.70 $\pm$ 7.2	5.47 $\pm$ 0.1	2.35 $\pm$ 0.2	-26.18 $\pm$ 0.8	15.89 $\pm$ 1.1
<i>Perca fluviatilis</i>	Perch	23	130.8 $\pm$ 42.9	1.82 $\pm$ 2.1	4.58 $\pm$ 7.8	-26.17 $\pm$ 1.3	16.6 $\pm$ 1.5
<i>Rutilus rutilus</i>	Roach	140	150.6 $\pm$ 34.4	5.97 $\pm$ 7.5	2.02 $\pm$ 1.6	-24.92 $\pm$ 2.6	14.3 $\pm$ 1.7
<i>Squalius cephalus</i>	Chub	158	181.9 $\pm$ 79.6	2.67 $\pm$ 1.9	1.6 $\pm$ 0.97	-24.85 $\pm$ 1.3	13.35 $\pm$ 1.8

Data presented as mean  $\pm$  standard deviation.

nutrient sampling ranged from weekly to monthly, with an average of 12 samples per locality per year (i.e., monthly sampling).

## 2.2. Stable isotope analysis

Samples of invertebrates and fish muscle tissue for isotopic analysis were oven dried at 60°C to constant mass prior to analysis. Samples were homogenized using ball mill (MM400, Retsch, Germany) and 0.5  $\pm$  0.05 mg of material was weighed into tin capsules. Total carbon and nitrogen content and isotopic ratios ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) were determined using a Delta V Advantage mass spectrometer coupled to Conflo IV and elemental analyzer Flash 2000 with TCD detector (all instrumentation by Thermo Fisher Scientific, Bremen, Germany)

at the Centre for Stable Isotope Research of the Charles University, Prague. The carbon and nitrogen isotope ratios are expressed following the delta notation, as follows:  $\delta^X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000$ , where, where X is  $^{13}\text{C}$  or  $^{15}\text{N}$ , respectively, and R is the relative amount of carbon or nitrogen isotopes ( $R = ^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ ). Isotope ratios were normalized using international standards; carbon isotope ratios were reported against the Vienna Pee Dee Belemnite (VPDB) scale, while nitrogen isotope ratios were reported against atmospheric  $\text{N}_2$ . In addition to repeated measurements of a series of international standards (IAEA-CH3, IAEA-CH6, IAEA-600, IAEA-N1, IAEA-N2, IAEA-NO3), after every 10th sample a glycine standard was included to provide calibration for elemental composition and serve as a quality control for isotopic measurement. Analytical precision was within  $\pm 0.2$  ‰ for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Table 2). As the lipid content was consistently low

TABLE 2 Mean stable isotope ratios ( $\pm$  standard deviation) at sampling sites.

Sampling site	Sampling site	$\delta^{13}\text{C}$ (‰) $\pm$ s.d.	$\delta^{15}\text{N}$ (‰) $\pm$ s.d.
1	Malšín	-23.29 $\pm$ 1.1	12.92 $\pm$ 1.0
2	Rájov	-22.66 $\pm$ 1.6	12.58 $\pm$ 0.8
3	Boršov	-21.46 $\pm$ 1.9	12.80 $\pm$ 1.1
4	Týn	-24.47 $\pm$ 1.5	13.40 $\pm$ 1.1
5	Davle	-25.11 $\pm$ 0.6	13.42 $\pm$ 2.0
6	Troja	-25.47 $\pm$ 1.2	13.85 $\pm$ 1.0
7	Libčice	-26.72 $\pm$ 0.9	14.09 $\pm$ 0.9
8	Vraňany	-26.34 $\pm$ 2.1	16.32 $\pm$ 1.4
9	Štětí	-26.64 $\pm$ 1.3	15.43 $\pm$ 0.9
10	Ústí	-26.08 $\pm$ 0.9	15.47 $\pm$ 0.9
11	Děčín	-25.8 $\pm$ 0.8	14.93 $\pm$ 1.7

in samples ( $C:N < 3.5$ ), lipid correction was not used (Post et al., 2007).

## 2.3. Data analyses

All statistical analyses were conducted using R 4.0.5 (R Core Team, 2021). To reveal food niche space, Bayesian ellipse analyses were used *via* the SIBER package (Stable Isotope Bayesian Ellipses in R<sup>3</sup>; Jackson et al., 2011). For each fish species, isotopic niche breadth was determined as standard ellipse area corrected for small sample size (SEAc) and total convex hull area (TA). We also used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to calculate trophic position and to evaluate trophic niche space of species (Layman et al., 2007). Relative position of species on  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  bi-plots was used to infer aspects of food web structure. To enable robust statistical comparisons among assemblages, we used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to describe six community-wide metrics as proposed by Layman et al. (2007), that reflect important aspects of trophic structure. The first four metrics were measures of the total extent of spacing within  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  bi-plot space, i.e., community-wide measures of trophic diversity. For each locality we calculated  $\delta^{15}\text{N}$  range (NR) as a measure of trophic height of the community and  $\delta^{13}\text{C}$  range (CR) as an estimate of the diversity of basal resources, total area of the convex hull encompassing the data points (TA) giving in indication of niche width of the community, mean distance to centroid (CD) as a measure of trophic diversity, mean nearest neighbor distance (MNND) providing a measure of density and clustering of species within the community, and standard deviation of MMND (SDNND) giving a measure of evenness of spatial density and packing. The final two metrics

reflect the relative positions of species within niche space and can be used to estimate the extent of trophic redundancy (MNND/SDNND; Layman et al., 2007; Jackson et al., 2011).

The trophic position of fish species was calculated as  $TP = [(\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{baseline}})/3.4] + 2$  (Cabana and Rasmussen, 1996), where aquatic invertebrates were used as a *baseline* (Vander Zanden and Rasmussen, 1999; Phillips et al., 2014). The constant 3.4‰ was used to reflect diet-tissue enrichment per trophic level (Minagawa and Wada, 1984). Nested ANOVA was used to compare mean values of trophic niche area and trophic position among ecological groups and river sites. As the data did not fulfil the criteria for parametric tests, logarithmic transformation was used to ensure normality. Simple linear regression models were used to examine relationships between the environmental variables and community metrics. To evaluate the influence of physico-chemical parameters on the trophic niche and trophic position of fish species, “lme4” (Bates et al., 2014) was used to fit linear mixed effects models LMMs and “lmerTest” (Kuznetsova et al., 2014) used to obtain value of ps for the fixed effects. We performed model selection based on the information-theoretic approach to assess the relative importance of all possible combination of predictor variables (Burnham and Anderson, 2002). Using Akaike Information Criterion corrected for small sample sizes (AICc) and best subset analysis in the package “leaps” (Lumley and Miller, 2004; Supplementary Table S2), we assessed relative performance of every combination of predictor variables. We included the variable “species” and “sampling site” as random effects in all models. *T*-tests were used to evaluate differences in trophic niche area among species and community metrics among sites.

## 3. Results

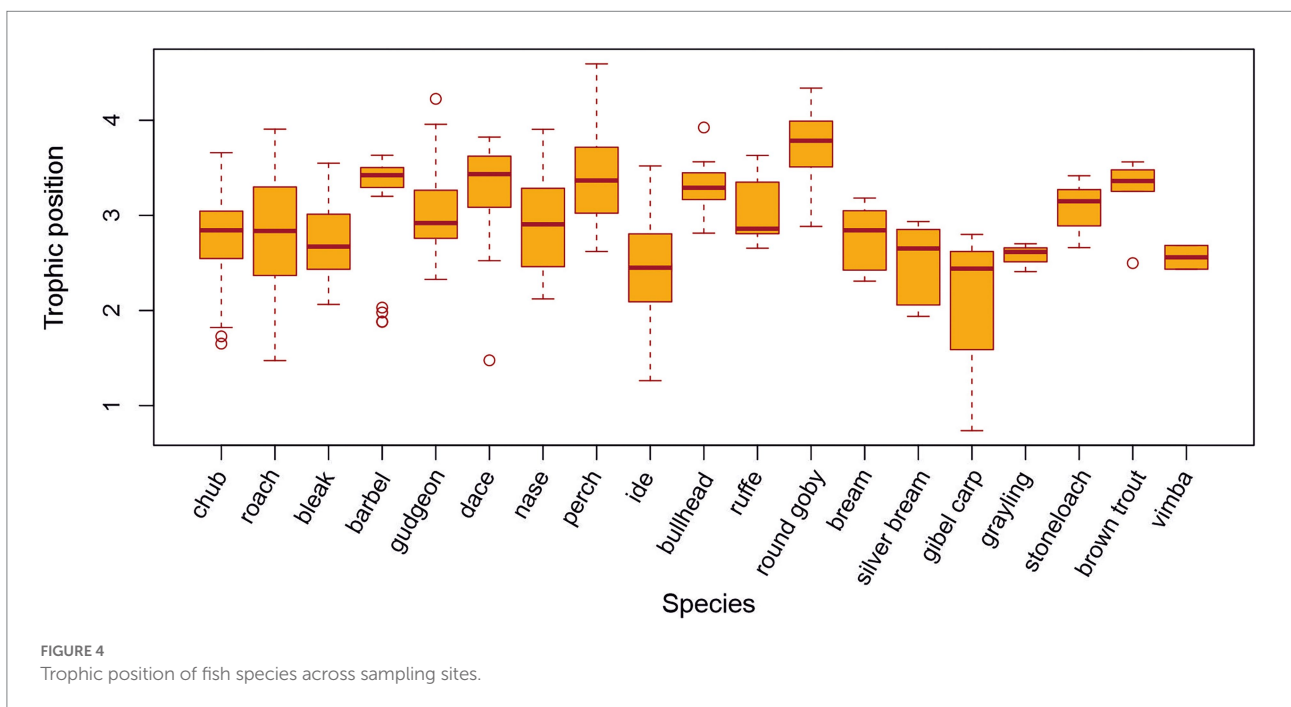
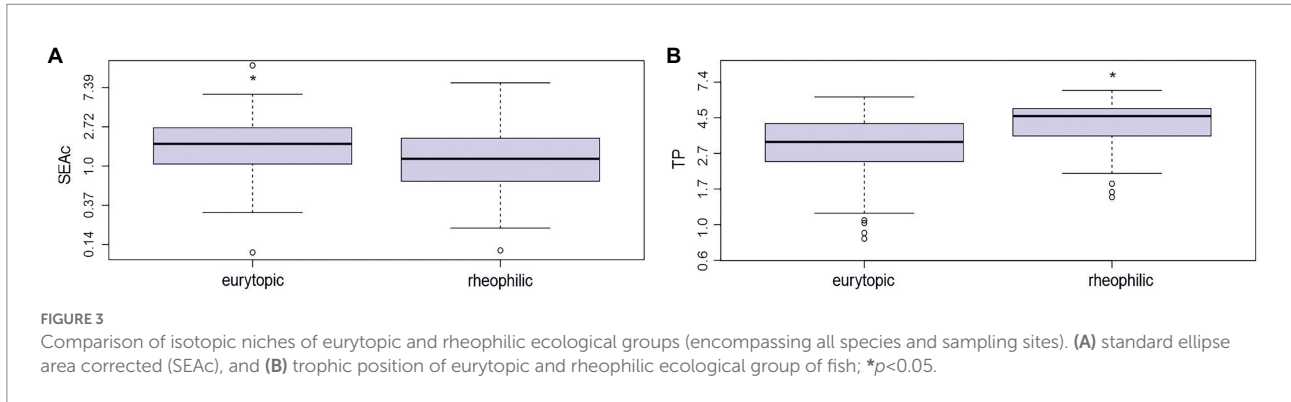
### 3.1. Trophic niche area of species

SEAc (Standard Ellipse Area Corrected; Jackson et al., 2011; Figure 3A) was significantly larger for eurytopic fish than rheophilic (Figure 3A;  $F_{1,74} = 1.902$ ;  $p = 0.038$ ). Total area of convex hull (TA) of eurytopic species was larger the for rheophilic species ( $F_{1,74} = 6.372$ ;  $p < 0.01$ ), indicating that eurytopic fish occupy a larger isotopic niche space than rheophilic fish. Mean SEAc was highest for gibel carp, common bream, eel, perch and silver bream (Table 1;  $t_{(18)} = 49$ ,  $p < 0.05$ ).

### 3.2. Trophic position

Rheophilic fish species occupied a significantly higher average trophic position (TP) than eurytopic species (Figure 3B;  $F_{1,699} = 0.3115$ ;  $p < 0.01$ ), although there was variation among species and sampling sites (Figure 4). Round goby, perch, dace, barbel, and bullhead occupied the highest mean trophic position of all species studied (Table 1; Figure 4;  $t_{(18)} = -4.0$ ,  $p < 0.05$ ).

<sup>3</sup> www.cran.r-project.org



### 3.3. Community wide metrics

$\delta^{15}\text{N}$  range (NR) provides a measure of the length of the longest food chain, where higher values suggest more trophic levels and a greater degree of trophic diversity. The NR was highest at sites S8 and S11 (Figure 5B). The highest  $\delta^{13}\text{C}$  range (CR), which reflects the diversity of resources exploited, was found at sites S2, S3 and S7, all on the Vltava river (Figure 5A), where total area (TA), which represents a measure of the total amount of niche space occupied, was highest also (Figure 5D). The lowest TA was observed at site S5. It was not possible to calculate community metrics for sites S5 and S7 due to the low diversity and abundance of fish at these sites. Mean CD is a metric which reflects the overall degree of trophic diversity in the food web, however, it is also a function of the degree of species spacing. CD was highest at sites S5 and S8 (Figure 5C). MNND and standard deviation of nearest neighbor distances (SDNND) are measures of diversity of trophic niche area of species

in a food web. MNND was highest at S5 (Figure 5E), and SDNND highest at sites S2, S3 (Figure 5F; Supplementary Table S3).

### 3.4. The effect of environmental variables on species trophic niche space

The effects of environmental parameters (pH, DO, TN,  $\text{N-NH}_4^+$ ,  $\text{P-PO}_4^{3-}$ , TP,  $\text{BOD}_5$ , COD, POM, DOM, conductivity and chl-*a*) on both individual (SEAc, TA, trophic position) and community metrics (NR, CR, TA, CD, MNND, SDNND) were evaluated. Of the 11 environmental variables tested, POM,  $\text{N-NH}_4^+$ ,  $\text{N-NO}_3$ - and total phosphorus were associated significantly with the trophic niche area of species, SEAc (Table 3). The results show that POM,  $\text{N-NH}_4^+$ , and  $\text{N-NO}_3$ - had a negative effect on SEAc, however total phosphorus (TP) had a positive effect on SEAc, suggesting that SEAc increased with

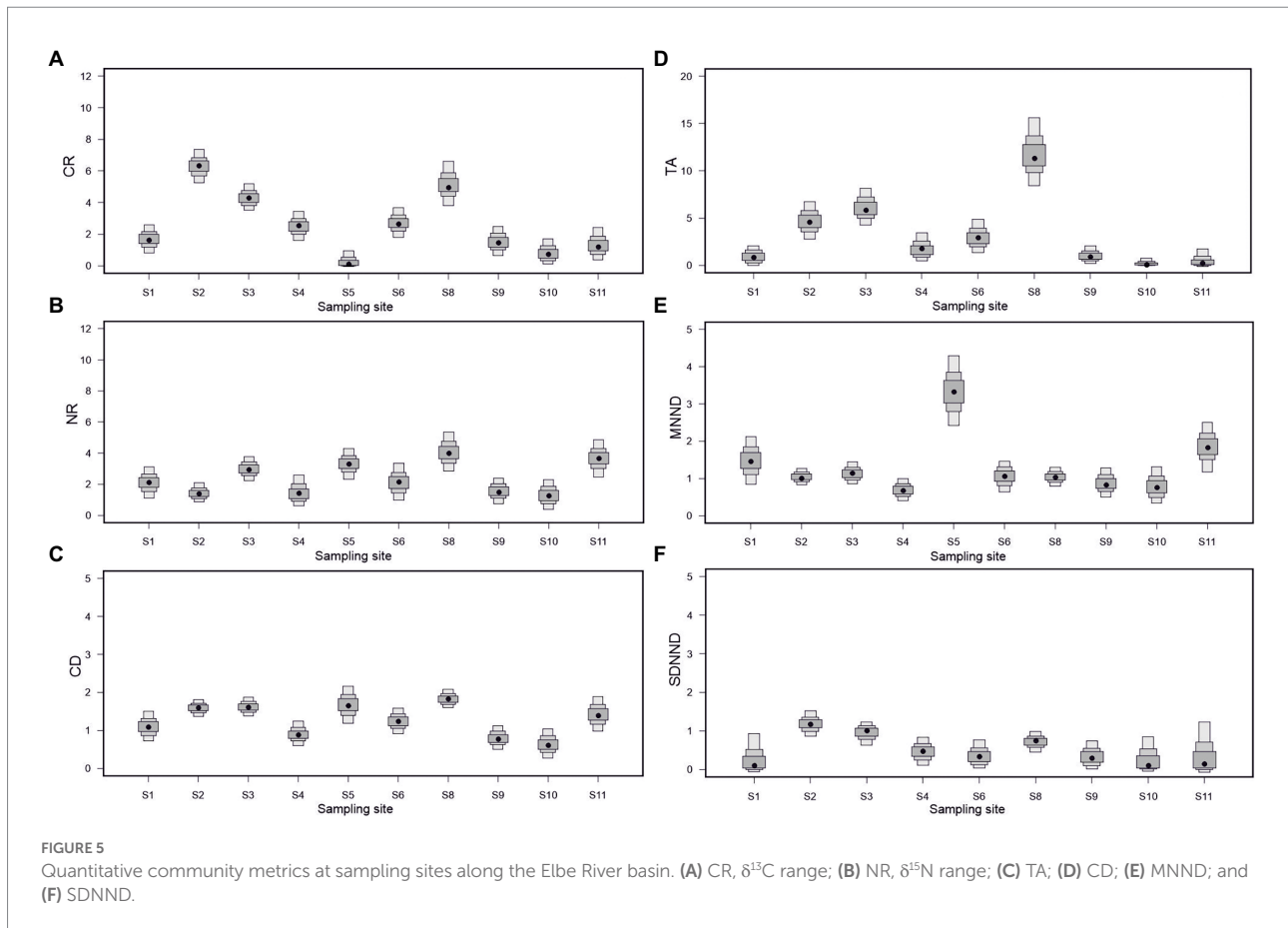


TABLE 3 Relationships between Standard Ellipse Area corrected (SEAc) and Trophic Position (TP) and physico-chemical parameters, estimated by the final linear mixed-effects model taking into account the effects of the species and sampling sites.

Model term	Estimate	Std. Error	df	t	p
<b>SEAc</b>					
POM	-0.1449	0.03566	7.85039	-4.063	0.004
N-NH <sub>4</sub> <sup>+</sup>	-27.00997	7.94757	10.24616	-3.399	0.007
Total phosphorus	78.51196	15.71166	9.04168	4.997	<0.001
N-NO <sub>3</sub> <sup>-</sup>	-0.85641	0.2766	9.7688	-3.096	0.012
<b>TP</b>					
COD	-0.18321	0.07646	11.05091	-2.396	0.035
N-NH <sub>4</sub> <sup>+</sup>	25.17287	9.5317	11.08512	2.641	0.023

TP. The results further shows that trophic position of species was positively associated with N-NH<sub>4</sub><sup>+</sup>, and negatively with COD. Evaluation of community level metrics shows that a measure of trophic diversity - mean CD, and a measure of density and clustering of species - MNND, were affected by environmental parameters, where a negative association between BOD<sub>5</sub> and CD, and COD and MNND (Table 4) were found. Other environmental parameters tested were found not

to be significantly associated with variation in either species or community level metrics.

## 4. Discussion

We predicted that eurytopic fish species would occupy wider trophic niches in riverine food webs than rheophilic species, as greater range of prey types can be accessed by omnivorous feeding. Based on previous evidence, eurytopic species should have a larger isotopic niche, indicating feeding across multiple trophic levels and a generalized diet based on a range of basal sources compared with more specialized rheophilic species (Persson, 1988; Kottelat and Freyhoff, 2007;). We found that rheophilic species occupied a narrower trophic niche space, suggesting greater dietary specialization (Araújo et al., 2011) and a smaller trophic niche size in a competitive environment (Van Valen, 1965; Human and Gordon, 1996; Olsson et al., 2009;). The largest mean trophic niche spaces were occupied by the eurytopic species gibel carp (*Carassius gibelio*), roach (*Rutilus rutilus*), and common bream (*Abramis brama*) whereas TA, SEAc were highest in gibel carp, eel (*Anquila anquila*) and perch (*Perca fluviatilis*). The larger trophic niche space of gibel carp, roach and common bream mostly reflected large carbon ranges as the result of a varied diet including macrophytes or detritus from terrestrial sources (Del Giorgio and France, 1996) and possibly littoral-based herbivorous resources (Vejříková et al., 2017).

**TABLE 4** Results of linear regression between environmental factors and mean nearest neighbour distance (MNND) and distance to centroid (CD).

term	R <sup>2</sup>	(Intercept)	Slope	Standard error (slope)	p-value
<b>MNND</b>					
COD	0.4593	1.28892	-0.05329	0.01909	0.027
<b>CD</b>					
BOD <sub>5</sub>	0.443	0.43969	-0.1284	0.05442	0.050

We further compared the trophic position between eurytopic and rheophilic species. Interestingly, despite narrower isotopic niche space, rheophilic fish species tended to occupy a higher trophic position than eurytopic species (Figure 3B), suggesting that these species use resources more enriched in <sup>15</sup>N. Our results are consistent with those observed by Champagne et al. (2022) who observed that the generalist consumer – creek chub (*Semotilus atromaculatus*) assimilated less terrestrial energy and occupied lower trophic positions. The highest trophic position was displayed by round goby, common dace and barbel. Our results suggest that on average these species were feeding higher in the food web, possibly through a greater reliance on terrestrial and/or aquatic macroinvertebrates. Common dace predominantly consumes aquatic and terrestrial insects (Hellawell, 1974), barbel feeds chiefly on benthic invertebrates, such as small crustaceans, insect larvae, molluscs, and mayfly larvae (Maitland and Campbell, 1992). The higher trophic position of perch and brown trout could be linked with a piscivory in these species (Kottelat and Freyhoff, 2007).

The relationship between community metrics and the structural variability of the sampling sites corroborates that the morphology of the stream and its surrounding landscape has important consequences for food web structure (Woodward and Hildrew, 2002; Wang et al., 2021). The highest N-ranges were found at sites S8 and S11 corresponding with the high variability of instream habitat structure and the surrounding terrestrial habitats. In contrast, it was not possible to obtain community metrics at site at site S5 and S7 due to the low diversity of the fish assemblages at these highly anthropogenically degraded sites (bank stabilization and homogenization of habitat). Niche diversification ( $\delta^{13}\text{C}$  range) was highest found at sites S2, S3 and S8 on the Vltava, where the total niche space occupied (total area) was highest also. Such finding may be explained by the observed heterogeneity of both in-river and adjacent habitats and the presence of macrophyte stands, which reflects a high diversity of resources in these less channelized reaches (Górski et al., 2016; Latli et al., 2018). Riparian zones are among the most diverse, and complex habitats (Naiman and Décamps, 2007): and the presented results demonstrate that the complexity of habitats may increase the overall trophic niche used by the species present.

Changes in the trophic structure of fish assemblages in response to ecosystem perturbations could indicate which pressures affect fish assemblages most. Nutrient concentrations

were associated with change in the trophic niche width of species (SEAc, TA), whilst changes in functional community structure (CD, MNND) were associated with change in biological and chemical oxygen demand, often associated with nutrient enrichment and increased productivity. Such results provide increased understanding of the effect of nutrient loading on the structure and composition of fish assemblages reported in previous studies (Kulišková et al., 2009; Hoffman et al., 2012; Baeta et al., 2017; Bierschenk et al., 2019; Wang et al., 2021). In our study, it has been shown that the nutrient concentration may influence the trophic niche space of species. Nitrate and ammonium have a negative effect on SEAc of species, whereas total phosphorus has a positive effect. Increased concentrations of inorganic nitrogen and phosphorus indicate water eutrophication associated with agriculture in the catchment (Roussel et al., 2004; Langhammer, 2010). Nutrient concentrations may influence the isotopic niche space of species through impacts on basal trophic resources where nutrients assimilated by primary producers are transferred to higher trophic levels (Roussel et al., 2004; Roulet and Moore, 2006; Bergfur et al., 2009; Baeta et al., 2017) further contributing to eutrophication (Weigelhofer et al., 2013). Nitrate contamination in the Elbe drainage basin has been a long-term issue. In the Czech Republic, N-NO<sub>3</sub>-concentrations have decreased slightly or remained constant since monitoring began in the 1960's (Ritter, 2010), and in some reaches exceeded the European Union (EU) standard of 50 mg.l<sup>-1</sup>. The fact that phosphorus concentration was more strongly associated with differences in the trophic niche space of fish species than chlorophyll-*a* concentration implies that nutrients from catchment land use (diffuse pollution) has probably a dominant effect rather than point source pollution (Mainstone and Parr, 2002). Indeed, diffuse pollution from fertilization, soil erosion and fish farming were identified as key pollutants of surface waters in Czech Republic (River Basin Management Plans reporting of the Czech Republic; EIONET)<sup>4</sup>.

Fish are particularly prone to the toxic effects of unionized ammonia (Servizi and Gordon, 1990; Handy and Poxton, 1993), although field demonstrations of the effect of ammonia on freshwater fish are rare. Ammonia is produced by the decomposition of organic matter through the activity of microorganisms, and its form varies with temperature, pressure and ionic concentration. The concentration of the toxic unionized form of ammonia (N-NH<sub>3</sub>) increases with increasing pH (Eddy, 2005). Increased concentrations of ammonia impair activity and behavior of fish, as ammonia interferes with nervous function and ionic regulatory processes (for review see Eddy, 2005; Kemp et al., 2011). Such negative impacts may influence the ability of fish to obtain food resources, decreasing the trophic niche area of fishes. Analogous to nitrogen, phosphorus can influence the isotopic composition of basal resources. However, it may also operate indirectly by affecting the abundance and community structure of invertebrates, a vital food source for fish (Henley et al., 2000; Nixon et al., 2001; Egler et al., 2012). Excessive

<sup>4</sup> <http://cdr.eionet.europa.eu/>



phosphate increases productivity, stimulating algal growth and increasing the supply of organic matter to water and sediments. Such processes are key drivers of the oxygen balance of water and sediments with subsequent detrimental effects on aquatic assemblages (Kemp et al., 2011).

A negative association between BOD<sub>5</sub> and CD, and COD and MNND were found, indicating that the oxygen demand is a key factor influencing community trophic structure. Excessive nutrients which trigger algal growth may lead to the lack of oxygen or anoxia, leading to deterioration of basal resource diversity (Nixon et al., 2001). For example, reduced oxygen availability may induce the development of invertebrate communities dominated by a few pollution-tolerant taxa (chironomids, oligochaetes), but less suitability as a food resource for fish (Mason, 1991; Egler et al., 2012). Consequently, low dissolved oxygen concentrations may reduce the realized trophic niche of fishes, especially those specialized on benthic invertebrates.

## 5. Conclusion

There is a growing recognition of a value of assessing functional responses of riverine ecosystems to environmental disturbances. As river fish communities are unprecedentedly affected by degradation and population loss, improved understanding of food web dynamics in anthropogenically modified rivers is urgently needed. The pattern observed here, where nutrient loading influenced both individual species and the trophic structure of fish assemblages strongly supports assertions that anthropogenic nutrient loading poses a substantial impact affecting the entire food web (Woodward and Hildrew, 2002; Warry et al., 2016). As rheophilic species may rely on both aquatic and terrestrial sources of food, the morphological structure of adjacent habitats will have a substantial impact on trophic niche use of these specialized fish species (Champagne et al., 2022). Such findings highlight the need for restoration of natural river habitat and remediation of structural degradation of adjacent river habitat, together with efforts to reduce the impact of agricultural runoffs and diffuse nutrient pollution on rivers.

## Data availability statement

The datasets presented in this article are not readily available because Environmental data are freely available at Czech Hydrometeorological Institute (<https://www.chmi.cz>). Trophic data are not publicly available due to restrictions. Requests to access the datasets should be directed to [petra.horka@natur.cuni.cz](mailto:petra.horka@natur.cuni.cz).

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## Ethics statement

The animal study was reviewed and approved by Ethical Committee, Charles University in Prague.

## Author contributions

PH: conceptualization, methodology, investigation, formal analysis, and writing—original draft preparation. ZM: methodology and investigation. KH: investigation and data curation. JK, KJ, and JR: investigation. JJ: writing—review and editing. All authors contributed critically to the drafts and gave final approval for publication.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.1076451/full#supplementary-material>

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