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LETTER

The interaction between warming and enrichment accelerates food-web simplification in freshwater systems

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Abstract

Nutrient enrichment and climate warming threaten freshwater systems. Metabolic theory and the paradox of enrichment predict that both stressors independently can lead to simpler food-webs having fewer nodes, shorter food-chains and lower connectance, but cancel each other's effects when simultaneously present. Yet, these theoretical predictions remain untested in complex natural systems. We inferred the food-web structure of 256 lakes and 373 streams from standardized fish community samplings in France. Contrary to theoretical predictions, we found that warming shortens fish food-chain length and that this effect was magnified in enriched streams and lakes. Additionally, lakes experiencing enrichment exhibit lower connectance in their fish food-webs. Our study suggests that warming and enrichment interact to magnify food-web simplification in nature, raising further concerns about the fate of freshwater systems as climate change effects will dramatically increase in the coming decades.

KEYWORDS
biochemical oxygen demand, connectance, fish, lake, maximum trophic level, stream, trophic interaction

INTRODUCTION

Freshwater ecosystems are particularly vulnerable to global change and are impacted by numerous threats such as land-use change and pollution (Danet et al., 2024; Dudgeon, 2019). Both of these threats are among the causes of nutrient enrichment (hereafter enrichment), which can harm aquatic life and water quality. The effects of climate change are expected to add to ongoing enrichment (Reid et al., 2019). To date,

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however, the complex interactions between enrichment and climate are not well-understood and pose particular challenges for conservation and restoration of freshwater ecosystems (Craig et al., 2017; Hering et al., 2015).

In nutrient-poor systems, moderate enrichment can stimulate primary production and consequently increase the relative importance of dietary specialists and the amount of energy flowing through the food-web (Fitch & Crowe, 2012; O'Gorman et al., 2012, Figure 1a(1)), but, further enrichment can theoretically destabilize consumer populations through the paradox of enrichment (where the amplitude of population fluctuations increases with nutrient input, leading to extinctions of consumers, and particularly specialist consumers, at high nutrient concentrations, Binzer et al., 2012, 2016; Rosenzweig, 1971, Figure 1a(2)). In parallel, warming is expected to disproportionately affect consumer populations, especially top-consumers with wider niche breadth, through metabolic effects. Indeed, most top-consumer species become less efficient at processing matter and energy at warmer temperatures because their metabolic losses often increase faster with temperature than their feeding rates (Bideault et al., 2021; Vucic-Pestic et al., 2011, Figure 1a(3)). In summary, high levels of enrichment can have negative impacts on higher trophic levels and specialist consumers when it leads to destabilizing fluctuations, whereas warming can negatively impact the top-consumers with wider niche breadth by reducing consumer efficiency. Both enrichment and warming are thus threatening higher trophic levels as well as specialist and generalist consumers, which can lead to a simplification of food-web structure (Nordström & Bonsdorff, 2017; O'Gorman et al., 2019). Although the direct effects of enrichment and temperature on food-web structure have been extensively studied, inconsistency in these effects has also been documented, highlighting the difficulty in finding general patterns (Mestre et al., 2022).

Warming and enrichment often occur simultaneously (Cross et al., 2015) and could hence have joint effects on food-web structure. Using dynamic simulation models, their interactive effect on food-web structure has been predicted to mitigate their negative individual effects (i.e. an antagonist effect), leading to a positive interaction between warming and enrichment on food-chain length (Binzer et al., 2012), and on food-web persistence and connectance (Figure 1b, Binzer et al., 2016). Indeed, higher enrichment might allow consumers to meet their higher energy demands in warmer environments (Tabi et al., 2019, Figure 1a(4)), while higher consumption rates due to warming might increase top-down control

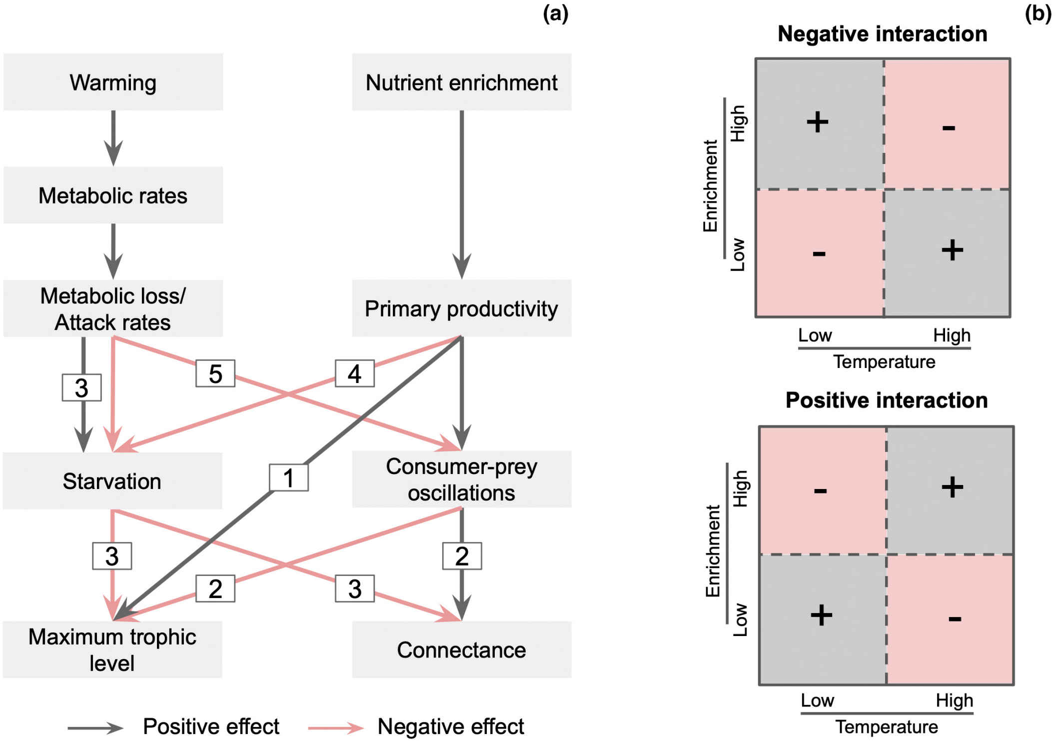

FIGURE 1 Warming and nutrient enrichment individual and interactive effects. (a) Conceptual diagram displaying the potential effects of warming and nutrient enrichment on maximum trophic level and connectance. Displayed numbers are referred to in the introduction. (b) Conceptual summary of two scenarios for effects of warming and enrichment on maximum trophic level and connectance. Grey squares with plus signs indicate a connectance and maximum trophic level above average, while red squares with negative signs indicate the opposite. Positive and negative interactions mean that the effect of warming changes with enrichment, and vice versa. Figure 5 shows that model predictions best match the negative interaction scenario.

(Kratina et al., 2012) and dampen higher oscillations and subsequent extinctions due to enrichment (Binzer et al., 2012; Sentis et al., 2017, Figure 1a(5)). Nevertheless, there is evidence that the simultaneous increase in nutrient inputs and temperatures can exacerbate eutrophication symptoms, leading to harmful algal blooms and oxygen depletion, which can disrupt the food-web structure (Moss et al., 2011; Rodgers, 2021; Figure 1b). The interactive effect of temperature and enrichment on food-web structure, as suggested by theoretical grounds, may thus diverge from empirical expectations. Therefore, it is important to assess whether these predictions, stemming from simplified energetic and demographic models, accurately forecast the intricate effects of warming and enrichment in natural settings.

Here, we examine the individual direct and interactive effects of temperature and enrichment on two key features of food-web structure previously assessed in theoretical models: food-chain length (Binzer et al., 2012)—a measure of the breadth of the vertical dimension of food-webs, and connectance (Binzer et al., 2016)—a measure of the level of generalism in food-webs. We used 13 years of freshwater fish community data at 629 sites in France to infer 3188 size-structured local food-webs. We inferred food-web structure based on fish taxonomy and body size to account for ontogenetic diet shifts, incorporating data regarding fish trophic ecology with seven basal resources (e.g. phytoplankton) from the literature alongside an allometric niche model (Bonnaffé et al., 2021). Two different types of freshwater ecosystems, lakes and streams, were included to better characterize how freshwater communities as a whole respond to environmental perturbations. Although lentic (lake) and lotic (stream) ecosystems have distinct characteristics (i.e. physical, geochemical and biological), we hypothesised that their food-web properties would be affected similarly by temperature and enrichment. We estimated individual direct effects of temperature and enrichment as well as their potential interactive effects on connectance and maximum trophic level and examined the relative strength of direct and interactive effects using a hierarchical Bayesian model with a spatial correlation matrix. Although the effects of warming and enrichment on the structure of food-webs are complex, we expected a decrease in the maximum trophic level and connectance in warmer and more enriched freshwater ecosystems as reported in previous empirical studies (Nordström & Bonsdorff, 2017; O'Gorman et al., 2019, 2023). As theoretical studies suggested that concomitant warming and enrichment should result in the cancellation of their individual negative effects on higher trophic level (Binzer et al., 2012, 2016), we expected a positive interaction between temperature and enrichment on food-web structure. However, empirical observations from experiments or from a few natural systems contrast with these theoretical predictions and suggest that the interactive effects of temperature and enrichment could be even more harmful to freshwater biodiversity than their individual effects (e.g. Kratina et al., 2012).

METHODS

Community data

Fish communities were surveyed as part of monitoring programmes related to the Water Framework Directive through standardized and comparable methods (Birk et al., 2012). Fish communities have been repeatedly sampled in France (across the seven different hydrographic basins (IGN/OFB, 2020)) from 2005 to 2017 by the French National Agency for Water and Aquatic Environments (sampling protocols are detailed in Appendix A).

Our final data set contains a total of 256 lake and 373 stream sites (Appendix A, Figure S1), with 3188 sampling events (2791 for streams and 397 for lakes). Most lake food-webs were sampled only once (median = 1 sampling event), while streams were sampled on multiple occasions (median = 7 sampling events). As food-web reconstruction was both taxonomy- and body size-based, we used taxonomic and body size information from captured fish during all sampling events. The captured fish were identified to the species level and individually measured, unless they were too numerous. In this case, body size classes were formed with individuals of the same species, and some individuals within each class were measured. The body size of individuals left unmeasured was estimated based on the assumption that body size within a class follows a normal distribution (for more details, see Danet et al., 2021).

Food-web inference and structure

Metaweb and defining nodes

We applied a metaweb method to obtain the composition and structure of local food-webs of fish communities. Our metaweb (a compilation of potential feeding interactions between all species found in our dataset) takes into account some intraspecific diet variation. Trophic interactions derived from the literature and an allometric model (see Section 'Defining links') were determined by both species identity and body size to account for ontogenetic diet shifts (i.e. changes in diet with life stage and body size). The method is extensively described in Bonnaffé et al. (2021) and Danet et al. (2021). To define metaweb nodes, we divided each fish species into nine body size classes evenly distributed in the range of their measured body size. Each body size class within a given species constitutes a 'trophic species', assuming that conspecifics of the same body size class share similar trophic interactions because trophic interactions are largely determined by predator–prey body size ratio in freshwater ecosystems (Brose et al., 2006). In addition to the fish trophic species, we added to the metaweb seven 'resource' nodes following Bonnaffé et al. (2021): detritus, biofilm, phytoplankton, zooplankton, macrophytes, phytobenthos, and zoobenthos, assuming that they were present at all sampling sites. The resulting metaweb contained 52 fish species divided into nine size classes and seven resource nodes, summing up to 475 nodes (i.e. $52 \times 9 + 7$).

Defining links

To establish fish–resource interactions within the metaweb, we referred to published information on fish diet across ontogeny (Bonnaffé et al., 2021; Danet et al., 2021). If literature indicated a fish–resource link for a specific ontogenetic stage, we considered it present—as in Bonnaffé et al. (2021), we used two or three size-dependent ontogenetic stages for each species. For fish species with piscivorous ontogenetic stages, we inferred fish-fish trophic links based on predator–prey body size ratios. A predation window for piscivores was set from 3% to 45% of the midpoint of the piscivore's body size range, establishing a trophic link between the piscivore and all the preys whose body size range midpoint falls within the piscivore's predation window.

Local food-webs and topology

For each sampling event, we inferred the food-web structure by extracting the trophic species and resources as well as their trophic links from the metaweb. To characterize the structure of each food-web, we computed two complementary network properties: connectance and maximum trophic level. Both metrics have been shown to capture most of the variation in food-web structure (Leclerc et al., 2023) and to be sensitive to temperature (Gibert, 2019; O'Gorman et al., 2019) and enrichment (Nordström & Bonsdorff, 2017; O'Gorman et al., 2012). Connectance is the proportion of realized interactions out of the maximum number of possible interactions (excluding cannibalism). Maximum trophic level is the highest trophic level occupied by a consumer in the food-web. The trophic level of a consumer-node is calculated as one plus the weighted average of the trophic levels of its prey-nodes (the trophic level of basal species being one). The two metrics were calculated using the 'NetIndices' R package (Kones et al., 2009).

Environmental variables

Water temperature and biological oxygen demand (BOD) were sampled within streams and lakes to represent warming and enrichment variables. BOD measures the loss of dissolved oxygen (mg/L) due to the degradation of organic matter by the ambient microbial community, and is commonly used to assess organic matter content in continental and coastal aquatic environments (Lv et al., 2022; Sepp et al., 2018). We found positive correlations between BOD, total phosphorus and total nitrogen in both streams and lakes (Appendix A, Figure S2), confirming that organic enrichment often results from inorganic enrichment, which can lead to eutrophication (Fitch & Crowe, 2012; O'Gorman et al., 2012). We thus used BOD as a single proxy variable for enrichment.

For the lakes, we computed the mean annual BOD from four measurements taken during the year over the euphotic zone at the maximum lake depth. However, some yearly BOD measurements were missing ($n = 288$, see Appendix B.1 for further details on imputation). We computed the mean annual water temperature using daily data from an epilimnion temperature model (Prats & Danis, 2019; Sharaf et al., 2023).

For the streams, we retrieved monthly water temperatures and BOD from the naïades database (https://naiades.eaufrance.fr/). We interpolated the values of these two variables using spatial stream network models (Hoef et al., 2014; Isaak et al., 2014) because environmental parameter assessments were conducted at locations different from fish community samplings (details on interpolation in Danet et al., 2021). We then computed annual average values for each stream.

At the end of the process, each fish sampling event that occurred between 2005 and 2017 was characterized by its mean annual water temperature and BOD.

Statistical analyses

We modelled the interactive effects of temperature and BOD on maximum trophic level and connectance of stream and lake food-webs using Bayesian mixed effect models. We chose a Bayesian framework as it helps with (1) dealing with missing information by treating 288 missing observations out of 3188 BOD measurements as random variables, and (2) accounting for potential spatial and temporal pseudo-replication in the data, which could arise from spatial correlations between nearby sites, and temporal correlations within sites, by introducing a custom variance–covariance matrix.

Linear model

We assumed that observations of connectance and maximum trophic level, $\boldsymbol{Y}_i$, were normally distributed with mean $\widehat{\boldsymbol{Y}}_i$, obtained from a linear model, and variance–covariance matrix $\boldsymbol{\Sigma}$, accounting for spatial and temporal correlations between neighbouring sites,

$$\boldsymbol{Y} \sim N\left(\widehat{\boldsymbol{Y}}, \boldsymbol{\Sigma}\right),$$

$$\begin{aligned}\hat{\boldsymbol{Y}}_i = {} & \theta_0 + \theta_1 \boldsymbol{type}_i + \theta_2 \boldsymbol{temp}_i + \theta_3 \boldsymbol{temp}_i^2 + \theta_4 (\boldsymbol{type}_i * \boldsymbol{temp}_i) \\ & + \theta_5 \boldsymbol{BOD}_i + \theta_6 \boldsymbol{BOD}_i^2 + \theta_7 (\boldsymbol{type}_i * \boldsymbol{BOD}_i) \\ & + \theta_8 (\boldsymbol{temp}_i * \boldsymbol{BOD}_i) + \theta_9 (\boldsymbol{type}_i * \boldsymbol{temp}_i * \boldsymbol{BOD}_i) \\ & + \theta_{10} \boldsymbol{rich}_i + \theta_{11} \boldsymbol{year}_i,\end{aligned} \tag{1}$$

where $\hat{\boldsymbol{Y}}_i$ is the predicted response (i.e. either connectance or maximum trophic level) for the i$^{\text{th}}$ observation, $\boldsymbol{\theta}_0$ is the intercept, $\boldsymbol{\theta}_{1-11}$ are the mean standardized coefficients, $\boldsymbol{temp}_i$ is the temperature, $\boldsymbol{type}_i$ is the ecosystem type (i.e. 0 for a stream and 1 for a lake), $\boldsymbol{BOD}_i$ is the biological oxygen demand, $\boldsymbol{rich}_i$ is the number of trophic (fish) species in the community, $\boldsymbol{year}_i$ is the year of the sampling event, implemented as a continuous variable to account for temporal trends. We included quadratic effects of temperature and BOD ($\boldsymbol{temp}_i^2$ and $\boldsymbol{BOD}_i^2$, Equation 1), to account for potential concave or convex relationships (as suggested by Bonnaffé et al., 2021; Leclerc et al., 2023). We included two-way and three-way interactions (indicated by an asterisk, Equation 1) to account for potential interactive effects of temperature, BOD, and ecosystem type. Finally, including effects of trophic species richness (Dunne, 2006; Shibasaki & Terui, 2024) and year allowed us to control for known external sources of change in the response variables. All variables were standardized with respect to their mean and standard deviation to enable the comparison of their respective effects. Estimates reported come from the full models to control for potential confounding factors, whether significant or not, and due to prohibitive fitting times (>1 week) of the model, which prevented term-by-term model simplification.

Bayesian estimation of the parameters

We computed the posterior density distribution of the parameters given the observations by defining a hierarchical Bayesian model. The only difference with a simple Bayesian model is the addition of a likelihood term for missing observation:

$$\begin{aligned} p(\boldsymbol{\theta}, \boldsymbol{Xmis}, \boldsymbol{\sigma}, \boldsymbol{\alpha}, \boldsymbol{\beta}, \boldsymbol{\mu}, \boldsymbol{\nu} \mid \boldsymbol{Y}) \propto {} & p(\boldsymbol{Y} \mid \hat{\boldsymbol{Y}}(\boldsymbol{\theta}, \boldsymbol{Xmis}), \boldsymbol{\Sigma}(\boldsymbol{\sigma}, \boldsymbol{\alpha}, \boldsymbol{\beta})) \\ & \times p(\boldsymbol{Xmis} \mid \boldsymbol{\mu}\boldsymbol{\nu}) \times p(\boldsymbol{\theta}) p(\boldsymbol{\sigma}) p(\boldsymbol{\alpha}) p(\boldsymbol{\beta}) p(\boldsymbol{\mu}) p(\boldsymbol{\nu}), \end{aligned} \tag{2}$$

where $\boldsymbol{p}(.)$ stands for density distributions, $\hat{\boldsymbol{Y}}(\boldsymbol{\theta}, \boldsymbol{Xmis})$ is the linear model (Equation 1) which depends on the mean standardized coefficients, $\boldsymbol{\theta}$ (e.g. effects of temperature, BOD), and vector of missing BOD values, $\boldsymbol{Xmis}$. The variance–covariance matrix, $\boldsymbol{\Sigma}(\boldsymbol{\sigma}, \boldsymbol{\alpha}, \boldsymbol{\beta})$, depends on the basin-specific standard deviation vector, $\boldsymbol{\sigma}$, and spatial correlation parameters, (intercept $\boldsymbol{\alpha}$ and decrease rate $\boldsymbol{\beta}$). This ensured that spatial correlations across sites and temporal correlations within sites (i.e. pseudo-replication) were appropriately captured by the model (see Appendix B.1). We chose uninformative priors for all parameters except for the mean and variance of missing BOD values ($\boldsymbol{\mu}$, $\boldsymbol{\nu}$), which were informed by observed BOD values (the results were robust to a change in BOD priors, Appendix B.4). We estimated the posterior density of the model parameters using single-chain differential-evolution Monte-Carlo, which is particularly suitable for computationally intensive sampling tasks (Bonnaffé, 2022; ter Braak, 2006; ter Braak & Vrugt, 2008). We computed the r^2 values following $\boldsymbol{r}^2 = 1 - \frac{\text{RSSq}}{\text{TSSq}}$ where RSSq is the residual sum of squares and TSSq is the total sum of squares. The residuals were obtained by subtracting the values of connectance or maximum trophic level predicted by the models to the observed values. We ensured normality of residuals by looking at histograms and quantiles of the residual distributions. We also verified that the distribution of missing BOD is similar to observed BOD by visual inspection (Appendix B, Figures S5 and S20). The details of the estimation of the spatial correlation between sites, the handling of missing data, the specification of the priors, and the implementation of the chains, are presented in Appendix B.1.

RESULTS

Topology of food-webs

The 3188 food-webs (397 from lakes and 2791 from streams) contained 1 to 25 fish species (mean (SD) = 8 (5)) and a number of nodes (i.e. the sum of fish trophic species and resources) ranging from 8 to 92 (mean (SD) = 32 (14), Table 1). Maximum trophic level between sampling sites varied between 2.9 and 4.5 (mean (SD) = 3.8 (0.2)) indicating that food-webs are structured vertically and could reach high trophic levels sustaining top predators. Connectance ranged from 0.05 to 0.24 (mean (SD) = 0.15 (0.03)), suggesting that the proportion of realized interactions within food-webs is low compared with the maximum number of possible interactions. Overall, there was a difference in maximum trophic level and connectance between lakes and streams. Lake food-webs had on average a higher maximum trophic level (Mean standardized coefficient ($\boldsymbol{\theta}_1$) [95% credible interval] = 0.80 [0.66, 0.94]; Figure 2a; Table 1) and a lower connectance ($\boldsymbol{\theta}_1$ = −0.50 [−0.64, −0.36]; Figure 2b; Table 1) than stream food-webs.

Interactive effects of temperature and BOD on maximum trophic level

We found a quadratic negative effect of temperature (Mean standardized coefficient ($\boldsymbol{\theta}_3$) [95% CI] = −0.02 [−0.03, −0.01]; Figure 2a) indicating that both cold and warm ends of the temperature range are associated with a lower maximum trophic level than in the middle of the gradient. Apart from this individual effect of temperature, we found a negative interaction between temperature and BOD on maximum trophic level in both lakes

TABLE 1 Summary of food-web and environmental properties for the sampled lakes and streams.

		Lake	Stream	All
Food-web properties				
Fish species richness	Mean (SD)	9 (2)	8 (5)	8 (5)
	Range	1–18	1–25	1–25
Number of nodes	Mean (SD)	36 (9)	32 (15)	32 (14)
	Range	10–64	8–92	8–92
Connectance	Mean (SD)	0.13 (0.02)	0.16 (0.03)	0.15 (0.03)
	Range	0.06–0.20	0.05–0.24	0.05–0.24
Maximum trophic level	Mean (SD)	4.0 (0.1)	3.8 (0.2)	3.8 (0.2)
	Range	3.2–4.5	2.9–4.4	2.9–4.5
Environmental properties				
Temperature	Mean (SD)	13.9 (1.9)	11.6 (1.8)	11.9 (1.9)
	Range	6.0–18.6	1.8–17.8	1.8–18.6
BOD	Mean (SD)	1.5 (0.9)	1.7 (0.6)	1.7 (0.6)
	Range	0.5–5.5	0.5–4.9	0.5–5.5
Total number of sites		256	373	629
Total number of fish sampling events		397	2791	3188

Note: The range indicates the minimum and maximum of the variable.

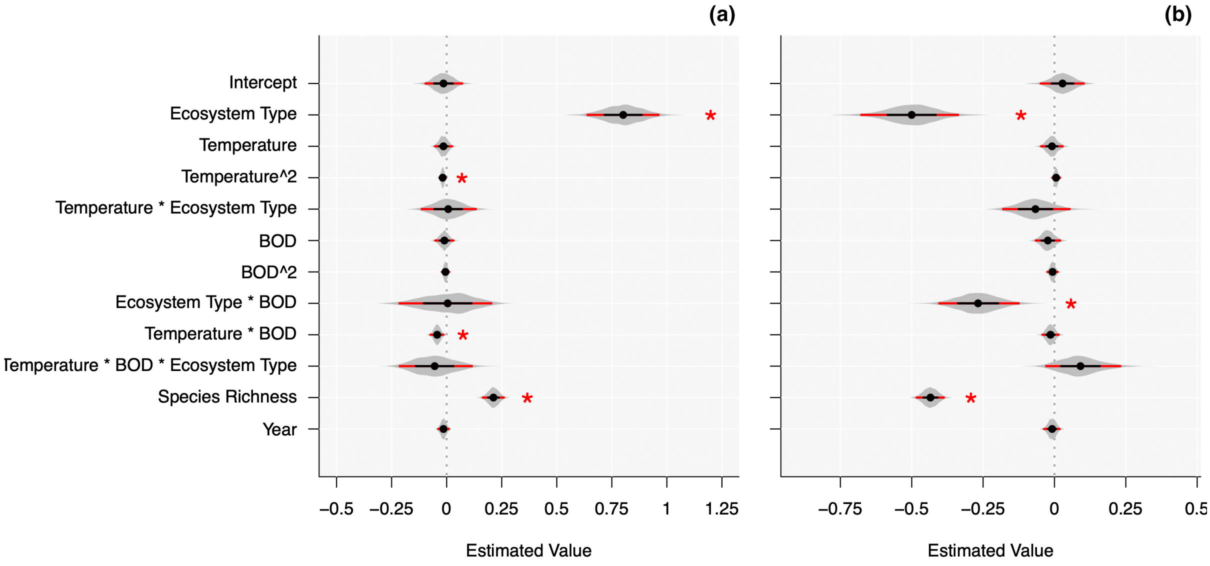

FIGURE 2 Credible interval of standardized estimated model parameters (θ) on maximum trophic level (a) and connectance (b). Credible intervals (CIs) correspond to the 5%–95% quantiles of the distributions of estimates, obtained by DEMC sampling of the posterior distribution (see Section 'Methods'). Significant effects are indicated by a black asterisk and correspond to effects of variables with a 95% CI not overlapping with 0. The variable *Ecosystem Type* refers to the type of ecosystem (i.e. stream or lake), *Species Richness* corresponds to the trophic species richness, *Year* is the effect of the sampling year, *Temperature* × *Ecosystem Type* denotes the interaction between temperature and ecosystem type, *Temperature^2* corresponds to a quadratic effect of temperature, *Temperature* × *BOD* × *Ecosystem Type* is the three-way interaction between temperature, enrichment, and ecosystem type. The shaded area displays the distribution of parameter estimates, the solid black line represents the standard deviation around the mean, indicated by a black dot, while the red solid line indicates the bounds of the 95% CIs.

and streams ($\boldsymbol{\theta}_8 = -0.04$ [−0.07, −0.02]; Figure 2a), implying that temperature and BOD did not dampen their individual negative effects on maximum trophic level (Figures 2a, 3 and 5). In both ecosystems, temperature increased the maximum trophic level at low BOD levels (Figure 3a,c, blue line), but reduced it at higher BOD levels (Figure 3a,c, green line). BOD increased the maximum trophic level at low temperature (Figure 3b,d, blue line), while reducing it at high temperature (Figure 3b,d, green line), in both lakes and streams. Overall, food-chains were shorter at warmer and more enriched sites and this effect did not differ between lakes and streams. We also found a positive effect of trophic species richness on maximum trophic level ($\boldsymbol{\theta}_{10} = 0.21$ [0.17, 0.25]; Figure 2a),

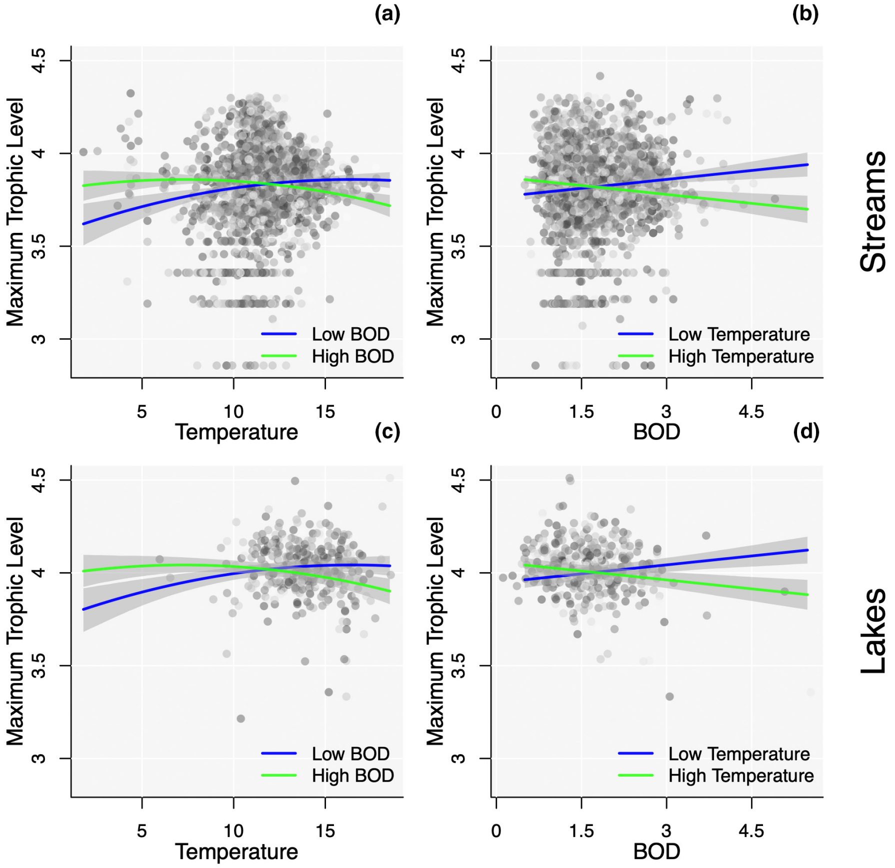

FIGURE 3 Interactive effects of temperature and biological oxygen demand (BOD) on maximum trophic level in stream food-webs (a & b) and lake food-webs (c & d). Lines display the predictions from the linear models, while the shaded areas correspond to the 95% credible interval of model predictions. Low (in blue) and high (in green) levels of BOD and temperatures correspond to the 5th and 95th quantiles of the observed distributions, ranging from 8°C and 16°C, and 0.5 and 2.96 mg/L, respectively. Dots are randomly assigned a transparency value for visual comfort. The r^2 of model predictions is $r^2=0.17$.

but no significant temporal trend ($\boldsymbol{\theta}_{11}$ = −0.01 [−0.04, 0.01]; Figure 2a).

Noninteractive effects of temperature and BOD on connectance

Connectance was not influenced by the individual effect of temperature (Mean standardized coefficient ($\boldsymbol{\theta}_2$) [95% CI] = −0.01 [−0.04, 0.02]), nor by the interactive effects of temperature and BOD ($\boldsymbol{\theta}_8$ = −0.01 [−0.04, 0.01]), regardless of ecosystem type (Figures 2b and 4). We only found significant effects of BOD on connectance that were dependent on ecosystem type as connectance decreased in more enriched lakes, but not in more enriched streams ($\boldsymbol{\theta}_7$ = −0.27 [−0.38, −0.15]; Figures 2b and 4b,d). We did not find a significant temporal trend ($\boldsymbol{\theta}_{11}$ = −0.01 [−0.03, 0.01]; Figure 2b) on connectance. However, we found a negative effect of trophic species richness ($\boldsymbol{\theta}_{10}$ = −0.43 [−0.47, −0.39]; Figure 2b).

We found that the negative interactive effects of temperature and enrichment were four times stronger than their direct effects on maximum trophic level (standardized coefficients, Appendix B, Table S1: temperature = −0.01, BOD = −0.01 versus temperature × BOD = −0.04). For connectance, the indirect negative effects were stronger than the direct effect of temperature but lower than the one of BOD (standardized coefficients, Appendix B, Table S2: temperature = −0.009, BOD = −0.023, versus temperature × BOD = −0.014).

DISCUSSION

One of the key questions about the effects of temperature increase and enrichment is about their combined effects on food-web structure, especially in natural settings. To answer this question, we assessed the individual and interactive effects of temperature and enrichment on the structure of freshwater food-webs. We found a quadratic negative effect of warmer temperature on maximum trophic level in both ecosystem types as well as a negative effect of enrichment on connectance only in lakes. Furthermore, in contrast with previous studies, we found evidence that higher temperature and enrichment interacted to further impact food-web structure.

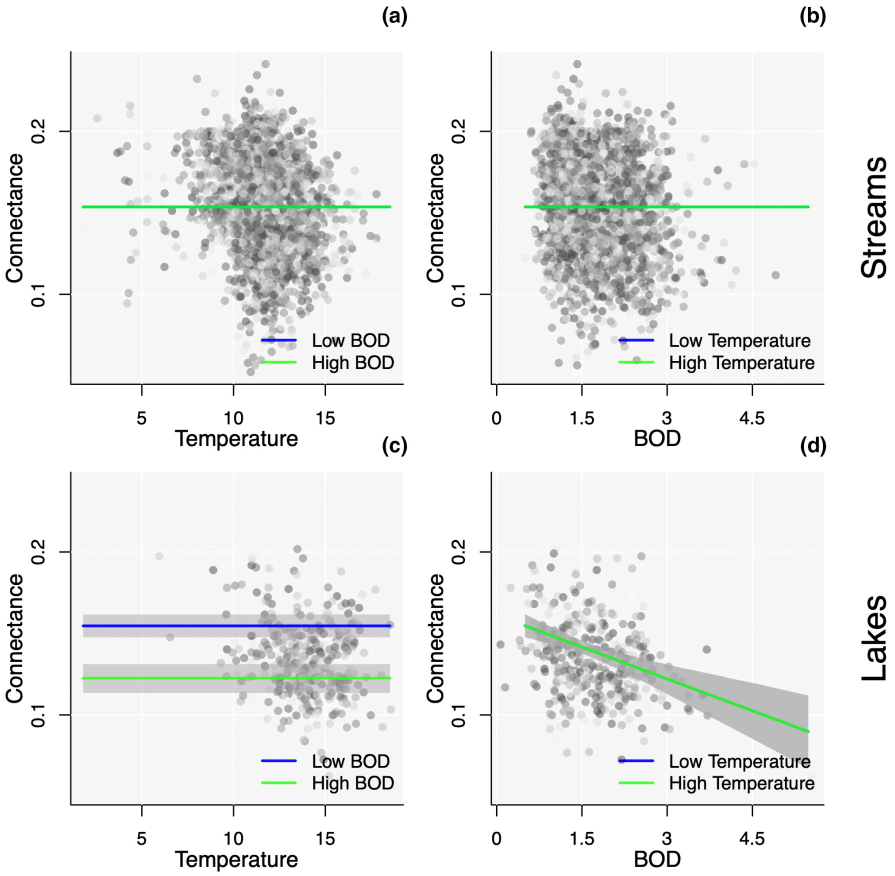

FIGURE 4 Interactive effects of temperature and biological oxygen demand (BOD) on connectance in stream food-webs (a & b) and lake food-webs (c & d). Lines display the predictions from the linear models, while the shaded areas correspond to the 95% credible interval of model predictions. Low (in blue) and high (in green) levels of BOD and temperatures correspond to the 5th and 95th quantiles of the observed distributions, ranging from 8°C and 16°C, and 0.5 and 2.96 mg/L, respectively. Dots are randomly assigned a transparency value for visual comfort. In panels (a), (b), and (d) the blue and green lines are overlaid. The r^2 of model predictions is $r^2 = 0.31$.

Effect of ecosystem type on food-web structure

Overall, we did not find any difference in the effects of enrichment, temperature, and their interaction across lakes and streams on maximum trophic level and connectance (apart from a negative effect of enrichment on connectance in lakes but not in streams). This suggests that warming and enrichment have generally consistent effects on food-web structure across both ecosystem types. Yet, we found that lakes display a higher maximum trophic level and lower connectance than streams, in line with previous studies (Canning & Death, 2019; Vander Zanden & Fetzer, 2007). Ecosystems experiencing a higher disturbance regime and environmental fluctuations, such as streams, are predicted to be less able to maintain long food-chains (Pimm & Kitching, 1987; Post, 2002). Differences in ecosystem size and productivity between streams and lakes might also explain the shorter food-chains found in streams, but it remains challenging to compare the ecosystem size of streams and lakes (i.e. open vs closed systems, Vander Zanden & Fetzer, 2007).

Higher connectance in streams than in lakes indicates that stream food-webs tend to contain more generalist trophic species (i.e. species with a large number of trophic links), which is in accordance with previous studies suggesting that generalist predators are more adapted to disturbance regimes (Mihuc & Minshall, 1995) and that disturbances affecting generalist predators have less impact on food-webs (Montoya et al., 2009). Altogether, our results suggest that differences in food-web structure between streams and lakes might be underpinned by differences in disturbance regimes (Post, 2002), which leads to streams having shorter food-chains but more generalist species than lakes.

Warmer temperatures but not enrichment were associated with shorter food-chains

We found a quadratic negative effect of temperature on the maximum trophic level (controlling for species richness and enrichment level), with both cold and warm ends of the temperature range associated with a lower maximum trophic level than in the middle of the gradient. Previous studies reported that species at higher trophic level were more sensitive to warming (Voigt et al., 2003) because they experienced a greater increase in metabolic activity with temperature than species at lower trophic levels (Binzer et al., 2012, 2016; Petchey et al., 2010; Sentis et al., 2017; Uszko et al., 2017). Consequently, top-consumers were predicted to suffer from starvation to the point where their energetic demands exceeded their energetic supply (Rall et al., 2010; Vucic-Pestic et al., 2011). At low temperature, top-consumers are also predicted to suffer from starvation resulting from a lower ingestion rate, due to lower attack rates and higher handling time at the lower extreme of the temperature gradient (Englund et al., 2011; Uszko et al., 2017).

In contrast, we did not find any individual effect of enrichment (linear or quadratic term, controlling for temperature values) on maximum trophic level. This might be due to the antagonistic effects of enrichment on food-web structure (Figure 1a (1) and (2)). On the one hand, enrichment can increase productivity and thus energy input to the system which in turn may support higher trophic levels (Lindeman, 1942). Further enrichment can also lead to high oscillations of primary producers, which in turn may destabilize consumer dynamics and can lead to a loss of higher trophic levels (‘paradox of enrichment’, Rosenzweig, 1971). These two effects might cancel each other along the enrichment gradient, which could explain the absence of an overall effect of enrichment in the studied food-webs.

We did not find evidence of any individual effect of temperature and enrichment on connectance, except for a negative effect of enrichment on connectance in lakes. This contrasts with theoretical studies that predict that warming could lead to a decrease in connectance (Binzer et al., 2016; O'Gorman et al., 2019). Because generalist consumers have weaker, albeit more, feeding links than specialists, metabolic theory predicts that generalists would be more vulnerable to starvation induced by the increase in metabolic demand with temperature, due to lower energy income from their weaker interactions (Binzer et al., 2016). However, foraging theory also predicts that connectance of systems characterized by a large degree of variation in body size, such as in aquatic food-webs, can be less sensitive to fluctuations in temperature because consumers should be able to switch prey (Petchey et al., 2010). In turn, enrichment is predicted to result in higher connectance as specialist consumers are more impacted by the paradox of enrichment (Rall et al., 2008). The absence of an effect of temperature and enrichment on connectance in streams could also come from limitations in our data. We focussed only on fish food-webs where resources (e.g. zooplankton and phytoplankton) are characterized by unique and always-present nodes. This could hence have reduced our capacity to discriminate the generalism of the food-webs and so to detect an overall effect of temperature and enrichment on food-web connectance.

Interactive effects of temperature and enrichment

We found that temperature and enrichment had a negative interactive effect on maximum trophic level, implying that warmer and more enriched freshwaters tended to have shorter food-chains than expected from the individual negative effects of temperature and enrichment. This result contrasts with previous findings from theoretical and experimental studies reporting that simultaneous effects of warming and enrichment should cancel out each other on top-consumer survival, food-chain length (Binzer et al., 2012), as well as on community persistence, and on biomass and its stability (Binzer et al., 2016; Tabi et al., 2019). Theory suggests that the increase in attack rates induced by warming should prevent the strong biomass fluctuations of consumers resulting from the paradox of enrichment (Rosenzweig, 1971), while enrichment should prevent warming-induced starvation of higher consumers (Tabi et al., 2019). If this was the case, both warming and enrichment should interactively support higher trophic level consumers and thus promote consumer species richness. Therefore, our results suggest that more complex mechanisms may be at play in natural settings.

The complex effects of temperature and enrichment might be explained by taking into account alternative constraints such as oxygen, food stoichiometry, or nonmonotonic relationships between metabolic rates and temperature. The depletion of oxygen caused by enrichment and warming (Jane et al., 2021; Rabalais et al., 2002), for which we found support in our data (Appendix C), can dampen the increase in metabolic activity with temperature. Larger bodied organisms are more susceptible to hypoxia (Rubalcaba et al., 2020), which should limit the potential of warming to dampen the destabilizing effect of enrichment on consumers. Enrichment can also change food stoichiometry, by decreasing food quality (i.e. higher C:P-ratios), and hence lead to food ‘quality starvation’ (Hessen, 2013; Hood et al., 2005), which in turn could enhance the starvation of consumers at warmer temperatures (Sentis et al., 2022). Finally, the hypothesis that metabolic and mortality rates of consumers scale monotonically with temperature does not hold over a large temperature range (Knies & Kingsolver, 2010), as primary producer growth rates and carrying capacity often follow hump-shaped or no relationship with temperature (Synodinos et al., 2021; Uszko et al., 2017). As the shape of those relationships are critical to determine not only the outcome of warming on food-web

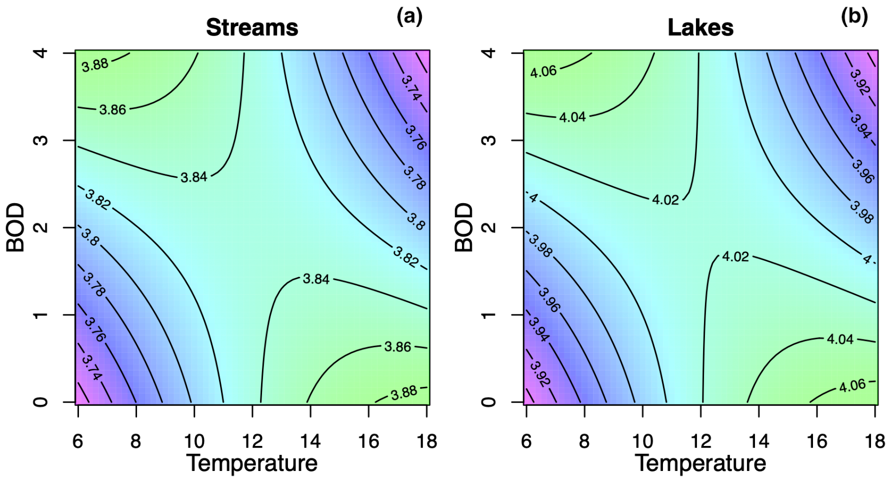

FIGURE 5 Estimated interactive effects of biological oxygen demand (BOD) and temperature on maximum trophic level in streams (a) and lakes (b). The model predicts that the maximum trophic level is maximized at either low temperature and high BOD, or high temperature and low BOD, and minimized when temperature and BOD are simultaneously low, or high, both in streams (a) and lakes (b). The contour lines represent predicted values of maximum trophic levels. No interactive effects were found for connectance so only maximum trophic level is presented in this figure. Predictions are obtained from the same model that generated predictions in Figure 3. Figure 1b provides a comparison point with our different initial hypotheses.

structure (Uszko et al., 2017) but also the potential for warming to dampen the paradox of enrichment, our results suggest that previous studies have thus likely overestimated the positive effects of simultaneous warming and enrichment on food-web dynamics. A complementary hypothesis to explain our results could be that the direct negative effects of temperature and enrichment outweigh the interactive effects. However, we found that interactive effects of temperature and enrichment on maximum trophic level were four times stronger than their individual counterparts, while the interactive effects on connectance were twice stronger than the single effect of enrichment. Altogether, this adds to the mounting body of evidence highlighting the importance of assessing the simultaneous effects of multiple stressors and their interactions (Simmons et al., 2021; van Moorsel et al., 2023).

We report a change in food-chain length along the temperature and enrichment ranges of about 0.2 (Figure 5), that is ~10%–13% compared to the whole range of food-chain length previously reported in streams and lakes (respective range: 1.5 and 2, Vander Zanden & Fetzer, 2007; Post et al., 2000). We also found that species richness was a strong predictor of maximum trophic level and connectance (Dunne, 2006; Shibasaki & Terui, 2024), such that the variations that we report should be understood as being the effects of temperature and enrichment on maximum trophic level independently from variation in species richness. We then expect more variations if the effect of species richness was not accounted for. Furthermore, we used a space-for-time approach, where changes in food-web structure along the spatial gradients of temperature and nutrient are likely accompanied by changes in species composition resulting from local adaptation and biogeographical history. In a scenario where climate change and nutrient enrichment is much faster than local adaptation or community turnover, we then expect that local changes in temperature and enrichment (i.e. at the site level) might lead to more dramatic changes in food-web structure than reported in the present study.

PERSPECTIVES AND CONCLUSION

Our study shows that warming leads to shorter food-chains in freshwater systems, and that this effect is even stronger in enriched conditions. Overall, our results indicate that the interactive effect between warming and enrichment might be more complex and deleterious than previously reported in theoretical models. While further investigations are needed to confirm the generality of our results, the decrease of food-chain length in warmer and enriched environments may have negative consequences on ecosystem functioning as the presence of higher trophic level is associated with higher community biomass and higher temporal stability in fish communities (Bonnaffé et al., 2021; Danet et al., 2021; Woods et al., 2020).

We used a food-web inference method with the best data available (i.e. individual body-size and allometric diet data at the species level), which can reproduce similar food-web structures as the one inferred from more direct assessments such as gut content (Canning & Death, 2019; Vander Zanden & Fetzer, 2007). Nevertheless, our inferred food-webs suffer a number of limitations. Like many other food-web models, our inference method does not account for change in diet related to foraging decisions (Beckerman et al., 2006) and, as a consequence, cannot substitute realized food diet data (e.g. Vander Zanden & Fetzer, 2007). Additionally, our food-webs do not encompass variations at the lower trophic levels, such as invertebrates, zoo- and phyto-plankton. We predict that integrating such data would give us further insights into the direct and interactive effects of temperature and enrichment on food-web structure, and would provide a more comprehensive comparison with previous theoretical and empirical studies (Binzer et al., 2016; Kratina et al., 2012). Despite those limitations, we believe that our data set enables reasonable comparison because our fish data comprises a large span of the trophic levels present in a typical food-web (from detritivores to strict piscivores). Also, food-chain length is highly constrained by trophic cascades (e.g. secondary extinction), such that unobserved extinctions in fish resources should be reflected in the structure of our fish food-webs. We further acknowledge that we focused on the effects of enrichment and temperature on food-web structure, but we expect that local or regional variation in anthropogenic threats such as habitat degradation, damming, water withdrawals, and non-native species introductions might also be major drivers of food-web structure that may also interact with temperature and enrichment. Studying interactions between global-change factors and these local/regional perturbations constitutes a promising avenue for further studies.

Overall, we hope that our study will stimulate future investigations on the complex interactive effects of warming and enrichment on food-webs and ecosystems. This research agenda is particularly urgent in freshwater systems that are already severely impacted by habitat degradation and will be even more impacted with the acceleration of climate change (Comte et al., 2021; Reid et al., 2019).

AUTHOR CONTRIBUTIONS

Willem Bonnaffé was involved in conceptualisation, methodology, software, formal analysis, validation, visualization, writing—original draft and writing—review and editing. Alain Danet was involved in conceptualisation, data curation, methodology, software, visualization, writing—original draft and writing—review and editing. Camille Leclerc was involved in conceptualisation, data curation, methodology, software, visualization, writing—original draft, writing—review and editing, and project management. Eric Edeline was involved in conceptualisation, methodology and writing-review and editing. Victor Frossard and Arnaud Sentis were involved in funding acquisition, conceptualisation, methodology and writing—review and editing.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

The R code to reproduce the analyses, along with all the original and derived data, is archived on Zenodo via GitHub (https://doi.org/10.5281/zenodo.12515498). The original temperature and fish data of lakes are available from the dashboard of Pole ECLA (http://dashboard.ecla.inrae.fr/). Temperature and fish data of streams as well as physico-chemical parameters of lakes and streams (i.e. BOD, total phosphorus and total nitrogen) are available on http://www.naiades.eaufrance.fr/. Shapefile of hydrographic basins is available on https://www.sandre.eaufrance.fr/atlas/srv/fre/catalog.search#/metadata/4714a793-dcd8-4528-bd6a-80bfdbee9728.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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