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# Species richness and food- web structure jointly drive community biomass and its temporal stability in fish communities

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Current biodiversity losses and further global change have the potential to affect ecosystems in complex ways (Loreau et al., 2001; Tilman et al., 2014). Biodiversity has indeed a major effect on ecosystem functions and their stability in response to perturbations (Duffy, 2009; Dunne, 2006; Hector, 1999; Hooper et al., 2005; Loreau et al., 2001). Understanding the relationship between biodiversity and ecosystem properties is thus crucial to better anticipate the impacts of global change.

Species richness has been found to increase primary productivity, community biomass and its temporal stability in various ecosystems and taxa, both experimentally and in natural settings (Cardinale et al., 2002; Franssen et al., 2011; Grace et al., 2016; Houlihan et al., 2018; Olivier et al., 2020; Pennekamp et al., 2018; Tilman et al., 1996, 2006). However, these studies mainly focused effects of food- web structure (but see Scherber et al., 2010). Conversely, theoretical works suggest that both species richness and food- web structure

## INTRODUCTION

### Abstract

Biodiversity– ecosystem functioning and food- web complexity– stability relationships are central to ecology. However, they remain largely untested in natural contexts. Here, we estimated the links among environmental conditions, richness, food- web structure, annual biomass and its temporal stability using a standardised monitoring dataset of 99 stream fish communities spanning from 1995 to 2018. We first revealed that both richness and average trophic level are positively related to annual biomass, with effects of similar strength. Second, we found that community stability is fostered by mean trophic level, while contrary to expectation, it is decreased by species richness. Finally, we found that environmental conditions affect both biomass and its stability mainly via effects on richness and network structure. Strikingly, the effect of species richness on community stability was mediated by population stability rather than synchrony, which contrasts with results from single trophic communities. We discuss the hypothesis that it could be a characteristic of multi- trophic communities.

### KEYWORDS

biomass, ecosystem functioning, fish, foodweb, natural settings, network structure, species richness, stability, synchrony, temperature

on communities composed of a single trophic level, generally primary producers, thereby ignoring the potential affect ecosystem properties such as productivity, total biomass and its temporal stability. For example, the presence of species at higher trophic levels may increase total primary production through top– down effects, which result in the selection of primary producers that are larger and more complementary in their use of resources (Wang & Brose, 2018). In communities including producers and consumers, the food- web connectance is predicted to modulate the diversity– productivity relationship (Thébault et al., 2007; Thébault & Loreau, 2003). Similarly, theoretical studies generally show strong links between food- web structure and stability (e.g., Duffy, 2009; Dunne, 2006; May, 1972; Neutel et al., 2007; Stouffer & Bascompte, 2011). Overall, theoretical models suggest that both species richness and food- web structure should affect community biomass and its stability, but empirical evidence of such effects is lacking.

While community stability is measured in many ways in theoretical studies, most empirical studies measure

community stability as the inverse of the coefficient of variation of community productivity, biomass or abundance, also called temporal stability (Kéfi et al., 2019). This stability metric is also well grounded in theory (e.g., Loreau & Mazancourt, 2008; Thébault & Loreau, 2005; Thibaut & Connolly, 2013) and can be decomposed into two components: population stability and synchrony (Thibaut & Connolly, 2013). Studies considering a single trophic level (Loreau & Mazancourt, 2008; Olivier et al., 2020; Tilman et al., 2006; Yachi & Loreau, 1999) as well as theoretical prediction for multi-trophic communities (Thébaud & Loreau, 2005) tend to highlight that asynchrony in population dynamics is key for the stabilising effects of species richness on community biomass. Theory predicts that higher food-web connectance may increase interaction strength and thereby increase population variability, counterbalancing the positive effect of species richness on the temporal stability of community biomass (Thébaud & Loreau, 2005). Predators can also have cascading effects on both population variability and synchrony at lower trophic levels (Shanafelt & Loreau, 2018; Teng & McCann, 2004). Overall, these theoretical studies show that the effects of species richness and food-web structure, such as connectance and average trophic level, are potentially conflicting or synergistic in such a way that they need to be simultaneously assessed.

The joint study of the effects of species richness and food-web structure on community biomass and its stability is important in the context of environmental changes. Recent studies comparing natural communities showed that environmental characteristics determine in part community biomass (Grace et al., 2016; Woodset al., 2020) and its temporal stability (Blüthgen et al., 2016; De Boeck et al., 2018; Franssen et al., 2011; Fried-Petersen et al., 2020; Hansen et al., 2013). The environment can affect ecosystem function or stability directly. For instance, larger freshwater ecosystems are expected to have more available resources and thus community biomass (Doi et al., 2009; Post et al., 2000), while agricultural intensification destabilises bird communities by decreasing population stability (Olivier et al., 2020). The effects of environment can also be mediated by changes in species richness and food-web structure. Larger ecosystems host food webs with higher diversity and trophic levels (e.g., McHugh et al., 2010), and temperature is also known to affect food-web diversity and structure (e.g., Bonnaffé et al., 2021; Edeline et al., 2013; Gauzens et al., 2020; O’Gorman et al., 2017). Environmental characteristics have thus to be accounted for if we are to tease apart the effects of species richness and food-web structure on community biomass and its temporal stability.

Stream fish communities constitute a good model to study the effects of network structure on community biomass and

its temporal stability because their trophic interactions are well known. A substantial body of literature supports that trophic interactions can be inferred through body size and diet information (Beckerman et al., 2006; Brose et al., 2019; Gravel et al., 2013; Jennings et al., 2001; Portalier et al., 2019). Using long-term monitoring of stream fish communities and inference of trophic interactions (Bonnaffé et al., 2021), we provide one of the first empirical tests of the expected relationship between biodiversity–ecosystem functioning and food-web complexity–stability accounting for environmental characteristics.

## **METHODS Data preparation and filtering**

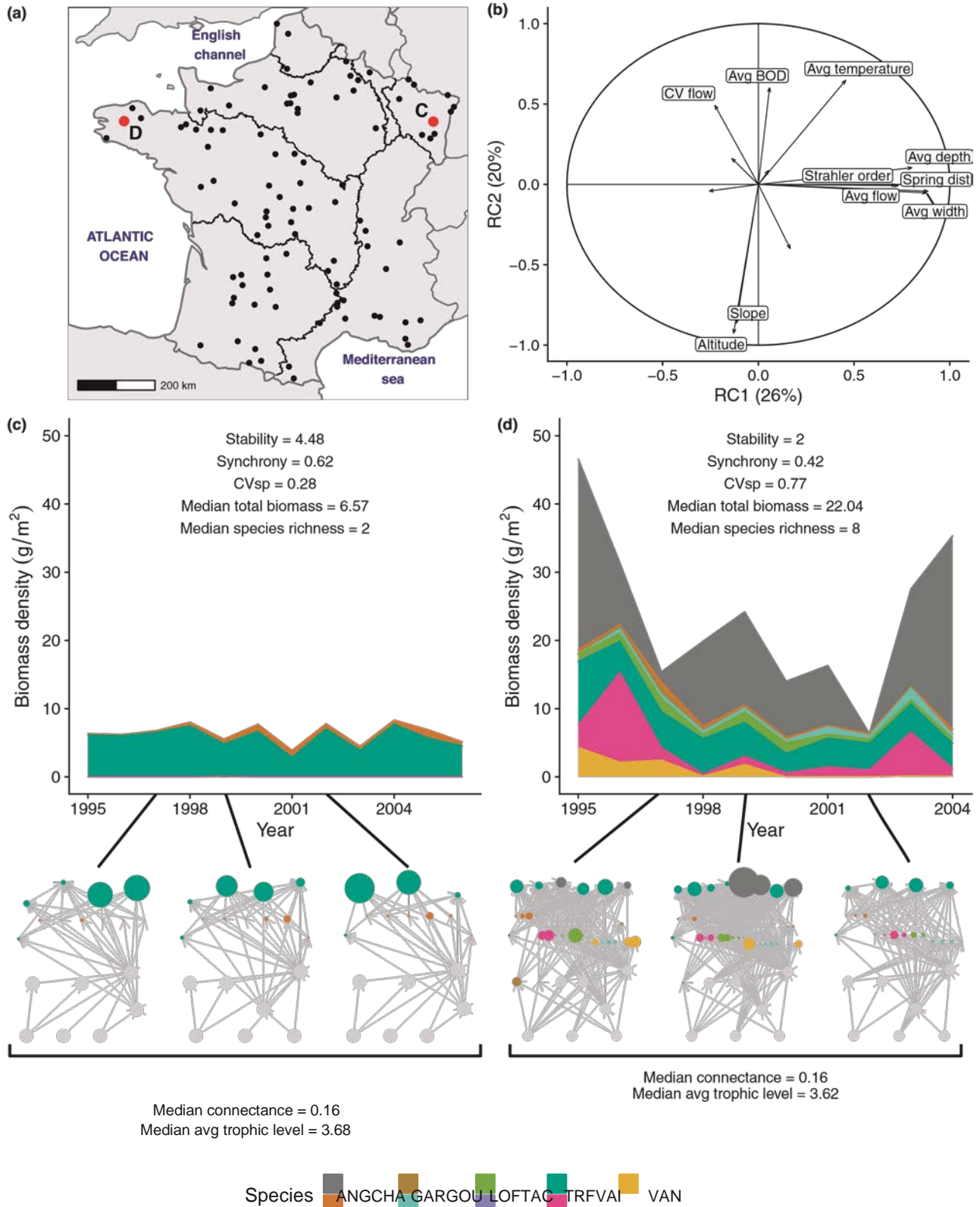
Fish communities were monitored across stream sections in metropolitan France over the period 1995–2018 by the French Office of Water and Aquatic Ecosystems (ONEMA) using electrofishing. Two different standardised protocols were used for small and large streams (detailed in Appendix B, part 1.1). In the case where a stream was sampled alternatively with one of the two sampling protocols, we only included data derived from the most frequently used sampling method. The sampling season spanned from late spring to autumn. There was low heterogeneity in the sampling month within stations, with the median sampling month being mid-August and the median standard deviation of the sampling month was 0.7 month, that is, 3 weeks.

We selected the stations that had been sampled for 10 years or more. As the concept of temporal stability often referred to the variability around an equilibrium point (Donohue et al., 2016), we selected the stations that did not show temporal trends in community biomass (detailed in Appendix B, part 2). However, the results were robust to the relaxation of this hypothesis (Figure S7). These selection steps resulted in 99 stations distributed over seven hydrographic basins (Figure 1a).

## **Community biomass and its temporal stability**

### **Biomass estimation**

The fishes collected by electrofishing were grouped in batches according to their body size class and species identity (Figure S1, Appendix B, part 1.1). When individuals were too numerous in a given batch, the body size of a subsample of the individuals was measured. The body size of the unmeasured individuals was inferred under the assumption that the body size of the individuals in a batch follows a normal distribution



**FIGURE 1** (a) Observation sites (black dots) were located across France and monitored on the period 1995–2018. The red dots show the location of C and D sites. Inner borders draw the limits of the hydrographic basins. (b) Principal component analysis performed on environmental variables. The first

axis was positively related to the stream size, and the second axis was related to the stream slope and altitude and negatively related to average water temperature and Biological Oxygen Demand (BOD). (c and d) Temporal dynamic of communities with examples of networks corresponding to the years 1997, 1999 and 2002. Each trophic species is represented by a node, and each colour represents a species (see Methods). Node size is proportional to the biomass of the trophic species. The seven resource nodes are coloured in grey. Species names corresponding to the three digit codes are found in Table S1 (Figure S1, Appendix B, part 1.2). The body mass of each individual was then estimated following the results of two meta- analyses on fishes (Froese, 2006; Lleonart et al., 2000), using an allometric law  $B_i = 0.01 \times l_i^{3.03}$ , with  $B$  as the body mass in grams,  $l$  the body size in millimetres and  $i$  the individual. Population biomass and community biomass at each sampling event were then calculated by summing individual body masses. To account for the variation in sampling effort among sites, population biomass and community biomass were corrected by the surface sampled (range 140– 2700 m<sup>2</sup>) and expressed in grams per square metre (g m<sup>-2</sup>). In the analysis, the community biomass of a site was defined as the median of the community biomass across sampled years.

## Stability measures

Temporal biomass stability was defined as the inverse of biomass variability. Variability was computed as coefficient of variation (CV) of the community biomass over time ( $CV_i = \sigma_i \mu_i^{-1}$ , with  $\sigma_i$  and  $\mu_i$  being respectively the standard deviation and the temporal average of the annual community biomass of the station  $i$ ). Then, temporal stability ( $S_i$ ) was equal to  $CV_i^{-1} = \mu_i / \sigma_i$ . The variability of community biomass ( $CV_{com,i}$ ) can be decomposed into a synchrony ( $\phi$ ) component and a weighted average population variability ( $CV_{sp,i}$ ) component according to Thibaut and Connolly (2013):

$$CV_{com,i} = CV_{sp,i} \sqrt{\phi_i} \quad (1)$$

To assess the mechanisms driving the stability of community biomass, we thus in addition measured the synchrony and the weighted average population variability  $CV_{sp,i}$ , the average CV at the population level in the station  $i$ , weighted by the relative biomass of the species populations,  $B_{k,i}$ .

Synchrony of the station  $i$ ,  $\phi_i$ , is the ratio between the variance of community biomass over time ( $\sigma_{XT,i}^2$ ) and the squared sum of the standard deviation of population biomass over time ( $\sigma_{Xk,i}$ ),  $i$  being the station  $i$  and  $k$  the species  $k$  (Loreau & Mazancourt, 2008). Synchrony varies from 0 to 1, 0 indicating complete asynchrony and 1 perfect synchrony. Consequently, the lower is synchrony, the higher are the compensatory dynamics.

$$CV_{sp,i} = \frac{\sum_k B_{k,i} CV_{k,i}}{\sum_k B_{k,i}} \quad (2)$$

$$= \frac{\sigma_{XT,i}^2}{\sum_k B_{k,i} CV_{k,i}^2} = \frac{\sigma_{XT,i}^2}{\sum_k B_{k,i} CV_{k,i}^2} \quad (3)$$

$$\phi_i = \frac{\sigma_{XT,i}^2}{\sum_k B_{k,i} CV_{k,i}^2} \quad (3)$$

## Species richness and food- web structure

### Species richness

Species richness in a given site was defined as the total number of species present across all the sampling events. We controlled species richness for sampling effort by dividing the total number of species by the total surface sampled in the given station. Species richness was then expressed in number of species per square metre sampled.

### Food- web inference

We determined the food- web structure in two steps (Bonnaffé et al., 2021): (1) we built a metaweb describing the trophic interactions among all possible fish size classes and species as well as with non- fish resource classes (Figure S2), then (2) we determined the food web corresponding to each sampling event by extracting from the metaweb the subset of fish species and size classes present at a given site and sampling event (Figure 1c,d).

The food web was inferred from body size and ontogenic diet shift following previous studies (Bonnaffé et al., 2021; Brose et al., 2019; Gravel et al., 2013; Poisot et al., 2016). The diet of stream fishes, as for many organisms, shifts throughout an individual's life and thereby with body size. For example, larvae and small juveniles feed on plankton, while adults may feed on algae and fishes, with bigger individuals eating bigger fishes. Each fish species was divided into nine body size classes, each corresponding to a trophic species (Appendix B, Figure S2). A trophic species constitutes a group of individuals from the same species and

size class, which are expected to share the same sets of prey and predators. Additionally, we added seven resource nodes present in the ontogenic food diet database: detritus, biofilm, phytoplankton, zooplankton, macrophages, phytobenthos and zoobenthos (grey nodes in Figure 1c,d). The trophic species and the resources constituted the 412 nodes of the metaweb, that is, 45 fish species divided into nine body size classes plus seven resource nodes. The inference of trophic interactions was shown to be more accurate when considering body size classes, that is, trophic species, than species (Jennings et al., 2001).

The feeding interactions of a trophic species were determined by both its species identity and its body size. The ontogenic fish diet database was filled according to fishbase (Froese & Pauly, 2021) and literature (Appendix A, Table S2). Each fish species had two or three life stages that are delimited by its body size range (Appendix B, Figure S2). The life stage of a fish trophic species was determined by the centre of its body size range, hereafter midpoint (Appendix B, Figure S2).

For a piscivorous trophic species, the fish– fish trophic links were defined in two steps and based on the body size ratio between predators and prey. First of all, the predation window of a piscivorous trophic species was defined as 3% to 45% of its midpoint (Claessen et al., 2002; Hart & Reynolds, 2008; Mittelbach & Persson, 1998). Then, a trophic link was set between the piscivorous trophic species and every trophic species whose midpoint in body size range was included in the predation window (Appendix B, Figure S2). The fish– resource trophic links were set between the trophic species and the resource nodes according to the food items of their size class. Lastly, the trophic links among resource nodes were set according to the literature (Allan & Castillo, 2007; Hart & Reynolds, 2008).

## Food- web structure

For each food web, corresponding to a particular site and year, we computed the connectance and mean trophic level. Food- web connectance describes the level of generalism in the network and is calculated as the actual number of interactions divided by the number of interactions if all species interact ( $C = L/N^2$ , with  $L$  and  $N$  being respectively the number of links and of nodes). The trophic level of the nodes was computed as one added to the average trophic level of its food items. The average trophic level  $T$  was computed as the average trophic level of the trophic species weighted by their biomass (excluding resource nodes for which we had no biomass information), so  $T = \sum_i^N B_i T_i / (\sum_i^N B_i)$ , with  $T_i$  and  $B_i$  being respectively the trophic level and the biomass of the node  $i$ . For each site, the median of connectance and average

trophic level over time was used in subsequent analysis (Figure 1c,d).

## Environmental variables

We characterised the sites by their altitude, slope, distance from source, stream width, depth and Strahler order, that is, its position in the stream network hierarchy. We obtained data on Biological Oxygen Demand (BOD), which is often related to enrichment and eutrophication in aquatic systems (Mallin et al., 2006), water temperature, flow and from the Naiades database ([www.naiad.es.eaufrance.fr](http://www.naiad.es.eaufrance.fr)). As data from Naiades are not collected on the same site as our fish sampling sites, we performed an interpolation of the water temperature and flow based on the spatial stream network models (Hoef et al., 2014; Isaak et al., 2014). The interpolation procedure is detailed in Appendix B (part 1.4).

We had one environmental variable value for each sampling event, except for water temperature for which records began in 2006. Then, we computed the average and temporal CV values of water temperature, flow, BOD, river width and depth. As habitat and environmental variables are often collinear, a principal component analysis (PCA) was performed on the 14 scaled variables. We kept in the analysis the two first principal components based on the elbow method on the eigenvalues distribution (Appendix B, Figure S5). The two first principal components explained 46% of the variance (Figure 1b). A varimax axis rotation was performed to maximise the representation of the environmental variables by the principal components (Kaiser, 1958; Revelle, 2019). The first axis represented a gradient from small to big streams, characterised by their width and depth, but also a gradient of distance from source. We reversed the values of the second axis, so that is represented a gradient of increasing average water temperature, average BOD and decreasing altitude and slope. Further descriptions of the variables are provided in Appendix B (part 1.4).

## Statistical analysis

We analysed the relationships among environment, species richness, food- web structure, community biomass and its temporal stability with structural equation models (SEMs), as they enable the assessment of potential direct and indirect relationships among multiple variables (Grace, 2008; Grace et al., 2014, 2016; Lefcheck, 2016). The SEM explains the median annual community biomass as a function of the environment, species richness and food- web structure (Maureaud et al., 2019; Woods et al., 2020). We assumed that the environment, species richness and food- web structure directly affect community biomass (Figure 2a), that species richness affects food- web structure (Dunne, 2006; Thébaud

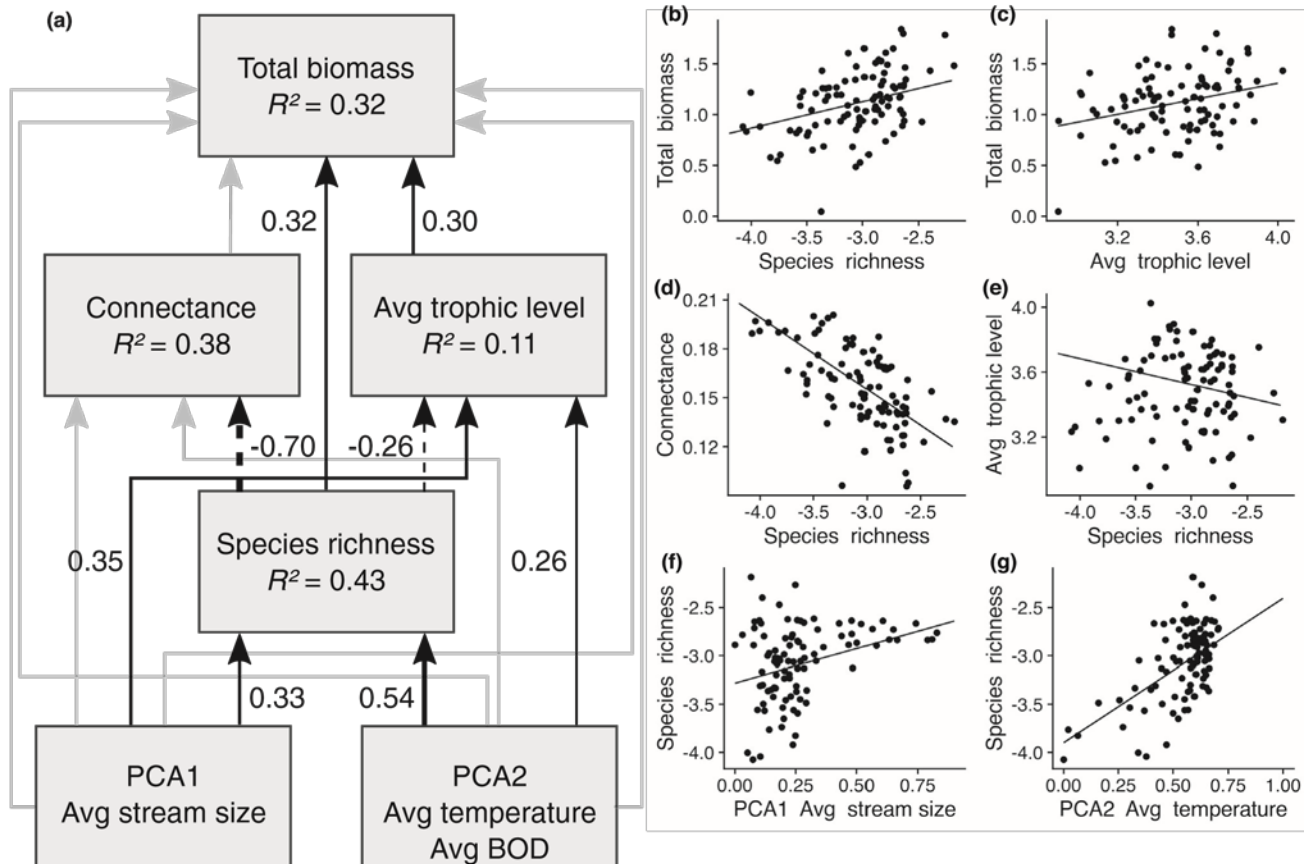
& Fontaine, 2010; Winemiller, 1989) and that environment affects species richness and food- web structure.

We used the same model structure to assess the drivers of temporal stability of community biomass (Figure 3a). Instead of the annual community biomass, we modelled the synchrony and population variability that in turn fully determined the temporal stability of community biomass. We linearised the mathematical relationship linking temporal stability of community biomass  $S_i$  to  $CV_{sp,i}$  and  $\phi$  by taking the log of temporal stability such as

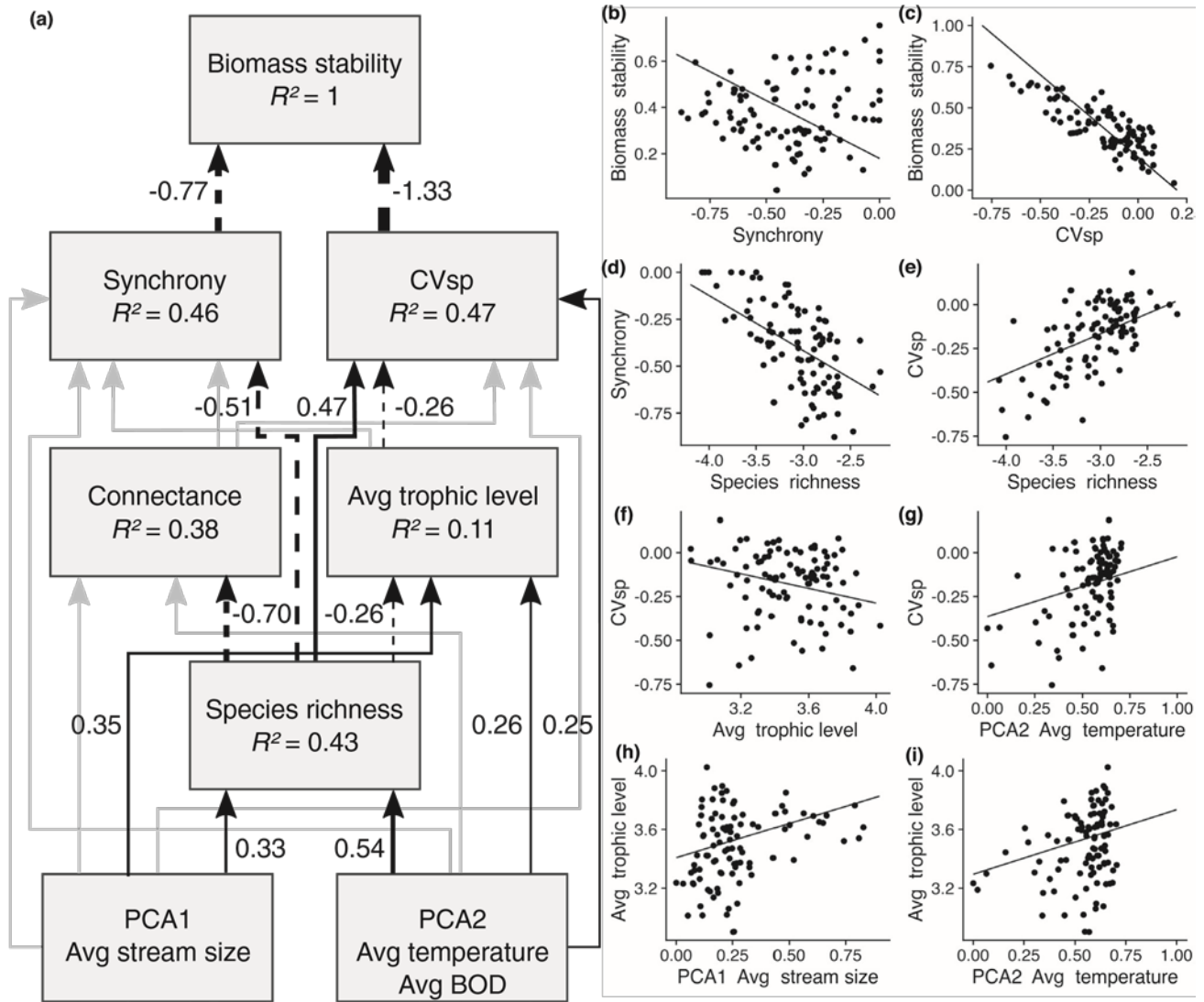
$$\log S_i = - \frac{1}{2} \log CV_{sp,i} - \frac{1}{2} \log \phi \quad (4)$$

The SEMs were based on Gaussian linear mixed- effects models. All variables except the connectance and average trophic level were log- transformed to fulfil model requirements (see residual plots and data transformation in Figures S5 and S6, Table S5, Appendix B). We set the seven hydrographic basins as a random effect on the intercept to account for their heterogeneity. We checked for the absence of multi- collinearity with variance inflation factor (Table S6, Appendix B). The slopes estimated by the SEMs and reported in the main text were standardised in order to compare their

magnitude ( $r_{\beta} = \frac{\beta}{\sigma_x}$ , with  $\beta$  being the unstandardised slope,  $\sigma_x$  and  $\sigma_y$  being respectively the standard deviation of the predictor variable  $x$  and of the response variable  $y$ ). Therefore, the standardised coefficients expressed the variation of  $x$  and  $y$  in standard deviation units. According to Equation (4), the unstandardised coefficients of synchrony and population variability determining temporal stability of community biomass are respectively  $-0.5$  and  $-1.0$ . When standardised, the relative comparison of those coefficients comes down to a comparison of the standard deviation of these two variables. The deviation from unstandardised effect values (i.e.,  $-0.5$  and  $-1.0$ ) indicates that one component of community stability displays more variations than the other and that the determinants of the more variable component will be those affecting community stability the most. The paths whose slope had a  $p$  value inferior or equal to 0.05 were reported in the main text; all the path values are presented in Tables S7 and S8. Indirect effects on community biomass and its temporal stability were computed by multiplying slopes along the path. Only significant direct slopes were included in the calculation of indirect effects. Total effects were computed as the sum of direct and indirect effects.



**FIGURE 2** Relationships among the predictors of community biomass. (a) Structural equation model for the median of annual community biomass (in grams by square metre). Dotted and solid arrows represent, respectively, negative and positive path coefficients. Non- significant paths are coloured in grey. The path coefficients are standardised.  $R^2$ , adjusted  $R^2$ ; Avg, average;  $CV_{sp}$ , weighted temporal coefficient of variation of the population biomass; PCA1 and PCA2, respectively the first and second axis of the principal component analysis performed on environmental variables (see Methods). (b– g) Significant bivariate relationships between variables of the structural equation model. Solid lines depict the predictions of the statistical model. See Figure S8 for a sensitivity analysis according to different station selection criteria



**FIGURE 3** Relationships among the predictors of the temporal stability of community biomass. (a) Structural equation model for the temporal stability of community biomass. Dotted and solid arrows represent, respectively, negative and positive path coefficients. Non-significant paths are coloured in grey. The path coefficients are standardised.  $R^2$ , adjusted  $R^2$ ; Avg, average; CVsp, weighted temporal coefficient of variation of the population biomass; PCA1 and PCA2, respectively the first and second axis of the principal component analysis performed on environmental variables (see Methods). The  $R^2$  for the temporal stability of community biomass is exactly one because the relation is deterministic (see Equation 4). (b–i) Significant bivariate relationships between variables of the structural equation model. Solid lines depict the predictions of the statistical model. See Figure S8 for a sensitivity analysis according to different station selection criteria

Environmental variables were interpolated with the openStars and SSN R packages (Hoef et al., 2014; Kattwinkel & Szöcs, 2020). Linear models and SEMs were computed with respectively the nlme and piecewiseSEM R packages (Lefcheck, 2016; Pinheiro et al., 2021). The codes used for the analysis and to generate the manuscript are accessible on GitHub (alaindanet/fishcom<sup>1</sup>). The analyses were performed with R version 3.6.3 (R Core Team, 2020).

## RESULTS

The SEMs explained a large part of the variation of species richness, connectance, synchrony, CV<sub>sp</sub> and community biomass (resp.  $R^2 = 0.43, 0.38, 0.46, 0.47$  and  $0.32$ ) but less so for mean trophic level ( $R^2 = 0.11$ ; Figures 2a and 3a). We found a negative relationship between species richness and mean trophic level ( $r_{\delta} = -0.26$ , with  $r_{\delta}$  meaning the standardised slope) and connectance ( $r_{\delta} = -0.7$ ; Figures 2a and 3a), meaning that a part of the effects of species richness on community biomass and its temporal stability went through the food-web structure. The relationships resulting from the SEM are robust to different

<sup>1</sup> <https://github.com/alaindanet/fishcom>



station selection criteria in the analysis, with different selections ranging in 65 to 403 stations (see sensitivity analysis, Figure S8).

**Species richness and average trophic level are positively correlated with community biomass**

**TABLE 1** Direct, indirect and total effects of environment, species richness, connectance and mean trophic level on community biomass and its temporal stability

SEM type	Variable	Direct	Indirect effects via					Total effect
			Species richness	Connectance	Avg trophic level	CVsp	Synchrony	
Community biomass	PCA1 avg stream size	NS	0.08	0	0.1	NA	NA	0.18
	PCA2 avg temperature	NS	0.13	0	0.08	NA	NA	0.21
	Species richness	0.32	NA	0	-0.08	NA	NA	0.25
	Connectance	NS	NA	NA	NA	NA	NA	0
	Avg trophic level	0.3	NA	NA	NA	NA	NA	0.3
	PCA1 avg stream size	NA	-0.1	0	0.12	0	0	0.02
Temporal stability of community biomass	PCA2 avg temperature	NA	-0.17	0	0.09	-0.33	0	-0.41
	Species richness	NA	NA	0	-0.09	-0.62	0.4	-0.31
	Connectance	NA	NA	NA	NA	0	0	0
	Avg trophic level	NA	NA	NA	NA	0.35	0	0.35

Indirect effects are computed by multiplying the path coefficients from the predictor to the response variables. For example, the indirect effect of species richness on biomass stability via its effect on CVsp is -0.62. The total effect of a predictor to a response variable is the sum of all paths. Only the significant direct effects were retained for the computation of indirect effects. NA values indicate that the corresponding paths do not exist in the specified structural equation model (SEM).

NS, statistically non-significant.

Species richness and mean trophic level had a significant

positive direct effect on community biomass ( $r_{\delta} = 0.32$  and  $r_{\delta} = 0.3$ , respectively; Figure 2a–c, Table 1), while connectance had no direct effect. The two PCA axes synthesising environmental variables had no significant direct effects on community biomass but indirect ones (Table 1). The first axis, related to the stream size, was positively linked to community biomass ( $r_{\delta} = 0.18$ ; Table 1), through both species richness and mean trophic level ( $r_{\delta} = 0.08$  and  $0.1$ , respectively; Figure 2f,g, Table 1). The second axis, related to the average annual temperature and BOD, was positively related to community biomass ( $r_{\delta} = 0.21$ ; Table 1), mainly through species richness ( $r_{\delta} = 0.13$ ; Figure 2g, Table 1). Warmer and enriched, that is, with higher BOD, streams contained more species and thus indirectly increased the biomass of the communities. The total effects of PCA1, PCA2 and species richness on community biomass were of the same magnitude.

### Temporal stability of annual community biomass

By its effects on synchrony and population variability ( $CV_{sp}$ ), species richness had a negative total effect on biomass stability ( $r_{\delta} = -0.31$ ; Table 1). This effect resulted from two opposite effects. On the one hand, species richness had a direct negative effect on synchrony ( $r_{\delta} = -0.51$ ; Figure 3a,b), thereby increasing stability ( $r_{\delta} = 0.4$ ). On the other hand, species richness had a positive direct effect on  $CV_{sp}$  ( $r_{\delta} = 0.47$ ; Figure 3a,c), thereby decreasing biomass stability ( $r_{\delta} = -0.62$ ; Table 1), which outweighed the stabilising effect of species richness via decreased synchrony. The negative effect of  $CV_{sp}$  on temporal stability was twice higher than the negative effect of synchrony (respectively  $r_{\delta} = -1.33$  and  $r_{\delta} = -0.77$ ; Figure 3a), which is as expected from the

### DISCUSSION Species richness increased community biomass but decreased its temporal stability

We found that species richness increased community biomass in line with the results in the plants and tree communities (Hector, 1999; Li et al., 2018; Tilman et al., 2014; Wu et al., 2015) as well as those found for fish communities (Maureaud et al., 2019; Woods et al., 2020) and for theoretical food-web models (Schneider et al., 2016). Theory suggests that the positive effect of species richness on community biomass might be induced by resource use complementarity (Carey & Wahl, 2011), which is driven by niche differentiation (Loreau, 1998; Loreau & Hector, 2001) or driven by the dominance of a highly productive species (i.e., positive selection effect; Loreau et al., 2001). Recent findings suggest that such positive selection effect (Loreau & Hector, 2001) is the main driver of the observed positive relationship between

mathematical decomposition of the stability of community biomass. Population variability and synchrony indeed contribute respectively to  $-1$  and  $-0.5$  when the coefficients are not standardised (Equation 4). Our result thus also means that the standard deviation of  $CV_{sp}$  is of roughly the same magnitude as the one of synchrony in this case.

The total effects of mean trophic level and species richness on temporal stability of community biomass were of the same magnitude (respectively  $0.35$  and  $-0.31$ ; Table 1). The mean trophic level had only a direct negative effect on  $CV_{sp}$  ( $r_{\delta} = -0.26$ ; Figure 3a,f) and thereby had a total positive effect on temporal stability ( $r_{\delta} = 0.35$ ; Table 1). Food webs in which community biomass is located on average at higher trophic levels thus tend to have higher stability of population and community biomass. Connectance had no significant direct effect on either  $CV_{sp}$  nor synchrony and thus no effect on temporal stability of community biomass (Figure 3a, Table 1).

The total effect of PCA2, related to average annual temperature and BOD, on temporal stability was of higher magnitude than the effects of species richness and mean trophic level (Table 1). The PCA2 had a total negative effect on the temporal stability of communities, meaning that higher temperature and BOD results in lower stability ( $r_{\delta} = -0.41$ ; Table 1). PCA2 had an indirect positive effect on temporal stability through a direct positive effect on mean trophic level ( $r_{\delta} = 0.09$ ; Figure 3i, Table 1). However, PCA2 had a negative effect on stability of community biomass through a direct positive effect on  $CV_{sp}$  and species richness (respectively  $r_{\delta} = -0.33$  and  $r_{\delta} = -0.17$ ; Figures 2g and 3g, Table 1). PCA1, related to stream size, had in contrast a very slight positive effect on stability of community biomass ( $r_{\delta} = 0.02$ ; Table 1). Warmer and larger streams tend to have more species, but the variability of their population biomass is respectively higher and lower, resulting in respectively lower and higher temporal stability of community biomass.

biomass and species richness in fish communities (Maureaud et al., 2019; Woods et al., 2020).

Contrary to most experimental and empirical results (Franssen et al., 2011; Olivier et al., 2020; Pennekamp et al., 2018; Tilman et al., 2006; Valencia et al., 2020, but see, Declerck et al., 2006), we found a negative relationship between species richness and stability of community biomass. This effect resulted from a combination of two effects, one on population synchrony and one on population variability, both of which contribute to the stability of community biomass. The negative effect of species richness on population synchrony we found, thereby increasing stability of community biomass, is in accordance with most studies on experimental grasslands (Isbell et al., 2009; Roscher et al., 2011) as well as natural communities such as birds, grasses, bats or butterflies (Blüthgen et al., 2016; Olivier et al., 2020, but see Declerck et al., 2006; Valencia et

al., 2020). Our result thus extend this relationship to multi-trophic communities.

The positive effect of species richness on population variability that we found, thereby destabilising communities, is more intriguing and does not fit the findings of a meta-analysis reporting more frequent negative effects of richness on population variability in multi-trophic communities (Jiang & Pu, 2009). Food-web theory predicts that the relationship between the temporal stability of populations and species richness depends on the strength of interactions and its distribution (Downing et al., 2020; McCann & Hastings, 1997; Thébault & Loreau, 2005), with stronger interactions promoting a negative relationship between species richness and stability. This might be the case in our study system, but this hypothesis remains to be directly tested. Alternatively, a positive richness-population variability relationship can come from an increased demographic stochasticity with increasing species richness (Loreau & Mazancourt, 2008).

In our study system, the destabilising effect of species richness via increased population variability was stronger than the stabilising effect via decreased synchrony. Further, as the effects of species richness on population variability and synchrony we found here were of similar amplitude, the balance between both pathways is governed by the relative standard deviation of population variability and synchrony, this because we used standardised coefficients (see Methods). The fish communities studied here therefore present a similar level of variation in population variability and synchrony, again contrasting with results on terrestrial animal communities that exhibited twice as much variation in population synchrony than in population variability (Olivier et al., 2020). This opens intriguing questions as to potential mechanisms constraining the variation range of population variability and synchrony among communities. Lower variation in population synchrony among the fish communities studied here might relate to their trophic structure, as theory predicts potential synchronising effect of generalist predators, such as piscivorous fishes, on prey dynamics (Huber & Gaedke, 2006; Raimondo et al., 2004). Trophic interactions might also raise synchrony between predators and preys (Figure S9; Bulmer, 1975), although predictions can vary depending on the distribution of interaction strengths (Huber & Gaedke, 2006; McCann & Rooney, 2009). Restricted variations in population synchrony among communities can also be fostered by low biomass evenness and thereby low portfolio effect (Doak et al., 1998; Thibaut & Connolly, 2013), but whether biomass evenness of stream fish communities is particularly low remains to be tested. Alternatively, aquatic ecosystems have been suggested to show greater population variability than terrestrial ones (Rip & McCann, 2011), which could translate in a greater variation range of population variability among aquatic communities than among terrestrial ones.

## **Average trophic level increased community biomass and its temporal stability, while connectance had no effect**

Our analysis further indicates that network structure, and in particular average trophic level, was strongly related to community biomass, as higher community biomass was found in communities with a higher average trophic level. These results are in accordance with the theoretical predictions (Schneider et al., 2016; Wang & Brose, 2018), proposing that predation selects for primary producers with higher resource use efficiency and enhance complementarity between primary producers (Wang & Brose, 2018).

Further, our results show that communities with higher average trophic level had lower population variability and were thereby more stable. This result is also in accordance with theoretical models predicting a higher stability of populations of higher trophic levels (Barbier & Loreau, 2019; Shanafelt & Loreau, 2018) or a damping effect of higher trophic levels on the variability of lower trophic level populations (McCann, 2000).

In contrast, we found that food-web connectance was not related to community biomass, which contradicts theoretical models suggesting that higher connectance is expected to lower community biomass by decreasing complementarity in resource use among species (Poisot et al., 2013; Thébault & Loreau, 2003). However, the effect of connectance on productivity remains poorly investigated.

Unexpectedly, we found no relationship between food-web connectance and stability of community biomass that contrasts with many theoretical results highlighting food-web complexity–stability relationships (e.g., Angelis, 1975; May, 1972; Thébault & Fontaine, 2010; but see Neutel et al., 2007), although they generally consider different stability concepts and metrics (Arnoldi et al., 2016). The lack of connectance effect on the temporal stability of community biomass might be related to the connectance metric we used, in particular the fact that it did not account for interaction strengths. Indeed, connectance stability relationship is expected to vary depending on the strength of trophic interactions (Thébault & Loreau, 2005). Further, in our dataset, resource nodes, that is, primary producers, decomposers and the benthic species, were highly aggregated, which might blur potential connectance differences among communities.

## **Environment had a strong effect on community biomass and its temporal stability**

We found that the larger as well as warmer and more enriched streams had higher community biomass and that this was mediated by higher species richness and average trophic level. Regarding the effect of ecosystem size, our results thus

support a classical theory of food- web ecology (Doi et al., 2009; Post et al., 2000). Larger freshwater ecosystems provide higher diversity of resources through habitat heterogeneity and then result in higher species richness and mean trophic level per surface unit, through complementarity in resource use (Doi et al., 2009; McHugh et al., 2010; Post et al., 2000). Regarding temperature and enrichment effect, our study joins the mounting body of works reporting the effect on the structure and biomass of aquatic systems (Allan & Castillo, 2007; Bonnaffé et al., 2021; Edeline et al., 2013; Emmrich et al., 2014; Hattab et al., 2016; Woods et al., 2020). However, current results do not show consensus (Dossena et al., 2012; Maureaud et al., 2019; Tabi et al., 2019; Yvon-Durocher et al., 2011), with potential antagonistic effects of temperature and enrichment as well as non- monotonic effects (O'Connor, 2009; Tabi et al., 2019; Uszko et al., 2017). Although we could not tease apart the respective effects of temperature and enrichment, our results indicate that in the range of observed covariation in temperature and enrichment, their joint effects result in a positive relationship with community biomass.

Our analysis further revealed that stream size had only a weak effect on the temporal stability of community biomass, while warmer and enriched streams exhibit less stable community biomass mainly via an increase in population variability. These results are in line with previous experiments showing that warming or enrichment decreases the temporal stability of communities (Kratina et al., 2012; Tabi et al., 2019). However, several studies have highlighted that the effects of temperature on stability can be complex and interact with those of enrichment (Binzer et al., 2012; Uszko et al., 2017).

## Network reconstruction: limits and perspectives

The lack of experimental or empirical studies considering the effects of both species richness and food- web structure on ecosystem functions can be explained by the challenges associated with manipulating both species richness and food- web structure experimentally (e.g., Sander et al., 2017) and by the fact that describing trophic interactions between species is highly labour intensive. These challenges are even more acute when studying the temporal stability of ecosystem properties, which requires time series. In this context, recent developments to predict trophic interactions among species (Beckerman et al., 2006; Gravel et al., 2013; Portalier et al., 2019), combined with observational long- term monitoring of ecological communities, offer a promising opportunity. They offer a way to maximise the amount of information that can be extracted from already collected empirical data but at the cost of their precision. Here, we built binary interaction networks based on the ratio

of body size between predator and prey, ignoring modulation of interactions strength depending on preferences or environmental factors. Refining the construction of interaction networks by, for example, integrating predator behaviour (Portalier et al., 2019) or developing more statistically flexible framework such as machine learning (Pichler et al., 2020) will certainly increase the accuracy of species interaction predictions. Although challenging, methods of food- web reconstruction have a great potential to increase our understanding of network structure effects on ecosystem function and dynamic in natural settings using available long- term empirical data.

## CONCLUSION

Our work contributes to bridging the gap between theoretical, experimental and empirical findings on the functioning and stability of communities. Our study extends the assessment of the effect of species richness on community biomass and its temporal stability to the case of freshwater food webs in natural settings. While our results are in accordance with numbers of studies showing a positive effect of richness on community biomass, they provide a contrasting example of a negative relationship between richness and stability of community biomass. Our results highlight population variability as key in transmitting effects of species richness, network structure and environmental gradients on community stability, opening stimulating questions about how the food- web structure and species richness drive population synchrony and variability.

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## AUTHOR CONTRIBUTIONS

AD, CF, MM and ET designed the study. WB designed the network inference method and collected the food diet data. AD performed the data analysis and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13857>

## DATA AVAILABILITY STATEMENT

The raw data used for the analysis are available on Zenodo: 10.5281/zenodo.5095656. The code used for the analysis and

to generate the manuscript is available on GitHub: (alaindanet/fishcom.git). The raw fish database is public and available upon request to eddy.cosson@afbiodiversite.fr and thierry.point@afbiodiversite.fr. The raw data of water temperature, flow and Biological Oxygen Demand are available on <http://www.naiad.es.eaufrance.fr/>

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## REFERENCES

- Allan, J.D. & Castillo, M.M. (2007) *Stream ecology: structure and function of running waters*, 2nd edition, New York: Chapman and Hall.
- Angelis, D.L. (1975) Stability and connectance in food web models. *Ecology*, 56(1), 238–243. <https://doi.org/10.2307/1935318>
- Arnoldi, J.-F., Loreau, M. & Haegeman, B. (2016) Resilience, reactivity and variability: a mathematical comparison of ecological stability measures. *Journal of Theoretical Biology*, 389, 47–59.
- Barbier, M. & Loreau, M. (2019) Pyramids and cascades: a synthesis of food chain functioning and stability. *Ecology Letters*, 22, 405–419.
- Beckerman, A.P., Petchey, O.L. & Warren, P.H. (2006) Foraging biology predicts food web complexity. *Proceedings of the National Academy of Sciences*, 103, 13745–13749.
- Binzer, A., Guill, C., Brose, U. & Rall, B.C. (2012) The dynamics of food chains under climate change and nutrient enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2935–2944.
- Blüthgen, N., Simons, N.K., Jung, K., Prati, D., Renner, S.C., Boch, S. et al. (2016) Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nature Communications*, 7, 10697.
- Bonnaffé, W., Danet, A., Legendre, S. & Edeline, E. (2021) Comparison of size-structured and species-level trophic networks reveals antagonistic effects of temperature on vertical trophic diversity at the population and species level. *Oikos*, 130(8), 1297–1309. <https://doi.org/10.1111/oik.08173>
- Brose, U., Archambault, P., Barnes, A.D., Bersier, L.-F., Boy, T., Canning-Clode, J. et al. (2019) Predator traits determine food-web architecture across ecosystems. *Nature Ecology & Evolution*, 3, 919–927.
- Bulmer, M.G. (1975) Phase relations in the ten-year cycle. *The Journal of Animal Ecology*, 44(2), 609.
- Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002) Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, 415, 426–429.
- Carey, M.P. & Wahl, D.H. (2011) Determining the mechanism by which fish diversity influences production. *Oecologia*, 167, 189–198.
- Claessen, D., Van Oss, C.V., de Roos, A.M. & Persson, L. (2002) The impact of size-dependent predation on population dynamics and individual life history. *Ecology*, 83(6), 1660–1675.
- De Boeck, H.J., Bloor, J.M.G., Kreyling, J., Ransijn, J.C.G., Nijs, I., Jentsch, A. et al. (2018) Patterns and drivers of biodiversity-stability relationships under climate extremes. *Journal of Ecology*, 106(3), 890–902.
- DeClerck, F.A.J., Barbour, M.G. & Sawyer, J.O. (2006) Species richness and stand stability in conifer forests of the Sierra Nevada. *Ecology*, 87, 2787–2799.
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E. & Thomson, D. (1998) The statistical inevitability of stability-diversity relationships in community ecology. *The American Naturalist*, 151(3), 264–276.
- Doi, H., Chang, K.-H., Ando, T., Ninomiya, I., Imai, H. & Nakano, S.-I. (2009) Resource availability and ecosystem size predict food-chain length in pond ecosystems. *Oikos*, 118(1), 138–144. <https://doi.org/10.1111/j.1600-0706.2008.17171.x>
- Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S. et al. (2016) Navigating the complexity of ecological stability. *Ecology Letters*, 19, 1172–1185.
- Dossena, M., Yvon-Durocher, G., Grey, J., Montoya, J.M., Perkins, D.M., Trimmer, M. et al. (2012) Warming alters community size structure and ecosystem functioning. *Proceedings of the Royal Society B: Biological Sciences*, 279, 3011–3019.
- Downing, A.L., Jackson, C., Plunkett, C., Lockhart, J.A., Schlater, S.M. & Leibold, M.A. (2020) Temporal stability vs. community matrix measures of stability and the role of weak interactions. *Ecology Letters*, 23, 1468–1478.
- Duffy, J.E. (2009) Why biodiversity is important to the functioning of real-world ecosystems. *Frontiers in Ecology and the Environment*, 7(8), 437–444.
- Dunne, J.A. (2006) The network structure of food webs. In: Pascual, M. & Dunne, J.A. (Eds.) *Ecological networks: linking structure to dynamics in food webs*. Oxford: Oxford University Press, pp. 27–86.
- Edeline, E., Lacroix, G., Delire, C., Poulet, N. & Legendre, S. (2013) Ecological emergence of thermal clines in body size. *Global Change Biology*, 19, 3062–3068.
- Emmrich, M., Pédrón, S., Brucet, S., Winfield, I.J., Jeppesen, E., Volta, P. et al. (2014) Geographical patterns in the body-size structure of European lake fish assemblages along abiotic and biotic gradients. *Journal of Biogeography*, 41(12), 2221–2233.
- Franssen, N.R., Tobler, M. & Gido, K.B. (2011) Annual variation of community biomass is lower in more diverse stream fish communities. *Oikos*, 120(4), 582–590.
- Fried-Petersen, H.B., Araya-Ajoy, Y.G., Futter, M.N. & Angeler, D.G. (2020) Drivers of long-term invertebrate community stability in changing Swedish lakes. *Global Change Biology*, 26(3), 1259–1270.
- Froese, R. (2006) Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. *Journal of Applied Ichthyology*, 22(4), 241–253.
- Froese, R. & Pauly, D. (2021) *FishBase*. Fisheries Centre, University of British Columbia.
- Gauzens B., Rall B.C., Mendonça V., Vinagre C. & Brose U. (2020) Biodiversity of intertidal food webs in response to warming across latitudes. *Nature Climate Change*, 10(3), 264–269.
- Grace, J.B. (2008) Structural equation modeling for observational studies. *The Journal of Wildlife Management*, 72(1), 14–22.
- Grace, J.B., Adler, P.B., Stanley Harpole, W., Borer, E.T. & Seabloom, E.W. (2014) Causal networks clarify productivity–richness interrelations, bivariate plots do not. *Functional Ecology*, 28(4), 787–798.
- Grace, J.B., Anderson, T.M., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S. et al. (2016) Integrative modelling reveals mechanisms linking productivity and plant species richness. *Nature*, 529, 390–393.
- Gravel, D., Poisot, T., Albouy, C., Velez, L. & Mouillot, D. (2013) Inferring food web structure from predator–prey body size relationships. *Methods in Ecology and Evolution*, 4(11), 1083–1090. <https://doi.org/10.1111/2041-210x.12103>
- Hansen, B.B., Grotan, V., Aanes, R., Saether, B.-E., Stien, A., Fuglei, E. et al. (2013) Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic. *Science*, 339(6117), 313–315. <https://doi.org/10.1126/science.1226766>
- Hart, P.J. & Reynolds, J.D. (2008) *Handbook of fish biology and fisheries: fisheries*, John Wiley & Sons. Available at: <https://onlinelibrary.wiley.com/doi/book/10.1002/9780470693919> [Accessed 11th August 2021].
- Hattab, T., Leprieux, F., Ben Rais Lasram, F., Gravel, D., Le Loc'h, F. & Albouy, C. (2016) Forecasting fine-scale changes in the food-web structure of coastal marine communities under climate change. *Ecography*, 39(12), 1227–1237. <https://doi.org/10.1111/ecog.01937>
- Hector, A. (1999) Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123–1127.
- Hoef, J.M.V., Peterson, E.E., Clifford, D. & Shah, R. (2014) SSN: an R package for spatial statistical modeling on stream networks. *Journal of Statistical Software*, 56(3), 1–45. <https://doi.org/10.18637/jss.v056.i03>

- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. et al. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35. <https://doi.org/10.1890/04-0922>
- Houlahan, J.E., Currie, D.J., Cottenie, K., Cumming, G.S., Findlay, C.S., Fuhlendorf, S.D. et al. (2018) Negative relationships between species richness and temporal variability are common but weak in natural systems. *Ecology*, 99, 2592–2604.
- Huber, V. & Gaedke, U. (2006) The role of predation for seasonal variability patterns among phytoplankton and ciliates. *Oikos*, 114, 265–276.
- Isaak, D.J., Peterson, E.E., Ver Hoef, J.M., Wenger, S.J., Falke, J.A., Torgersen, C.E. et al. (2014) Applications of spatial statistical network models to stream data: spatial statistical network models for stream data. *WIREs Water*, 1, 277–294. <https://doi.org/10.1002/wat2.1023>
- Isbell, F.I., Polley, H.W. & Wilsey, B.J. (2009) Biodiversity, productivity and the temporal stability of productivity: patterns and processes. *Ecology Letters*, 12, 443–451.
- Jennings, S., Pinnegar, J.K., Polunin, N.V.C. & Boon, T.W. (2001) Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, 70(6), 934–944. <https://doi.org/10.1046/j.0021-8790.2001.00552.x>
- Jiang, L. & Pu, Z. (2009) Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. *The American Naturalist*, 174, 651–659.
- Kaiser, H.F. (1958) The varimax criterion for analytic rotation in factor analysis. *Psychometrika*, 23(3), 187–200. <https://doi.org/10.1007/bf02289233>
- Kattwinkel, M., Szöcs, E., Peterson, E. & Schäfer, R.B. (2020) Preparing GIS data for analysis of stream monitoring data: the R package openSTARS. *PLoS One*, 15(9), e0239237. <https://doi.org/10.1371/journal.pone.0239237>
- Kéfi, S., Domínguez-García, V., Donohue, I., Fontaine, C., Thébault, E. & Dakos, V. (2019) Advancing our understanding of ecological stability. *Ecology Letters*, 22, 1349–1356.
- Kratina, P., Greig, H.S., Thompson, P.L., Carvalho-Pereira, T.S.A. & Shurin, J.B. (2012) Warming modifies trophic cascades and eutrophication in experimental freshwater communities. *Ecology*, 93, 1421–1430.
- Lefcheck, J.S. (2016) piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210x.12512>
- Li, S., Lang, X., Liu, W., Ou, G., Xu, H. & Su, J. (2018) The relationship between species richness and aboveground biomass in a primary *Pinus kesiya* forest of Yunnan, southwestern China. *PLoS One*, 13, e0191140.
- Leonart, J., Salat, J. & Torres, G.J. (2000) Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology*, 205, 85–93.
- Loreau, M. (1998) Biodiversity and ecosystem functioning: a mechanistic model. *Proceedings of the National Academy of Sciences*, 95, 5632–5636.
- Loreau, M. & de Mazancourt, C. (2008) Species synchrony and its drivers: neutral and nonneutral community dynamics in fluctuating environments. *The American Naturalist*, 172, E48–E66.
- Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A. et al. (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804–808.
- Mallin, M.A., Johnson, V.L., Ensign, S.H. & MacPherson, T.A. (2006) Factors contributing to hypoxia in rivers, lakes, and streams. *Limnology and Oceanography*, 51(1, part 2), 690–701. [https://doi.org/10.4319/lo.2006.51.1\\_part\\_2.0690](https://doi.org/10.4319/lo.2006.51.1_part_2.0690)
- Maureaud, A., Hodapp, D., van Denderen, P.D., Hillebrand, H., Gislason, H., Spaanheden Dencker, T. et al. (2019) Biodiversity–ecosystem functioning relationships in fish communities: biomass is related to evenness and the environment, not to species richness. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20191189.
- May, R.M. (1972) Will a large complex system be stable? *Nature*, 238, 413–414.
- McCann, K.S. (2000) The diversity–stability debate. *Nature*, 405(6783), 228–233. <https://doi.org/10.1038/35012234>
- McCann, K. & Hastings, A. (1997) Re-evaluating the omnivory–stability relationship in food webs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 264, 1249–1254.
- McCann, K.S. & Rooney, N. (2009) The more food webs change, the more they stay the same. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1789–1801.
- McHugh, P.A., McIntosh, A.R. & Jellyman, P.G. (2010) Dual influences of ecosystem size and disturbance on food chain length in streams. *Ecology Letters*, 13, 881–890.
- Mittelbach, G.G. & Persson, L. (1998) The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(6), 1454–1465. <https://doi.org/10.1139/f98-041>
- Neutel, A.-M., Heesterbeek, J.A.P., van de Koppel, J., Hoenderboom, G., Vos, A.N., Kaldewey, C. et al. (2007) Reconciling complexity with stability in naturally assembling food webs. *Nature*, 449, 599–602.
- O’Gorman, E.J., Zhao, L., Pichler, D.E., Adams, G., Friberg, N., Rall, B.C. et al. (2017) Unexpected changes in community size structure in a natural warming experiment. *Nature Climate Change*, 7(9), 659–663. <https://doi.org/10.1038/nclimate3368>
- O’Connor, M.I. (2009) Warming strengthens a herbivore–plant interaction. *Ecology*, 90(2), 388–398. <https://doi.org/10.1890/08-0034.1>
- Olivier, T., Thébault, E., Elias, M., Fontaine, B. & Fontaine, C. (2020) Urbanization and agricultural intensification destabilize animal communities differently than diversity loss. *Nature Communications*, 11, 2686.
- Pennekamp, F., Pontarp, M., Tabi, A., Altermatt, F., Alther, R., Choffat, Y. et al. (2018) Biodiversity increases and decreases ecosystem stability. *Nature*, 563, 109.
- Pichler, M., Boreux, V., Klein, A.-M., Schleuning, M. & Hartig, F. (2020) Machine learning algorithms to infer trait-matching and predict species interactions in ecological networks. *Methods in Ecology and Evolution*, 11(2), 281–293. <https://doi.org/10.1111/2041-210x.13329>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2021) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–152. Available at: <https://CRAN.R-project.org/package=nlme> [Accessed 11th August 2021].
- Poisot, T., Cirtwill, A.R., Cazelles, K., Gravel, D., Fortin, M.-J. & Stouffer, D.B. (2016) The structure of probabilistic networks. *Methods in Ecology and Evolution*, 7(3), 303–312. <https://doi.org/10.1111/2041-210x.12468>
- Poisot, T., Mouquet, N. & Gravel, D. (2013) Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs. *Ecology Letters*, 16(7), 853–861. <https://doi.org/10.1111/ele.12118>
- Portalier Sébastien, M.J., Fussmann Gregor, F., Loreau, M. & Cherif, M. (2019) The mechanics of predator–prey interactions: first principles of physics predict predator–prey size ratios. *Functional Ecology*, 33(2), 323–334. <https://doi.org/10.1111/1365-2435.13254>
- Post, D.M., Pace, M.L. & Hairston, N.G. (2000) Ecosystem size determines food-chain length in lakes. *Nature*, 405, 1047–1049.
- R Core Team. (2020) R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Available at: <https://www.R-project.org/> [Accessed 11th August 2021].
- Raimondo, S., Turčáni, M., Patočka, J. & Liebhold, A.M. (2004) Interspecific synchrony among foliage-feeding forest Lepidoptera species and the potential role of generalist predators as synchronizing agents. *Oikos*, 107(3), 462–470.
- Revelle, W. (2019) Psych: procedures for psychological, psychometric, and personality research. R package. Available at: <https://CRAN.R-project.org/package=psych> [Accessed 11th August 2021].
- Rip, J.M.K. & McCann, K.S. (2011) Cross-ecosystem differences in stability and the principle of energy flux: cross-ecosystem differences in stability. *Ecology Letters*, 14(8), 733–740.
- Roscher, C., Weigelt, A., Proulx, R., Marquard, E., Schumacher,



- J., Weisser, W.W. et al. (2011) Identifying population- and community-level mechanisms of diversity– stability relationships in experimental grasslands. *Journal of Ecology*, 99(6), 1460– 1469.
- Sander, E.L., Wootton, J.T. & Allesina, S. (2017) Ecological network inference from long- term presence– absence data. *Scientific Reports*, 7, 7154.
- Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M. et al. (2010) Bottom- up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, 468, 553– 556.
- Schneider, F.D., Brose, U., Rall, B.C. & Guill, C. (2016) Animal diversity and ecosystem functioning in dynamic food webs. *Nature Communications*, 7, 12718.
- Shanafelt, D.W. & Loreau, M. (2018) Stability trophic cascades in food chains. *Royal Society Open Science*, 5, 180995.
- Stouffer, D.B. & Bascompte, J. (2011) Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences*, 108(9), 3648– 3652.
- Tabi, A., Petchey, O.L. & Pennekamp, F. (2019) Warming reduces the effects of enrichment on stability and functioning across levels of organisation in an aquatic microbial ecosystem. *Ecology Letters*, 22, 1061– 1071.
- Teng, J. & McCann, K.S. (2004) Dynamics of compartmented and reticulate food webs in relation to energetic flows. *The American Naturalist*, 164, 85–1 00.
- Thébault, E. & Fontaine, C. (2010) Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science*, 329, 853– 856.
- Thébault, E., Huber, V. & Loreau, M. (2007) Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos*, 116, 163– 173.
- Thébault, É. & Loreau, M. (2003) Food- web constraints on biodiversity-ecosystem functioning relationships. *Proceedings of the National Academy of Sciences*, 100, 14949– 14954.
- Thébault, E. & Loreau, M. (2005) Trophic interactions and the relationship between species diversity and ecosystem stability. *The American Naturalist*, 166, E95– E114.
- Thibaut, L.M. & Connolly, S.R. (2013) Understanding diversity– stability relationships: towards a unified model of portfolio effects. *Ecology Letters*, 16(2), 140– 150.
- Tilman, D., Isbell, F. & Cowles, J.M. (2014) Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, 45(1), 471– 493.
- Tilman, D., Reich, P.B. & Knops, J.M.H. (2006) Biodiversity and ecosystem stability in a decade- long grassland experiment. *Nature*, 441, 629– 632.
- Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718– 720.
- Uszko, W., Diehl, S., Englund, G. & Amarasekare, P. (2017) Effects of warming on predator- prey interactions — A resource- based approach and a theoretical synthesis. *Ecology Letters*, 20(4), 513– 523.
- Valencia, E., de Bello, F., Galland, T., Adler, P.B., Lepš, J., E- Vojtkó, A. et al. (2020) Synchrony matters more than species richness in plant community stability at a global scale. *Proceedings of the National Academy of Sciences*, 117, 24345– 24351.
- Wang, S. & Brose, U. (2018) Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. *Ecology Letters*, 21, 9– 20.
- Winemiller, K.O. (1989) Must connectance decrease with species richness? *The American Naturalist*, 134(6), 960– 968.
- Woods, T., Comte, L., Tedesco, P.A. & Giam, X. (2020) Testing the diversity– biomass relationship in riverine fish communities. *Global Ecology and Biogeography*, 29(10), 1743– 1757.
- Wu, X., Wang, X., Tang, Z., Shen, Z., Zheng, C., Xia, X. et al. (2015) The relationship between species richness and biomass changes from boreal to subtropical forests in China. *Ecography*, 38, 602– 613.
- Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences*, 96, 1463– 1468.
- Yvon- Durocher, G., Montoya, J.M., Trimmer, M. & Woodward, G. (2011) Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. *Global Change Biology*, 17(4), 1681– 1694.

## SUPPORTING INFORMATION

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