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# Linking intraspecific variability in trophic and functional niches along an environmental gradient

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## Abstract

1. Intraspecific trophic variability has important ecological and evolutionary implications, and is driven by multiple interacting factors. Functional traits and environmental conditions are important in mediating the trophic niche of individuals because they determine their ability to consume certain prey, their energetic requirements, and resource availability. In this study, we aimed at investigating the interacting effects of functional traits and environmental conditions on several attributes of trophic niche in natural populations.

2. Here, we quantified intraspecific variability in the trophic niche of 12 riverine populations of European minnow (*Phoxinus phoxinus*) using stable isotope analyses. Functional traits (i.e. morpho-anatomical traits) and environmental conditions (i.e. upstream–downstream gradient, forest cover) were quantified to identify the determinants of (1) trophic position and resource origin, (2) trophic niche size, and (3) trophic differentiation (β-diversity) among populations.

3. We demonstrated that trophic position and resource origin covaried with functional traits related to body size and locomotion performance, and that the strength and shape of these relationships varied according to local environmental conditions. The trophic niche size also differed among populations, although no determinant was identified. Finally, trophic β-diversity was correlated to environmental differentiation among sites.

4. Overall, the determinants of intraspecific variability in trophic niche appeared highly context-dependent, and related to the interactions between functional traits and environmental conditions. Because populations are currently facing important environmental changes, understanding this context-dependency is important for predicting food web structure and ecosystem dynamics in a changing world.

**KEYWORDS**
functional traits, intraspecific diversity, stable isotopes, streams, trophic niche

## 1 | INTRODUCTION

The integration of resource exploitation in community ecology has a longstanding history and has provided robust bases in the understanding of species coexistence, notably through niche partitioning (Tilman, 1982). Intraspecific trophic niche variation (variation in diet observed among individuals within a species) is ubiquitous in animals, and has strong ecological and evolutionary

implications (Araújo, Bolnick, & Layman, 2011; Bolnick et al., 2003; Van Valen, 1965). Intraspecific diet variation is often associated with morphological and behavioural traits (Skulason & Smith, 1995; Smith & Skulason, 1996), and allows populations to adapt to environmental variations (e.g. consumption of alternative resources in harsh environmental conditions). Intraspecific variation in trophic niche is also important for the dynamics of communities and ecosystems (Bolnick et al., 2003, 2011). Indeed, variability in consumer diet can result in differences in the density of their prey, with cascading effects on lower trophic levels (Des Roches et al., 2018; Raffard, Santoul, Cucherousset, & Blanchet, 2019; Terborgh & Estes, 2010). Therefore, quantifying intraspecific trophic niche variability in wild populations, and identifying its determinants is necessary to understand how organisms adapt to and affect their environment.

Trophic niche variability among individuals can be driven by several factors related to their phenotypes and local environmental conditions (Araújo et al., 2011; Schluter, 1995). Commonly, ecologists have used functional traits as a proxy for the ecological niche of species, and to predict the role of organisms in ecosystems (Díaz et al., 2013; Villéger, Brosse, Mouchet, Mouillot, & Vanni, 2017; Violle et al., 2007). Functional traits are expected to be tightly linked to potential trophic niches, as they govern the ability of organisms to detect and acquire trophic resources (Sibbing & Nagelkerke, 2001; Villéger, Miranda, Hernández, & Mouillot, 2010; Zhao, Villéger, Lek, & Cucherousset, 2014). Body size can strongly vary among individuals (both within and among life-stages), and it is one of the most important functional traits since it is associated with metabolism, energetic requirements, morphology, and the capacity to handle and consume specific resources (Hildrew, Raffaelli, & Edmonds-Browns, 2007; Vrede et al., 2011; Zhao et al., 2014). Thereby, body size strongly contributes to functional niche variability and probably affects individual trophic niche (Vander Zanden, Shuter, Lester, & Rasmussen, 2000). It is necessary to investigate the links between functional and trophic niches to understand the mechanisms underlying the ecological role of intraspecific variability.

Environmental heterogeneity is an additional important driver of individual trophic niche (Rosenblatt & Schmitz, 2016; Zandonà et al., 2017). Local environmental conditions induce physiological stress on individuals, and contribute to shape their trophic niche either by modifying their metabolic needs (e.g. temperature) or by modulating resource availability (e.g. intra- and interspecific competition, Cucherousset, Aymes, Santoul, & Céréghino, 2007; Hawlena & Schmitz, 2010; Boersma et al., 2016). However, the effects of environmental conditions on individual trophic niche might be highly context-dependent since the same environmental pressures can also modulate functional traits (Díaz et al., 2013). This might lead to complex relationships between individual trophic niche, functional traits, and environmental conditions. For instance, communities harbouring species with similar functional traits (i.e. high functional redundancy) might be trophically dissimilar because environmental conditions differ, leading to different constraints on organisms (Pool et al., 2016). Simultaneously quantifying environmental and
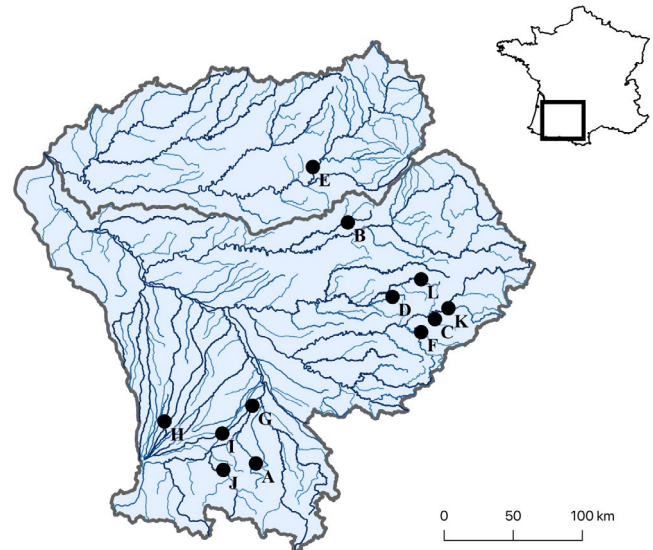


**FIGURE 1** Distribution of the 12 studied populations (A–L) in the Garonne basin, France [Colour figure can be viewed at wileyonlinelibrary.com]

functional variability is therefore necessary to fully appreciate the determinants of the trophic niche in wild populations.

Here, we investigated the functional and environmental determinants of trophic niche variability among wild populations, using the European minnow (*Phoxinus phoxinus*) as a model organism. We studied wild populations in 12 temperate rivers distributed across a large river basin (Figure 1) that differed in their environmental conditions (i.e. water temperature, river width, canopy cover, and land use). We used stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) to quantify trophic niche, and we focused on three parameters describing the trophic niche of populations: (1) trophic position (TP) and resource origin (RO); (2) trophic niche size (i.e. α-diversity); and (3) trophic niche differentiation among populations (i.e. β-diversity). We first assessed the effects of environmental factors and functional traits on the variation in TP and in RO among populations. We expected that functional traits mediate the ability of individuals to forage for specific resources and that the environment can affect the TP and RO of individuals because it may change their energetic requirements and prey availability. For instance, TP of individuals could depend on their ability to consume large prey through gap size limitation (Carroll, 2004; Karpouzi & Stergiou, 2003). Secondly, we assessed the relationship between trophic and functional niche sizes within populations and environmental conditions, and we expected a positive relationship between trophic and functional niche size (Pool et al., 2016). Since functional traits (in particular body size) might determine individual diets (e.g. preferred prey) by constraining their capacity to detect, capture, and consume resources, individuals displaying different functional traits should display different diet. Hence, within-population variation in functional traits should increase the diversity of consumed resources, which should ultimately increase trophic niche size (Svanbäck & Bolnick, 2005). Finally, we quantified the association between trophic, functional and environmental differentiations among populations. For instance, along the

upstream–downstream gradient, spatial differentiation in environmental conditions should lead to functional and trophic niche differentiation among populations, because individuals face different abiotic and biotic pressures. We therefore expected that populations sharing similar environmental conditions should display similar functional and trophic niches.

## 2 | METHODS

### 2.1 | Model species and study sites

The European minnow (*P. phoxinus*) is a generalist cyprinid fish found in water generally around 17°C, including streams, temperate rivers and mountain lakes (Frost, 1943; Keith, Persat, Feunteun, & Allardi, 2011). European minnows are small-bodied fish that often occur in schools, and preferably occupy shallow waters with gravel and sand as main substrate. They reach sexual maturity at approximately 2 years, spawn in spring and summer when temperatures exceed 15–17°C, and their longevity is about 4–5 years. They are omnivorous fish and feed primarily on small invertebrates, although filamentous algae and plant debris have also be reported in their diet (Collin & Fumagalli, 2011; Frost, 1943). European minnows display a high level of phenotypic and genetic differentiation among populations inhabiting different areas. This differentiation can be due to both plastic and selective adaptation to environmental conditions, or to the effect of drift (Collin & Fumagalli, 2015; Raffard, Cucherousset, et al., 2019).

We focused on an environmental gradient varying in water temperature, river width, altitude, canopy cover and land use, which has previously been shown to affect the phenotype of European minnows (Raffard, Cucherousset, et al., 2019), and hence potentially their trophic niche. For instance, temperature can affect the physiological requirements of individuals (Rosenblatt & Schmitz, 2016), river width is related to habitat size and resource heterogeneity, and the canopy cover of a river is linked to the amount of allochthonous inputs available to predators (Bartels et al., 2012; Evangelista, Boiche, Lecerf, & Cucherousset, 2014). To assess phenotypic and trophic niche variability, European minnows were sampled in 12 rivers located in the Garonne basin in southwestern France using electrofishing (DK 7000; Figure 1, Table S1). Rivers were selected based on a priori knowledge about their environmental characteristics (i.e. position in the drainage, river width and water temperature) to optimise the level of environmental variability between rivers. In June 2016, we sampled approximately 100 adult minnows in each river along a *c.* 200 m long river stretch to ensure representativeness of habitat heterogeneity. Minnows were sampled in several habitats (e.g. shallow riffles or deep pools) to cover the heterogeneity of each site, and included individuals occurring in schools as well as isolated individuals. Between 20 and 27 adult individuals were randomly collected from the pool of sampled individuals for further analyses to obtain a representative sample of each population. Fish were euthanised in the field using an overdose of anaesthetic (benzocaine:

25 mg/L), transported to the laboratory on ice, and subsequently frozen at −20°C until processing. Overall, a total of 305 individuals (mean number of individuals/populations ± *SE* = 25.41 ± 0.63) were analysed for trophic niche variation. In addition, we sampled benthic invertebrates in three different locations (e.g. along the shore, in riffles, and lower water velocity areas) within each river using Surber nets (mesh size = 0.5 mm). This enabled us to obtain stable isotope baselines, so that stable isotope values of fish could be corrected, thus ensuring robust comparisons among sites (Jackson & Britton, 2014; Post et al., 2007). The contents of the three Surber nets were pooled and frozen at −20°C. Then, invertebrates were sorted, and identified to Baetidae and Heptagenidae. We focused on these two taxa because they were present in each river. We obtained 3–6 samples for each river by pooling multiple specimens of either Baetidae or Heptagenidae (depending upon the number of individuals available and their size). Then samples were oven-dried at 60°C for 48 hr.

In each river, five environmental variables (water temperature, river width, altitude, canopy cover, and land use: urban, forest, or agricultural) were measured. Water temperature was recorded daily from July to September 2017 using automatic sensors (HOBO©, one measurement every hour). River width was measured at five locations in each river, and these five measurements were averaged. Canopy cover was assessed visually using a score ranging from 1 to 5:1 for a low canopy cover (0–25%) and 5 for a high canopy cover (75–100%). The altitude was recorded from existing maps (www.geoportail.gouv.fr). Land use was quantified as the percentage of urban, forest, or agricultural land in an area of 500 m diameter around the sampling river using GIS and the Corine Land Cover database (National Institute of Geographical Information). Environmental variation among sites was summarised using a principal component analysis (PCA, *ade4* package in R, Chessel, Dufour, & Dray, 2007; R Core Team, 2013). The first two axes of the PCA explained 75% of the total variation. The first axis represented 54% of the total variation (hereafter referred to as *upstream–downstream gradient*) and was positively correlated with temperature (loading value = 0.84), width (0.84), urban cover (0.80) and negatively correlated with altitude (−0.68), canopy cover (−0.81), and agricultural cover (−0.74). The second PCA axis represented 21% of the total variation (hereafter referred to as *forest cover*) and was negatively correlated with the percentage of forest cover surrounding each site (−0.96; Figure S1).

### 2.2 | Functional niche

In March 2017, fish were unfrozen and weighed for body mass (*M*) to the nearest 0.01 g. Then, a set of 15 morpho-anatomical traits (Figure S2) were measured for each individual (Zhao et al., 2014). These traits included mouth depth, mouth width, and body width measured to the nearest 0.01 mm using a digital calliper. Fish were imaged from the side and additional traits were obtained through image analyses using the software ImageJ©: body length, body depth, body depth at the level of pectoral fin insertion, mouth distance from the bottom of the head, head depth, eye diameter,

distance between the centre of the eye and the bottom of the head, caudal peduncle minimal depth, caudal fin depth, pectoral fin length, and distance between the insertion of the pectoral fin to the bottom of the body. Finally, gut length was measured following dissection. The 15 morpho-anatomical traits were then used to calculate 10 morphological ratios (Table S2) describing functional traits in fish (Villéger et al., 2010; Zhao et al., 2014).

The 10 morphological traits and body mass were synthesised using a PCA (*ade4* package in R, Chessel et al., 2007; R Core Team, 2013). Three axes explaining 51% of the total variation in functional traits were then used for subsequent analyses (Table 1). *Functional axis 1* (24% variation explained) was associated with individual body mass (loading = 0.87), oral gape surface (−0.58), and body transversal surface (−0.83). Hence, functional axis 1 mainly described individual body size (Table 1). *Functional axis 2* (14% variation explained) was associated with the position of the pectoral fin, the body transversal shape, and the eye size of individuals (Table 1). This axis could describe the capacity to detect prey and locomotion capacity of individuals. *Functional axis 3* (13% variation explained) was associated with the position of the mouth and the eye, and could describe the position of fish in the water column (e.g. deeper pools versus faster flowing water with shallow depth), suggesting that individuals displaying the highest values on this axis were probably more benthic (Villéger et al., 2010).

## 2.3 | Stable isotope niche

A sample of dorsal muscle was collected from each individual, oven-dried at 60°C for 48 hr and analysed for stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) at the Cornell Isotope Laboratory (COIL, Ithaca, NY,

**TABLE 1** Loading values of the functional traits on each of the three selected principal component axes

| Functional traits | Axis 1 (24%) | Axis 2 (14%) | Axis 3 (13%) |
|---|---|---|---|
| Body mass | **0.87** | 0.25 | 0.08 |
| Oral gape surface | **−0.58** | 0.10 | **−0.46** |
| Oral gape shape | 0.16 | **0.47** | **−0.44** |
| Oral gape position | 0.36 | −0.06 | **−0.61** |
| Relative gut length | 0.28 | −0.01 | −0.02 |
| Eye size | −0.16 | **−0.64** | −0.01 |
| Eye position | 0.49 | **−0.45** | **−0.56** |
| Body transversal shape | **−0.40** | **0.43** | **−0.42** |
| Body transversal surface | **−0.83** | −0.31 | 0.01 |
| Pectoral fin position | 0.21 | **−0.54** | −0.31 |
| Caudal peduncle throttling | 0.45 | −0.15 | 0.29 |

*Note:* Bold values represent variables that contribute >10% to the axis.

U.S.A.). As stated above, stable isotope values were corrected for each population using the $\delta^{15}N$ and $\delta^{13}C$ values of Ephemeroptera (Baetidae and Heptagenidae) following Olsson, Stenroth, Nyström, and Granéli (2009) and Jackson and Britton (2014). The TP of each individual was calculated as:

$$TP = \frac{\delta^{15}N_i - \delta^{15}N_{base}}{3.4} + 2.$$

where $\delta^{15}N_i$ is the $\delta^{15}N$ value of each individual, $\delta^{15}N_{base}$ the mean $\delta^{15}N$ of baseline invertebrates, 3.4 the fractionation factor between trophic levels, and 2 the TP of baseline invertebrates in each stream (Post et al., 2007).

Then, we corrected the $\delta^{13}C$ to describe the RO with the following equation:

$$RO = \frac{\delta^{13}C_i - \delta^{13}C_{base}}{CR_{base}}$$

where $\delta^{13}C_i$ is the $\delta^{13}C$ value for each individual fish, $\delta^{13}C_{base}$ the average $\delta^{13}C$ value of baseline invertebrates (Baetidae and Heptagenidae), and $CR_{base}$ the range of $\delta^{13}C$ values occupied by invertebrates calculated as $\delta^{13}C_{max} - \delta^{13}C_{min}$ (Jackson & Britton, 2014; Olsson et al., 2009). $\delta^{13}C_{base}$ and $CR_{base}$ were calculated for each stream separately using three to six samples per site (Figures S3 and S4).

## 2.4 | Statistical analyses

We first tested for differences in trophic (i.e. TP and RO) and functional niches (i.e. the three functional axes) among populations using a multiple analysis of variance with permutations (PERMANOVA) (Anderson, 2001). Two independent models were run on trophic axes and functional axes separately; in each of these models, population identity was the fixed effect. Analyses were performed using the *adonis* function from the *vegan* package in R (Oksanen, Kindt, Legendre, & O'Hara, 2019).

We then tested the effects of the upstream–downstream gradient, forest cover, and functional axes on TP and RO using linear mixed effect models (package *lme4* in R, Bates, Maechler, Bolker, & Walker, 2014). Trophic position and RO were set as dependent variables (separately), the upstream–downstream gradient, the forest cover, the three functional axes and the resulting interactions between upstream–downstream gradient, forest cover, and functional axes were set as fixed effects. The cross-products between environmental conditions and functional axes were included because we assumed that relationships between trophic niche and functional traits could be environment-dependent. Population identity was used as a random effect, allowing us to assess variation among populations while accounting for variation within populations (Bolker et al., 2009). A model selection procedure using the Akaike information criteria (AIC) was performed and all models falling within a $\Delta AIC < 14$ were then used in a model averaging procedure (Burnham, Anderson, &

Huyvaert, 2011; Symonds & Moussalli, 2011). This allowed the mean coefficient (i.e. slope) associated with each predictor variable to be calculated, along with the sum of the Akaike weight ($\Sigma w$) of the models in which the target variable appeared. The latter indicates the probability that the predictor variable is a component of the best model (Burnham & Anderson, 2002; Symonds & Moussalli, 2011).

To identify the factors determining trophic niche size of populations (i.e. α-diversity), we calculated the trophic niche size (i.e. stable isotope niche size) by measuring the convex hull area of all individuals within each population (Layman, Arrington, Montaña, & Post, 2007). Firstly, TP and RO values were scaled between 0 and 1 (across the fish from the 12 populations) to give the same weight to both variable when computing trophic niche size (Cucherousset & Villéger, 2015). Secondly, we calculated trophic niche size on 1,000 bootstraps using a subsample of 15 individuals in each population (corresponding to 75% of all individuals in the population with the lower number of individuals analysed for stable isotopes) to avoid potential bias due to differences in sample sizes among populations. We calculated the median value and the 95% confidence interval (CI) from the 1,000 bootstraps for each population. The same approach was used to calculate the functional niche size using convex hull volume on the three functional axes. The associations between trophic niche size, functional niche size and environmental conditions were tested using bivariate linear models with trophic niche size set as a dependent variable and functional niche size or environmental conditions (upstream–downstream gradient or forest cover) as explanatory variables.

The factors determining trophic β-diversity (i.e. trophic niche differentiation) were then identified by quantifying stable isotope differentiation using the Mahalanobis distance (i.e. a distance measurement accounting for variance and covariance within populations) between centroids (mean TP and RO for each population; Schmidt, Harvey, & Vander Zanden, 2011) of each pair of populations (Pool et al., 2016). Functional β-diversity and environmental differentiation were calculated using the same approach on the three functional traits axes, and on their environmental values (i.e. upstream–downstream gradient and forest cover), respectively. Lastly, we calculated the hydrographic distance (i.e. distance along the river network) among sites to test whether populations that were geographically close displayed similar trophic and functional niches. The associations between trophic and functional β-diversity, environmental differentiation and hydrographic distance were tested using multiple regression on distance matrices (Lichstein, 2007) (package *ecodist* in R, Goslee & Urban, 2007). Trophic β-diversity was set as dependent variable and functional β-diversity, environmental differentiation and hydrographic distance were set as explanatory variables. Finally, we assessed whether functional β-diversity was associated with environmental differentiation and hydrographic distance using multiple regression on distance matrices.

## 3 | RESULTS

Trophic position and RO differed significantly among populations (pseudo-$F_{11, 293}$ = 74.762, $p$ < 0.001, Figure 2a and Figure

S5). Specifically, some populations were positioned higher in the food web (maximum TP = 3.59 ± 0.02 *SE*) than others (minimum TP = 2.55 ± 0.02 *SE*). Resource origin (from −1.53 ± 0.08 to 0.70 ± 0.06; Figure 2a) and functional traits also differed significantly among populations (pseudo-$F_{11,293}$ = 12.465, $p$ < 0.001, Figure 2b). In particular, variability on functional axis 1 suggested that adult fish from different populations displayed different size structure, and average body size (Table 1, Figures 2b and S5).

The TP of individuals was positively affected by the interaction between functional axis 2 (i.e. associated with the detection and locomotion capacities of individuals) and the upstream–downstream gradient axis ($\Sigma w$ > 0.98). Specifically, the slope of the relationship between functional axis 2 and TP was the highest in downstream areas (Figure 3b). Trophic position was also slightly negatively associated with the functional axis 1 ($\Sigma w$ = 0.79, Table 2). This suggested that larger individuals tended to display a lower TP (Figure 3a). The RO was negatively related to the functional axis 2 (i.e. the detection and locomotion capacities of individuals, Table 2, Figure 3c) and to the functional axis 1, although the direction of this latter relationship varied along the upstream–downstream gradient (Table 2, Figure S6).
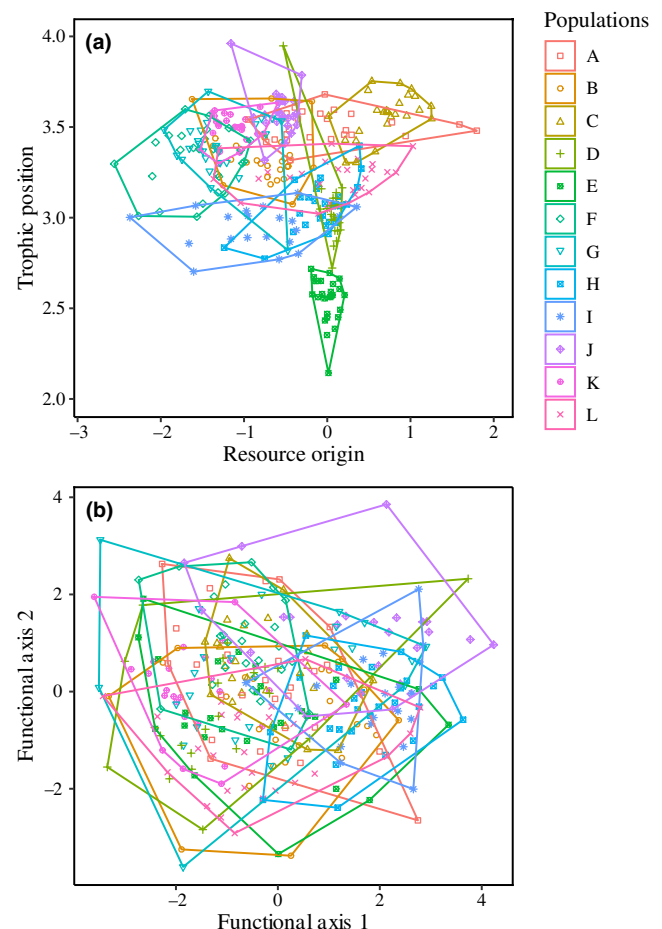


**FIGURE 2** Distribution of each individual from the 12 studied populations and the convex hull area in the (a) trophic (trophic position and resource origin) and (b) functional (PC axes 1 and 2) niche spaces [Colour figure can be viewed at wileyonlinelibrary.com]
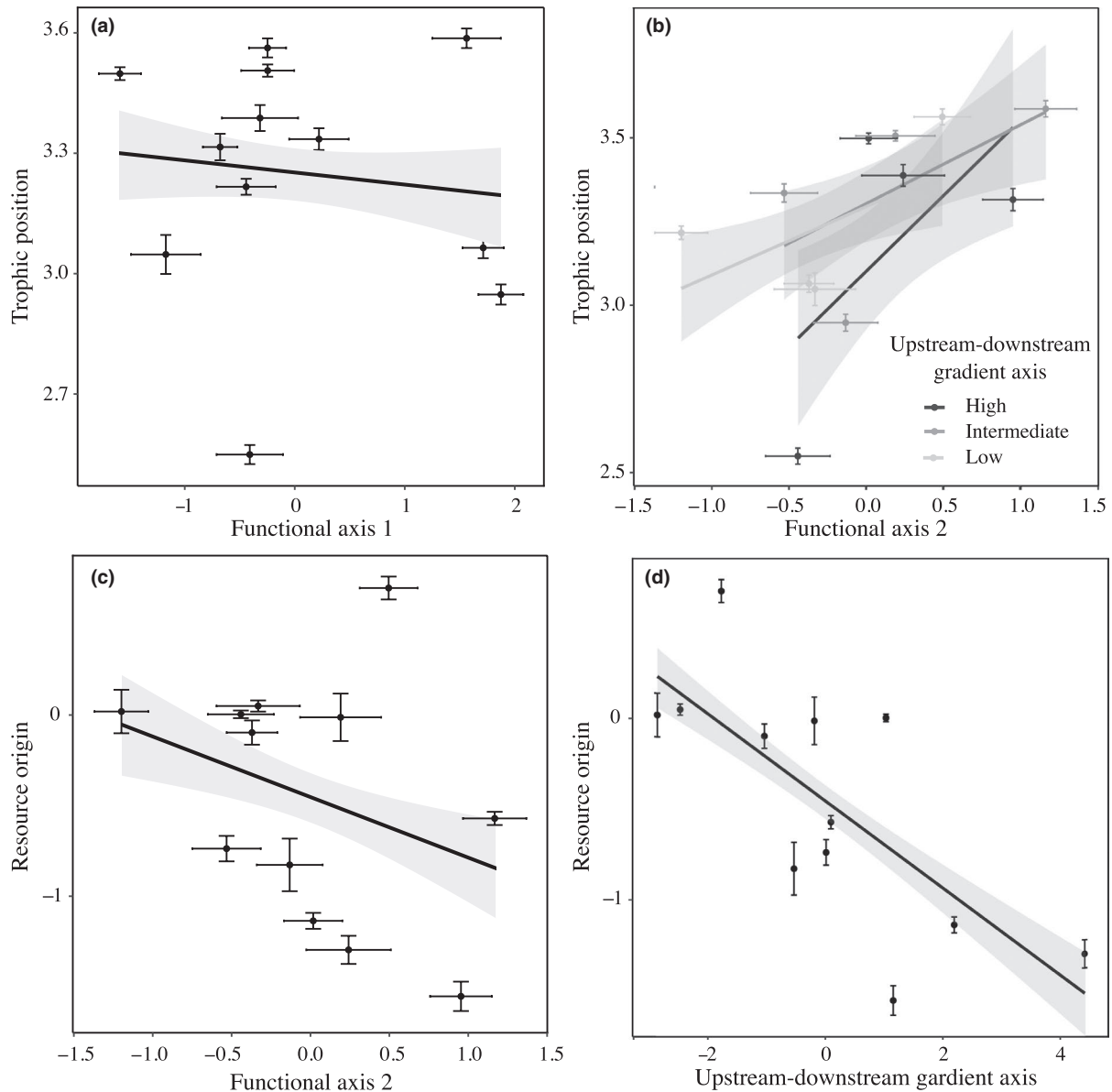
**FIGURE 3** Relationships between (a) functional axis 1 and trophic position, (b) functional axis 2 and trophic position in three categories of upstream–downstream gradient axis (high values representing downstream rivers), (c) functional axis 2 and resource origin, and (d) upstream–downstream gradient axis and resource origin. Error bars and shaded areas represent ± 1 *SE*, and lines represent the slopes of the bivariate relationship among the plotted variables

Trophic niche size varied from 0.011 (95% CI = 0.007–0.015) to 0.073 (CI = 0.051–0.088) among populations (Figures 2 and S7). A similar range of variation was observed among populations for the functional niche size (0.014 [CI = 0.008–0.021] to 0.062 [CI = 0.036–0.093], Figures 2 and S7). There was no significant relationship between trophic and functional niche sizes ($F_{1,10}$ = 0.107, $p$ = 0.749) or environmental conditions ($F_{1,10}$ = 0.062, $p$ = 0.807 and $F_{1,10}$ = 1.665, $p$ = 0.225 for upstream–downstream gradient and forest cover, respectively). In addition, there was no significant relationship between functional niche size and environmental conditions ($F_{1,10}$ = 0.652, $p$ = 0.476 and $F_{1,10}$ = 0.200, $p$ = 0.664, for upstream–downstream gradient and forest cover, respectively).

Trophic β-diversity was significantly and positively related to environmental differentiation ($R^2$ = 0.132, $p$ = 0.019, Table 3), indicating

that populations experiencing similar environmental conditions displayed more similar trophic niches (Figure 4a). In contrast, trophic β-diversity was related to neither functional β-diversity ($R^2$ < 0.001, $p$ = 0.373) nor hydrographic distance ($R^2$ = 0.108, $p$ = 0.102; Table 3, Figure 4b). Finally, functional β-diversity was related to neither hydrographic distance nor environmental differentiation (Table 3).

## 4 | DISCUSSION

The present study revealed the existence of important trophic and functional niche variability among wild populations of European minnow distributed along a strong environmental gradient. We further showed that TP and RO were linked to functional traits associated

**TABLE 2** Results of the model averaging procedure used to determine the best predictors of trophic niche (TP: trophic position, RO: resource origin)

| | TP | | RO | |
|---|---|---|---|---|
| | Σw | β ± SE | Σw | β ± SE |
| Functional axis 1 | **0.79** | **−0.011 ± 0.005** | **0.95** | **−0.019 ± 0.018** |
| Functional axis 2 | 0.99 | −0.005 ± 0.007 | **0.90** | **−0.047 ± 0.022** |
| Functional axis 3 | 0.71 | −0.006 ± 0.007 | 0.39 | −0.0002 ± 0.022 |
| Upstream–downstream | 0.99 | 0.021 ± 0.042 | **1.00** | **−0.246 ± 0.044** |
| Forest cover | 0.79 | 0.062 ± 0.066 | **0.99** | **−0.270 ± 0.069** |
| Functional axis 1 × upstream–downstream | 0.18 | 0.002 ± 0.003 | **0.85** | **−0.021 ± 0.008** |
| Functional axis 1 × forest cover | 0.20 | 0.006 ± 0.005 | 0.56 | −0.024 ± 0.0141 |
| Functional axis 2 × upstream–downstream | **0.98** | **0.013 ± 0.003** | 0.37 | −0.0131 ± 0.011 |
| Functional axis 2 × forest cover | 0.15 | 0.001 ± 0.006 | 0.24 | −0.011 ± 0.019 |
| Functional axis 3 × upstream–downstream | 0.14 | 0.002 ± 0.004 | 0.12 | 0.012 ± 0.011 |
| Functional axis 3 × forest cover | 0.55 | 0.016 ± 0.006 | 0.07 | −0.004 ± 0.019 |

Σw represents the sum of the Akaike weight (i.e. the relative importance of the variable), and β is the averaged estimate of model coefficient of variables over models in which the variables appeared. Variables with a high importance (i.e. Σw > 0.70 and β that did not overlap 0) are displayed in bold.

**TABLE 3** Results of the multiple regressions on distance matrices to determine the predictors of trophic and functional β-diversity

| | Trophic β-diversity | | | Functional β-diversity | | |
|---|---|---|---|---|---|---|
| | Estimate | $R^2$ | p | Estimate | $R^2$ | p |
| Full model | — | 0.251 | **0.038** | — | 0.082 | 0.223 |
| Functional β-diversity | 0.329 | <0.001 | 0.373 | — | — | — |
| Environmental differentiation | 0.984 | 0.132 | **0.019** | −0.276 | 0.064 | 0.096 |
| Hydrographic distance | <0.001 | 0.108 | 0.102 | <0.001 | <0.001 | 0.782 |

$R^2$ of the full model (with all variable included) and associated p-values are also provided. Significant p-values are displayed in bold.

with individual size and locomotion performance. Environmental conditions also played an important role by directly shaping trophic niche and by modulating the relationships between trophic niche and functional traits. Furthermore, the results confirmed that trophic β-diversity (among populations) was probably attributable to environmental differentiation among rivers rather than to functional differentiation among populations. Finally, the size of the trophic niche also differed among populations, although no determinant was clearly identified.

The relationship between trophic niche and functional traits has attracted a lot of investigations, and previous studies have mainly focused on the relationships between TP and individual body size (Arim, Bozinovic, & Marquet, 2007; Hildrew et al., 2007; Woodward et al., 2005). Interestingly, we found a slightly negative relationship between the functional axis 1 and TP, indicating that larger individuals may actually tend to occupy lower TPs. Smaller minnows may preferentially consume animal-based resources, which contain higher protein and lipid contents suitable for sustaining their higher metabolic rate (relative to body size). Whereas larger individuals may

consume higher proportion of periphyton and small plant fragments (Frost, 1943; Michel & Oberdorff, 1995). This result supports empirical studies on other organisms suggesting that the relationship between body size and TP is variable, both among and within species (Akin & Winemiller, 2008; Jackson et al., 2017; Vander Zanden et al., 2000). This relationship is probably context-dependent and can be mediated by multiple factors including ontogeny, energetic limitations, and environmental heterogeneity (Jackson et al., 2017; Potapov, Brose, Scheu, & Tiunov, 2019; Zhao et al., 2014). Hence, considering intraspecific variability may modify food web inferences since body size does not consistently predict TP.

Contrary to our expectations (Pool et al., 2016), the trophic niche size of populations was not related to functional niche size. Although we found variability in the trophic niche size among populations, it was associated neither with the functional niche width nor with environmental characteristics of the rivers. Primarily, the relatively low number of populations we sampled may have prevented us from detecting trends in trophic niche width among populations. Adding more populations to the analyses would increase statistical power
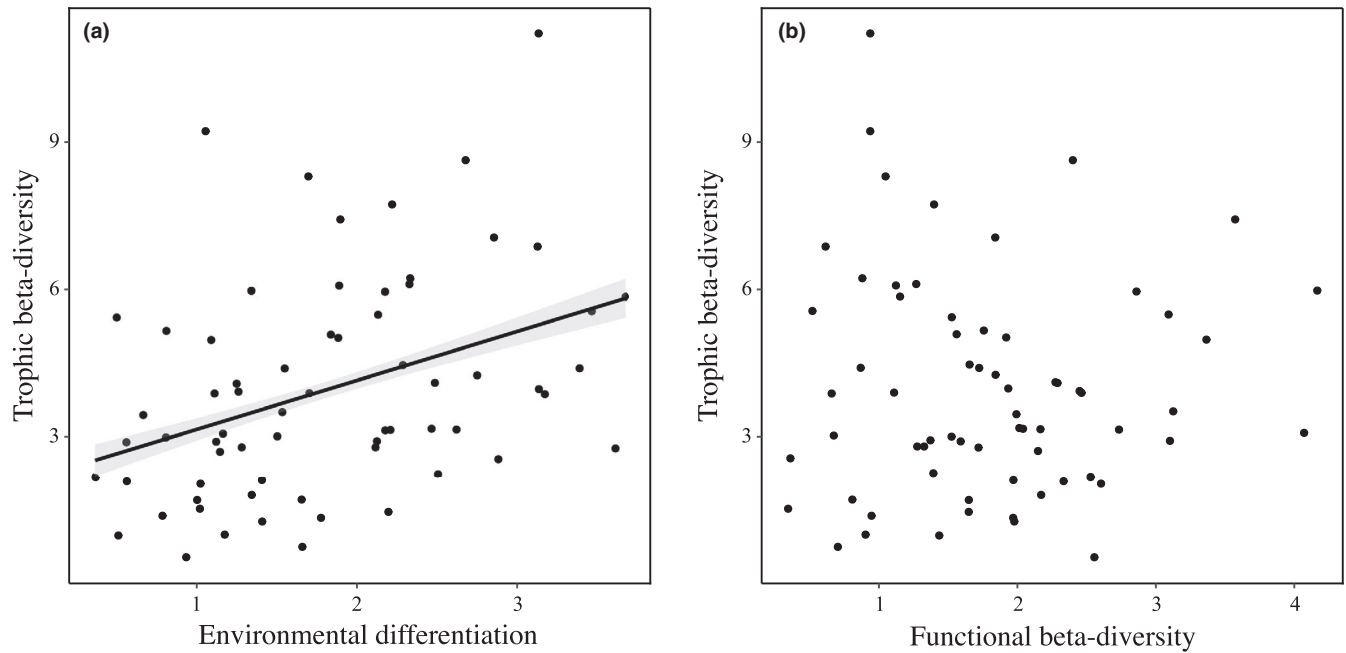
**FIGURE 4** Relationships between (a) environmental differentiation and trophic β-diversity, and between (b) functional and trophic β-diversity. Shaded area represents ± 1 *SE*

and hence the likelihood if identifying the determinants of trophic niche size. Alternatively, environmental conditions that were not quantified in the present study may have influenced trophic niche size. Specifically, invertebrate (resources) and fish (competition and predation) community composition are important drivers of the use of resources. Firstly, the diversity and abundance of available resources can modulate the number of ecological opportunities, which is expected to affect trophic niche size (Araújo & Costa-Pereira, 2013; Evangelista et al., 2014; Vrede et al., 2011). For instance, the diversity of invertebrates in rivers could have explained the trophic niche size of populations. Seasonal variation in resource availability might be an important factor shaping trophic niche size. Indeed, many freshwater invertebrates have a seasonal life cycle (e.g. Plecoptera and Ephemera), which can lead to temporal variation in individual diet (e.g. Hasegawa, Yamazaki, Ohta, & Ohkuma, 2012). Secondly, trophic niche size is also dependent on the other fish species present in the community. Biotic interactions, such as competition and predation, can constrain or induce shifts in TP and the type of resources consumed (Cucherousset et al., 2007; Zandonà et al., 2017), which could ultimately affect the trophic niche size. Therefore, further investigations are needed to understand how spatial and temporal variability in environmental conditions shapes trophic niche size in wild populations.

We found that environmental heterogeneity influenced trophic variability among populations. Firstly, environmental conditions can mediate the relationship between trophic and functional niche. Here, TP was associated with an individual's capacity to detect and capture prey, and this relationship was mediated by the environmental gradient observed from upstream to downstream. Secondly, environmental conditions can also affect trophic niche independently of functional traits. Our results showed

that, despite potential links between trophic niche and functional traits taken individually, functionally similar populations did not have a similar trophic niche when quantifying β-diversity, an approach that accounts for the overall trophic and functional niche. This confirms previous findings at the community level (Pool et al., 2016), and suggests that individuals may therefore display some degree of trophic versatility in regard to their functional traits, causing an overall mismatch between trophic and functional niches (Bellwood, Wainwright, Fulton, & Hoey, 2006). The effects of environmental conditions on trophic niche can be direct and indirect. On the one hand, direct effects can occur if abiotic conditions affect (qualitatively and quantitatively) the energetic requirements of individuals. In our system, direct effects are likely to occur because we have previously shown that temperature directly affected body size and metabolic rate of European minnows (Raffard, Cucherousset, et al., 2019). Such effects might subsequently modulate the resource selection of individuals (Rosenblatt & Schmitz, 2016). On the other hand, environmental conditions might also affect trophic niche indirectly. For instance, abiotic conditions can shape prey community structure (e.g. the occurrence or abundance of a specific prey, Altermatt, Seymour, & Martinez, 2013), modulating the resource availability for minnows, and ultimately constraining their diet. Quantifying the relative contribution of direct and indirect effects of abiotic conditions on the trophic niche of wild populations remains an important research topic that requires further investigations.

To conclude, it is important to understand intraspecific patterns in trophic niche variability as it is linked to individual fitness (Bolnick & Araújo, 2011; Cucherousset et al., 2011; Darimont, Paquet, & Reimchen, 2007) and to ecosystem functioning (Harmon et al., 2009). Our results demonstrated that predicting intraspecific trophic niche

based on functional traits and environmental characteristics is not trivial. Other phenotypic characteristics, such as behaviour or metabolism, can determine the energetic needs of individuals and ultimately their trophic niche (Gorokhova, 2018). Investigating such functional traits and their interactions with the environment should provide further insights into the determinants of intraspecific trophic niche variability.

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## AUTHOR CONTRIBUTIONS

A.R., S.B., F.S. and J.C. designed the study. A.R. and S.B. performed fieldwork, and A.R. performed trait measurement. A.R. performed statistical analyses with contributions from S.B. and J.C. A.R., F.S. and J.C. interpreted and discussed the results. A.R. and J.C. wrote the first draft of the paper. All authors corrected and improved the manuscript, and approved this version.

## DATA AVAILABILITY STATEMENT

Data are available upon personal request.

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## SUPPORTING INFORMATION

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