Decadal biodiversity trends in rivers reveal recent community rearrangements

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Decadal biodiversity trends in rivers reveal recent community rearrangements

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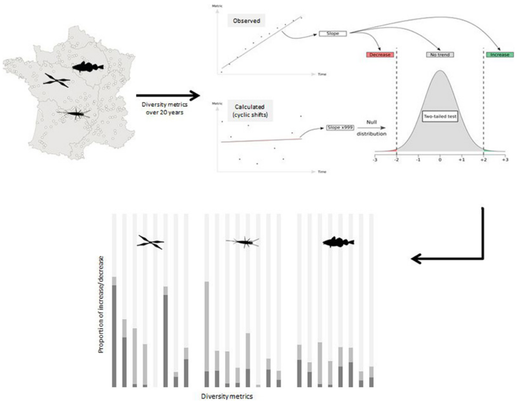
HIGHLIGHTS

- Water management over the past decades decreased nutrient loads in French streams.
- A recovery of sensitive taxa was observed for diatoms, macroinvertebrates and fish.
- Diatom richness declined over time, while macroinvertebrate richness increased.
- A shift from planktonic to benthic dominance of diatoms occurred.
- This shift induced functional changes in macroinvertebrates and fish communities.

GRAPHICAL ABSTRACT



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ABSTRACT

While it is recognized that biodiversity currently declines at a global scale, we still have an incomplete understanding of local biodiversity trends under global change. To address this deficiency, we examined the recent decadal trends in water quality and biodiversity (taxonomic and functional) of key river organisms (diatoms, macroinvertebrates and fish) in France. We implemented regression, RLQ and fourth-corner analyses. Our results showed that nutrient loads tended to decrease, diatom richness tended to decline and macoinvertebrate richness tended to increase. The recovery of sensitive taxa in all three groups suggested a successful outcome of water quality management in France over the past decades. Our study further revealed consistent rearrangements within river communities, with a decrease in the ratio of planktonic to benthic diatoms, and corresponding functional changes in macroinvertebrate and fish trait composition, indicative of a trophic cascade in response to changes in environmental conditions.

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1. Introduction

Many scientific opinions converge on the idea that a "6th phase of mass extinction" is in progress (Brook et al., 2008). Half of the ice-free land surface has been converted to agricultural or urban areas and one-third of the forest has been destroyed (Ellis and Ramankutty, 2008). Since 1600, 906 known species have become extinct (IUCN, 2015). Although this represents a small fraction of the eight million existing eukaryotic species, the corresponding extinction rate is 100 to 1000 times higher than the baseline rates from fossil records (Ceballos et al., 2015). Biodiversity loss in the Anthropocene is global and affects all ecosystems, but freshwaters are particularly vulnerable, threatened by much higher extinction rates compared to terrestrial habitats due to water pollution, flow modifications, climate change, species invasions and over-exploitation (Ricciardi and Rasmussen, 1999; Jenkins, 2003; Dudgeon et al., 2006; Wiens, 2016; WWF, 2020). Therefore, it is critical to evaluate the trends in freshwater biodiversity in order to develop effective conservation strategies (Turak et al., 2017).

There are several challenges with measuring freshwater biodiversity responses to global change, arising from limited research duration, scope, and number of metrics (Alahuhta et al., 2019). While biodiversity decline at a global scale is well-established, at a local scale, communities may undergo only compositional shifts, such as the replacement of locally rare species by common ones, without any decrease in richness (Dornelas et al., 2014; Hillebrand et al., 2018). This prompted scientists to broaden their view of anthropogenic effects as causing not only biodiversity loss but also biodiversity rearrangements (Blowes et al., 2019; Magurran et al., 2019). Thus, to adequately evaluate biotic responses to global change, community aspects such as temporal turnover (temporal beta-diversity), rarity, dominance and evenness (species abundance distribution) should be explored in addition to species richness (Mason et al., 2005).

Changes of nutrient levels and climate are among the strongest drivers of freshwater biodiversity and composition (Jeppesen et al., 2010a, 2010b; Rosset et al., 2010). Decades of nutrient enrichment due to agriculture and urbanization have impacted biodiversity worldwide (Song et al., 2009). In streams, high nutrient levels in agricultural watersheds tend to increase local diversity but cause widespread regional biodiversity declines (species loss and biotic homogenization) in diatoms, insects, and fish compared to nutrient-poor forested watersheds (Budnick et al., 2019). Eutrophication can also increase algal biomass and primary production (Elser et al., 2007), and thus promote consumer diversity by enhancing the availability of food for herbivores (Cook et al., 2018). However, in highly eutrophic conditions, oxygen and light depletion resulting from an excessive primary productivity, together with the increasing abundance of toxin producing species, create harmful conditions for consumers (Wang et al., 2021). Climate warming, known to enhance primary production, tends to exacerbate the negative effects of eutrophication (Woodward et al., 2010). However, following the adoption of stricter environmental policies under the Water Framework Directive (European Parliament. Directive 2000/60/EC, 2000), many freshwaters have experienced re-oligotrophication (Jeppesen et al., 2005a, 2005b; Pomati et al., 2012). Nevertheless, it is still unclear how re-oligotrophication impacts freshwater biodiversity and the functional relationships between producers and consumers, particularly in a global change context (Flaim et al., 2016; Verbeek et al., 2018).

Temporal biodiversity trends vary across organismal groups (Alahuhta et al., 2019) due to differences in sensitivity to nutrients and temperature (Bouraï et al., 2020), but also due to differences in diets (Gossner et al., 2013), dispersal capacities (Jourdan et al., 2019), and generation times (Korhonen et al., 2010). Nevertheless, studies on recent stream diatom, and to a lesser extent, fish community dynamics are still scarce (Alahuhta et al., 2019). Temporal changes in fish communities are generally a result of species loss (Kuczynski et al., 2018), introduction (Loewen et al., 2020) and/or expansion of non-native species under warming conditions (Gurevitch and Padilla, 2004). Macroinvertebrates, which are most commonly explored (Alahuhta et al., 2019), show diverse local temporal diversity trends both negative (Poff et al., 2010) and positive (Floury et al., 2018).

Understanding how cross-taxon relationships vary among the different aspects of diversity, especially from a functional point of view, gives deep insights into the way the freshwater realm faces global changes (Andersen et al., 2020). Changes in water quality or habitat conditions usually result in differences in the availability of food resources, with direct impacts on feeding habits and reproduction strategies (Woodward and Hildrew, 2002; Lainé et al., 2014). Trophic and reproductive guilds should thus provide a consistent way for determining if taxonomically distant groups have functionally concordant responses to changing environmental conditions even if the respective taxonomic responses diverge (Milošević et al., 2017). Nevertheless, temporal multi-taxa analyses of stream biodiversity are rare (but see Pilotto et al., 2020), limiting our understanding of the consequences of global change for freshwaters.

The aim of the present study was to characterize the decadal trends of diatom, macroinvertebrate and fish communities, and their responses to recent changes in stream physico-chemistry and climate. This time span is appropriate for investigating ecological responses without strong interference of most evolutionary processes (Rosenzweig, 1995). We selected a set of metrics to measure key aspects of biodiversity trends over the last decades, including taxonomic and functional richness, evenness, temporal beta-diversity, functional dispersion and numbers of winners vs. losers. We made the following predictions. First, we anticipated significant environmental changes over the period, reflecting both global warming and the implementation of the Water Framework Directive, with direct impacts on organisms based on their tolerance to nutrients and temperature. Second, we expected strong but group-specific diversity shifts in this environmental context, with marked differences between primary producers and consumers. Third, in response to global change, we hypothesized functional concordance among the different groups in terms of feeding habits and reproduction strategies.

2. Materials & methods

2.1. Biological data

Our dataset encompasses benthic diatom, macroinvertebrate and fish samples from respectively 258, 253 and 222 distinct sites from rivers in France (Fig. 1). Samples were collected from 1994 to 2013 as part of the national aquatic ecosystem monitoring program following standard protocols, implemented under the Water Framework Directive (available on the Naïades website, http://naiades.eaufrance.fr/). Sampling frequencies for each biological group are reported in Fig. S1. All taxa were described by a set of traits related to environmental preference, life history, reproduction strategy and trophic position (when appropriate). Among them and according to Violle et al. (2007), we considered as functional trait "any morphological, physiological or phenological feature measurable at the individual level."

2.1.1. Diatom dataset

There were 2613 diatom samples collected following a standard protocol (NFT 90–354, AFNOR, 2016). Stones were scraped during the warm and low flow period, between May and October, to reduce seasonal variability in species assemblages. Diatoms were identified in permanent slides at 1000 x magnification by examining 400 cleaned frustules. Krammer and Lange-Bertalot (1986–1991) and Lange-Bertalot (1995–2015, 2000–2013) were used as main identification references. Taxonomic standardization at the species level was performed for 977 species with Omnidia 5.3 software (www.omnidia.fr; Lecointe et al., 1993). All taxa were described by nine traits (Table 1), five related to preference for oxygen levels and tolerance of organic matter and nutrients (Carayon et al., 2019), and four guilds (low profile, high profile, motile, planktonic) (Passy, 2007 and Omnidia software).

2.1.2. Macroinvertebrate dataset

Macroinvertebrates were collected according to the Multi-Habitat Sampling NF T90–350 standard protocol (AFNOR, 2004a) from 1996 to 2006

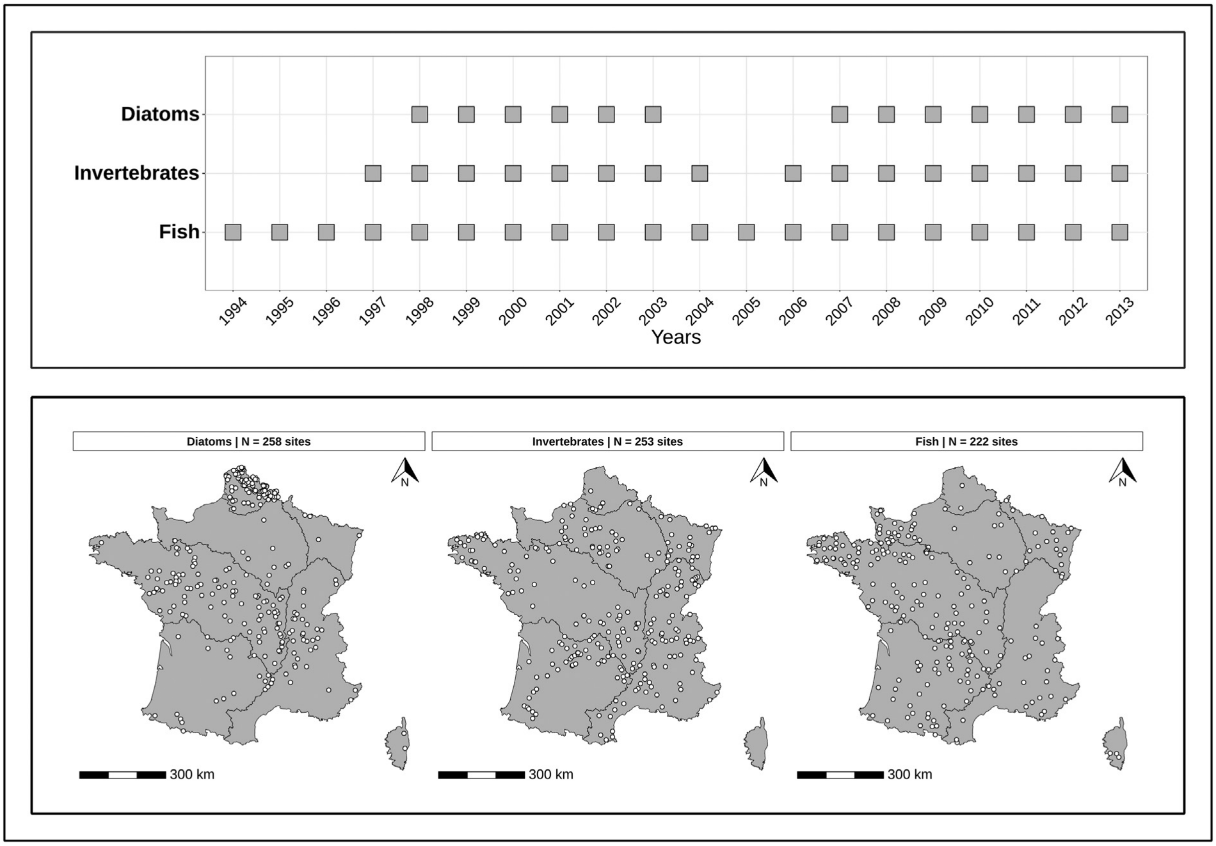


Fig. 1. Temporal and spatial distribution of the study sites.

and to the Multi-Habitat Sampling XP T90–333 standard protocol from 2007 to 2013. Only samples comparable between these two protocols, i.e. those taken from the most biogenic habitats, were analysed. There were 2868 samples taken with a Surber net (sampling area 0.05m^2, mesh size 500 μm) during summer low flow conditions from eight pre-defined habitats at each site. Macroinvertebrates were sorted, counted and identified at the family (NF T90–350) or genus level (XP T 90–388). All data, comprising 133 different families, were analysed at the family level. Each family was described by nine traits (Tachet et al., 2010) related to life-cycle properties, feeding, reproduction and tolerance to eutrophication and temperature (Table 2).

2.1.3. Fish dataset

There were 3638 fish samples, collected by electrofishing during the low flow period following a standard protocol (T90–344, AFNOR, 2004b). Each individual was identified to species and there were 49 recorded species. In case of multi-pass electrofishing, only fish caught in the first pass were considered in order to limit bias relative to single-pass samples. Density was calculated as number of individuals per unit area.

We used eleven traits related to tolerance (habitat degradation, oxygen and temperature), status (native vs exotic), trophic guilds and reproduction strategies to describe each species (Logez et al., 2013; Poulet et al., 2011; Pont et al., 1995; Bergerot et al., 2013; Froese and Pauly, 2010; Freyhof and Kottelat, 2007; Keith et al., 2011) (Table 3).

2.2. Environmental data

Physico-chemical data were gathered by the French Water Agencies and included water pH, specific conductance (at 20 °C, mS.cm^{-1}), dissolved oxygen concentration (O_2, mg.L^{-1}), dissolved oxygen saturation (% O_2), biological oxygen demand (BOD5, mg of O_2 consumed per liter during 5 days of incubation at 20 °C), total phosphorous (Ptot, mg.L^{-1}), orthophosphate (PO_4, mg.L^{-1}), ammonium (NH_4, mg.L^{-1}), nitrate (NO_3, mg.L^{-1}), and nitrite (NO_2, mg.L^{-1}). Since physico-chemical data were not systematically measured at the time of biological sampling, we calculated the median values of all environmental variables measured during the 45 days before and the 15 days after the biological sampling date within a 5-kilometer distance upstream and downstream of the sampling site. Sixteen fish samples without corresponding physico-chemical data were removed. Climatic variables were extracted from the SAFRAN database (Vidal et al., 2010) and included mean, minimum and maximum air temperature (°C) and cumulative solid and liquid precipitations (mm). We calculated an annual average value for each climatic variable for each site.

2.3. Data analyses

All analyses were performed with R 3.6.1 software (Team, 2019).

2.3.1. Biodiversity indices

We assessed the diversity of each community (diatom, fish and macroinvertebrate) for each sampling year at each site using a set of metrics: taxonomic richness (S), evenness Shannon-Wiener index H′, temporal beta-diversity (taking the first sampling time point as a baseline), functional richness (FRic) and evenness (FEve, the evenness of abundance distribution in a trait space), following Villéger et al. (2008), and functional dispersion (FDis, the mean distance in multidimensional trait space of individual species to the centroid of all species), following Laliberté and Legendre (2010). Functional metrics were calculated based on all available information related to traits. All traits had equal weighting in the analysis. Diatom and fish traits were treated as categorical variables and macroinvertebrate traits as fuzzy variables. Categorical traits were input as factors and were ordered when appropriate (e.g., size classes, preferences along environmental gradients). Traits coded as fuzzy variables were treated according to the recommendations of the “Handbook of Trait-Based Ecology” (de Bello et al., 2021a) by first computing Gower dissimilarity (trait dissimilarity between species) before computing the final Gower distance (gawdis function from the 'gawdis' package, de Bello et al., 2021b). The three functional local diversity metrics were calculated with the dbFD function of 'FD' package (Laliberté and Legendre, 2010). Values obtained for diatoms, macroinvertebrates and fish could not be compared given that functional metrics calculated with the dbFD function were highly correlated with taxonomic richness. Shannon-Wiener H′ was calculated using the diversity function of 'vegan' package (Oksanen et al., 2019). Temporal beta-diversity was measured with Baselga's partitioning approach (with Sørensen index, based on presence/absence data) disentangling turnover (species replacement) from nestedness (species gain or loss) (Baselga, 2010) (beta.div.comp function of 'adespatial' package, Dray et al., 2019).

2.3.2. Biodiversity trends

We fitted linear regression models for each metric against time and calculated the slope to measure the strength of temporal change. The assumptions of the linear models were graphically checked to ensure normality and homogeneity of the residuals (histograms and QQplots) (here and in Sections 2.3.3. and 2.3.4.). For beta-diversity, we chose a baseline approach that compares each sample with the first one in the time series of the site considered. An increase in temporal beta-diversity means that the deviation of sampled communities from the baseline community increases though time. Taking the first sampling date as a baseline may introduce a bias if this sample is an outlier. To ensure that this is not the case, we examined the first three samples as a baseline. As the results were not much different (results not shown), we retained the longer time series and kept the first sampling date as a baseline. To test whether the temporal diversity trends were significant, we compared the calculated slopes to those obtained from null models (999 draws): Following Magurran et al. (2018), we used cyclic shift permutations (cyclic_shift function of the 'codyn' package, Hallett et al., 2016). A cyclic shift permutation preserves single-species temporal autocorrelation while varying species abundances (Magurran et al., 2018; Henderson and Magurran, 2014). To assess the significance of trends, we carried out two-sided *Z*-tests comparing the observed slopes to those obtained from the null distribution. *P*-values were adjusted to account for multiple testing, with the false discovery rate method (Dray et al., 2014) (here and in Sections 2.3.3. and 2.3.4.).

2.3.3. Physico-chemical and climatic trends

For each site, we fitted a linear model for each environmental variable against time and calculated the slope to measure the strength of temporal change in physico-chemical and climatic conditions. To test whether these trends were significant, we compared (z-tests) the calculated slopes to slopes obtained from null models (999 draws), computed using free permutations.

2.3.4. Winners and losers

In order to better understand the changes observed in community patterns, we analysed the temporal dynamics of each species (diatoms and fish), family (macroinvertebrates) and trait. Winners and losers are taxa or traits that significantly increase or decrease within the time period (Domisch et al., 2011). We fitted linear models of each species/family or trait abundances against time and calculated the slope to measure the strength of temporal change. To test whether community structural and trait dynamics significantly differed from random fluctuations, we again compared the calculated slopes to those obtained from null models (999 draws, cyclic shifts) and computed two-sided *Z*-tests of the observed slope to the one obtained from the null distribution.

2.3.5. Relationships between traits and environmental variables

According to Dray et al. (2014), we used the RLQ analysis (Dolédec et al., 1996) combined with the fourth-corner approach (Legendre et al., 1997; Dray and Legendre, 2008) to identify the main relationships among environmental variables, species abundances and traits (methods implemented in the 'ade4' package, Dray and Dufour, 2007). This quantitative assessment links traits to environmental variables, but with no consideration of temporal trends.

The RLQ method analyzes information contained in three tables: table R with measurements of environmental variables, table L with species abundances, and table Q with species traits. The RLQ analysis is a simultaneous ordination of those three tables, allowing for mixed continuous and categorical variables. The interpretations were based on the variances explained by the first two RLQ axes, and significance was assessed based on 999 permutations. We calculated sample scores (environmental gradients) and species scores (trait syndromes) on those axes.

The fourth-corner approach tests multiple pairwise associations between traits and environmental variables separately. The combination of the two methods results in applying the fourth-corner tests directly on the outputs of the RLQ method (sample scores and species scores). A correlation matrix between environmental variables and traits is obtained. As these relationships are mediated by species composition, two null hypotheses must be tested before any interpretation of the results: i) the distribution of species with fixed traits is not influenced by environmental conditions (model 2) and ii) the species composition of sites with fixed environmental conditions is not influenced by the species traits (model 4) (Dray and Legendre, 2008). Significance of the trait-environment relationships was checked via 999 permutations. *P*-values were adjusted to account for multiple testing, with the false discovery rate method (Dray et al., 2014).

3. Results

3.1. Community trends

Temporal changes in diversity varied depending on the metric, biological group, and site (Fig. 2, Table S2). Only taxonomic and functional richness displayed noteworthy temporal trends. These changes mainly concerned diatoms and macroinvertebrates.

In diatoms, temporal changes were observed in species and functional richness, decreasing in 50% and 44% of sites, respectively. The other diversity metrics displayed no trends in the majority of sites, although total beta-diversity showed an increase in more sites (21% of sites) compared to a decrease (1% of sites). In macroinvertebrates, family richness had a positive temporal trend in 40% of sites, and functional richness increased in the majority of sites (70%). All other diversity metrics showed no temporal trends. In fish, diversity metrics exhibited no temporal trends in most sites.

3.2. Environmental trends

Physico-chemical trends revealed an overall improvement in water quality, with decreasing nutrient concentrations (total phosphorus, orthophosphates and ammonium) and biological oxygen demand frequently observed in all three datasets. For example for diatoms, orthophosphate concentrations and biological oxygen demand respectively decreased from 0.60 $mg.L^{-1}$ and 3.27 $mg.L^{-1}$ in 1998 to 0.12 $mg.L^{-1}$ (decrease of 80%) and 1.12 $mg.L^{-1}$ (decrease of 66%) in 2013 (annual mean values, all sampling sites considered). Concerning climate conditions, no change occurred across sites (Fig. 2b, Table S3).

3.3. Winners and losers

3.3.1. Diatoms

While the majority of diatoms exhibited no temporal trends (65%), more species showed declining (160 species) than increasing trends in abundance (74 species) (Table S4). Regarding diatom environmental preferences, we observed a significant increase of sensitive forms (Table 1). This trend was detected across almost all observed attributes such as oxygen requirements, saprobity, trophic state, organic nitrogen and nitrates. Regarding diatom guilds, the most striking result was a temporal shift from motile/planktonic (significantly decreasing) to low profile (significantly increasing).

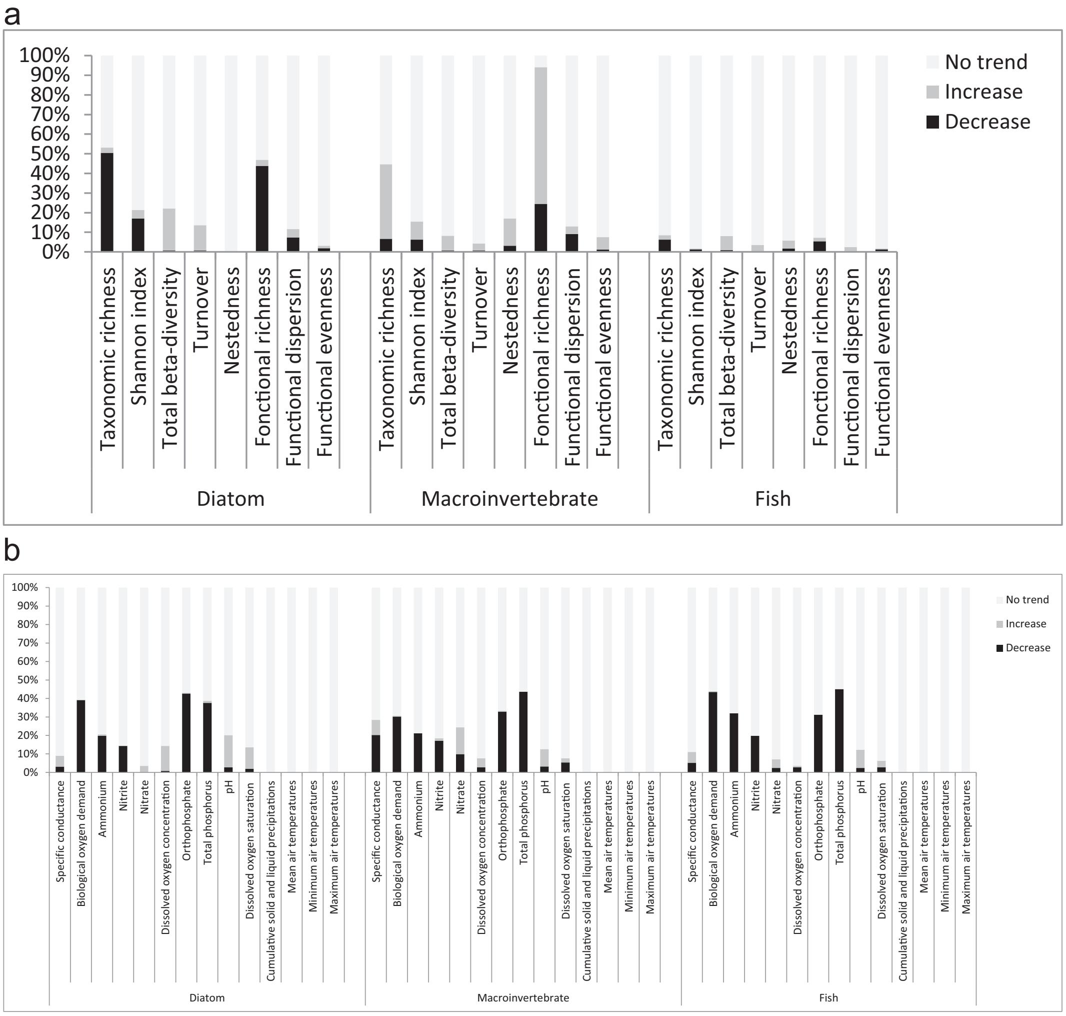


Fig. 2. a. Trends for diversity metrics in diatoms, macroinvertebrates and fish (% of sites on the y-axis). **b**. Environmental trends.

3.3.2. Macroinvertebrates

Contrary to diatoms, invertebrate families abundance showed more increasing trends (15 families) than declining trends (8 families) while 75% of the families showed no trend (Table S5). The *Gammaridae*, *Elmidae* and *Brachycentridae* were favored, whereas the *Erpobdellidae* and *Rhyacophilidae* showed a significant decline.

Macroinvertebrate feeding on other living macroinvertebrates, including predator and piercer feeding groups, declined, while those feeding on living microphyte, including scrapers, increased in number (Table 2). Families with eutrophic and α-mesosaprobic preferences also decreased while oligotrophic and oligosaprobic families increased. In parallel, an increasing trend was observed for thermophilic families at the expense of eurythermic ones. We also noticed the growing abundance of families with small size, long life cycles and ovoviviparity.

3.3.3. Fish

The majority of fish species showed no trend in abundance (Table S6). All species showing significant local declines were native with wide distribution in French watercourses. Only two species significantly increased in abundance, including *Pseudorasbora parva*, recently introduced in France.

Similar to diatoms and macroinvertebrates, there was a clear abundance decline in fish groups possessing tolerance, e.g. to water pollution, habitat degradation, or with omnivorous diet (Table 3). Conversely, most groups associated with intolerance or ecological specialization showed a significant positive trend. In addition, species feeding in the water column showed declines in abundance compared to benthic species exhibiting an opposite trend.

Many traits also showed diverging responses. In particular, species with intermediate body size, intermediate or long lifespan, high relative fecundity, small egg size, without parental care to eggs or young stages showed a significant decline. In contrast, short lifespan, low relative fecundity, large egg size and parental care significantly increased.

3.4. Trait-environment relationships

The combined RLQ and fourth-corner analysis revealed the variability between traits within each group, and the role of environmental parameters in this variability. The first two RLQ axes summarized the relationships between traits and environmental variables: 93.1% and 4.2% of the cross-covariance for axes 1 and 2 respectively for diatoms, 48.6% and 34.3% for macroinvertebrates, and 88.9% and 8.9% for fish.

For diatoms, almost all the cross-covariance was represented by the first RLQ axis. Its left (negative) part characterized saprobous and eutrophic taxa, taxa tolerant to oxygen depletion, planktonic forms, and to a lesser extent, motile and high profile forms (Fig. S7a). Such taxa were mostly found in sites with high levels of nutrients, conductivity and organic matter (Fig. S7b). The right (positive) part of the axis identified taxa sensitive to oxygen depletion, nutrient and organic matter enrichment, and low profile forms. Those taxa were found in sites with high dissolved oxygen concentrations, and low

Table 1

Trends in diatom trait abundances over time (no trend: =; decreasing: ↓; increasing: ↑; N.C.: not calculated). Decreasing trends are represented by red cells, increasing trends by green cells.

Type of trait	Trait	Modality	Thresholds	Modality occ. (%)	Slope	Trend	Two-sided test (p-value)
Autecological properties	Oxygen requirements *(Oxygen saturation, %)*	Low	< 83	2.09	-0.068	=	0.066
		Moderate	≥ 83 - 91	39.32	-0.665	↓	0.005
		High	≥ 91 - 96	38.18	0.265	↑	0.005
		Very high	≥ 96	20.41	0.479	=	0.058
	Saprobity *(BOD5, mg.L^{-1})*	Oligosaprobous	< 1.14	13.71	0.533	↑	0.008
		Mesosaprobous	≥ 1.14 - 1.56	49.72	0.151	=	0.094
		β-mesosaprobous	≥ 1.56 - 2.14	31.06	-0.322	↓	0.005
		α-mesosaprobous	≥ 2.14 - 2.90	5.07	-0.362	↓	0.005
		Polysaprobous	≥ 2.90	0.44	N.C.	N.C.	N.C.
	Trophic state *(Orthophosphates, mg.L^{-1})*	Oligotrophic	< 0.11	15.52	0.550	↑	0.031
		Oligo-mesotrophic	≥ 0.11 - 0.16	10.24	N.C.	N.C.	N.C.
		Mesotrophic	≥ 0.16 - 0.21	17.44	-0.042	=	0.464
		Meso-eutrophic	≥ 0.21 - 0.30	31.49	-0.170	=	0.258
		Eutrophic	≥ 0.30 - 0.43	18.61	0.031	=	0.636
		Eutro-hypereutrophic	≥ 0.43 - 0.56	5.17	-0.123	↓	0.008
		Hypereutrophic	≥ 0.56	1.53	-0.135	↓	0.005
	Organic nitrogen *(Organic nitrogen, mg.L^{-1})*	N_{org} oligotrophic	< 0.57	20.93	0.349	=	0.170
		N_{org} oligo-mesotrophic	≥ 0.57 - 0.73	48.38	0.336	↑	0.011
		N_{org} mesotrophic	≥ 0.73 - 0.88	24.08	-0.241	↓	0.011
		N_{org} eutrophic	≥ 0.88 - 1.20	6.16	-0.413	↓	0.005
		N_{org} hypereutrophic	≥ 1.20	0.45	-0.022	=	0.058
	Nitrates *(Nitrates, mg.L^{-1})*	Oligonitrophilous	< 6.10	6.60	0.509	↑	0.005
		Oligo-mesonitrophilous	≥ 6.10 - 10.64	23.49	-0.205	=	0.146
		Mesonitrophilous	≥ 10.64 - 13.91	31.16	-0.236	=	0.061
		Eunitrophilous	≥ 13.91 - 17.84	37.93	N.C.	N.C.	N.C.
		Hypernitrophilous	≥ 17.84	0.82	N.C.	N.C.	N.C.
Functional traits	Guilds	Low profile	36.78		0.801	↑	0.005
		High profile	14.40		0.018	=	0.636
		Motile	42.52		-0.381	↓	0.005
		Planktonic	6.30		-0.418	↓	0.005

levels of nutrients and BOD5. According to RLQ results, sites with higher annual temperatures were mostly impacted, higher order rivers.

For macroinvertebrates, the positive part of the first RLQ axis distinguished saprobic families, feeding on dead animals, microinvertebrates and vertebrates, shredders, with polyvoltinism, long life cycle and ovoviviparity (Fig. S7c), mostly found in sites with high conductivity and high levels of nutrients (Fig. S7d). The negative part of this axis identified small sized oligosaprobic families, with diverse reproduction strategies, mainly feeding on microphytes and small detritus (scrapers, filter feeders), found in sites with high dissolved oxygen concentrations.

The second RLQ axis appeared to reflect the position of sites along the longitudinal gradient of the river (upstream-downstream gradient), related to temperature and oxygen availability. This axis globally discriminates psychophilic, xenosaprobic and oligotrophic families (Fig. S7e), found in low temperature and high dissolved oxygen conditions (Fig. S7f) from thermophilic, mesotrophic and mesosaprobic families also showing polyvoltinism.

For fish as for diatoms, almost all the cross-covariance was represented by the first RLQ axis. On the negative part of the axis, there were planktivorous and omnivorous taxa, taxa tolerant to oxygen depletion and habitat degradation, eurythermal and exotic species, and taxa with long lifespan, large body size, medium to high fecundity and small egg size (Fig. S7g). These taxa were mostly found in sites with high levels of nutrients, conductivity and organic matter (Fig. S7h). The right part of the axis identified small species, intolerant to habitat degradation and oxygen depletion, stenothermal, as well as insectivorous species, and species with low fecundity, parental care and large egg size. Those species were detected predominantly in oxygen rich sites.

The global test of the RLQ analysis found highly significant relationships between species distributions and environmental variables for all

Table 2

Trends in macroinvertebrate trait abundances over time (no trend: =; decreasing: ↓; increasing: ↑; N.C.: not calculated). Decreasing trends are represented by red cells, increasing trends by green cells.

Trait	Modality	Modality occ. (%)	Slope	Trend	Two-sided test (p-value)
Trophic level	Oligotrophic	37.94	0.160	↑	0.006
	Mesotrophic	42.59	-0.052	=	0.201
	Eutrophic	19.47	-0.105	↓	0.006
Temperature	Psychrophilic	21.88	0.080	=	0.187
	Thermophilic	17.57	0.097	↑	0.006
	Eurythermic	60.55	-0.178	↓	0.006
Saprobity	Xenosaprobic	11.08	0.031	=	0.418
	Oligosaprobic	29.99	0.075	↑	0.006
	α-mesosaprobic	17.61	-0.095	↓	0.006
	β-mesosaprobic	38.52	-0.004	=	0.873
	Polysaprobic	2.79	0.000	=	0.421
Maximum potential size	≤ 0.25 cm	0.32	-0.004	=	0.421
	> 0.25 – 0.5 cm	17.59	0.261	↑	0.012
	> 0.5 - 1 cm	41.14	-0.190	↓	0.032
	> 1 - 2 cm	21.06	-0.153	↓	0.006
	> 2 - 4 cm	19.37	0.092	=	0.156
	> 4 - 8 cm	0.40	0.009	=	0.339
	> 8 cm	0.13	-0.015	↓	0.006
Life-cycle duration	≤ 1 year	73.79	-0.183	↓	0.026
	> 1 year	26.21	0.184	↑	0.026
Voltinism	< 1	2.50	N.C.	N.C.	N.C.
	1	47.41	-0.089	=	0.156
	> 1	50.09	0.155	=	0.069
Reproduction strategy	Ovoviviparity	27.90	0.298	↑	0.006
	Isolated eggs, free	3.09	-0.022	=	0.268
	Isolated eggs, cemented	11.98	-0.084	=	0.259
	Clutches, free	15.07	-0.076	=	0.141
	Clutches, cemented or fixed	35.70	-0.003	=	0.934
	Clutches, in vegetation	1.10	-0.068	↓	0.006
	Clutches, terrestrial	4.57	-0.030	=	0.141
	Asexual reproduction	0.58	-0.015	=	0.223
Food consumed	Microorganisms	0.85	-0.002	=	0.144
	Detritus < 1mm	22.21	0.007	=	0.930
	Dead plant ≥ 1mm	14.70	0.073	=	0.144
	Living microphytes	25.95	0.110	↑	0.006
	Living macrophytes	9.31	0.008	=	0.903
	Dead animal ≥ 1mm	4.59	0.014	=	0.263
	Living microinvertebrates	11.34	0.016	=	0.340
	Living macroinvertebrates	10.86	-0.212	↓	0.006
	Vertebrates	0.19	-0.014	↓	0.006
Feeding group	Absorber	0.00	N.C.	N.C.	N.C.
	Deposit feeder	10.63	-0.045	=	0.061
	Shredder	31.23	0.181	=	0.069
	Scraper	26.62	0.144	↑	0.049
	Filter-feeder	17.68	0.073	=	0.340
	Piercer	1.82	-0.109	↓	0.006
	Predator	10.13	-0.227	↓	0.006
	Parasite	1.89	-0.017	↓	0.029

biological groups (model 2, *p*-value <0.001). Relationships between species composition and traits (model 4) were significant for diatoms (p-value <0.001) and fish (p-value = 0.02), but not for macroinvertebrates (p-value = 0.07). Consequently, significant associations between traits and environmental conditions were only considered for diatoms and fish.

According to the fourth corner results, oligosaprobous, oligonitrophilous and oligotrophic diatoms with high oxygen requirements were positively correlated with the first RLQ axis for environmental variables (Fig. 3a). We consistently found a significant and negative association of conductivity, BOD5, NH_4, NO_2, NO_3, PO_4 and Ptot with the first RLQ axis for traits (Fig. 3b).

For fish, stenothermal taxa, taxa intolerant to habitat degradation, large life forms, taxa with low fecundity and large egg size were negatively correlated with the first RLQ axis for environmental variables, while taxa that were eurythermal, tolerant to habitat degradation, medium-sized forms and with small egg size were positively correlated (Fig. 4a). BOD5, NH_4, PO_4 and Ptot were positively correlated with the first RLQ axis for traits (Fig. 4b).

4. Discussion

Using a comprehensive national dataset on the decadal temporal trends in the environment and community properties and trait distribution of three major freshwater groups, we made several important observations.

Table 3

Trends in fish trait abundances over time (no trend: =; decreasing: ↓; increasing: ↑; N.C.: not calculated). Decreasing trends are represented by red cells, increasing trends by green cells.

Trait	Modality	Modality occ. (%)	Slope	Trend	Two-sided test (p-value)
Tolerance to oxygen depletion	Tolerant	14.03	-0.220	↓	0.014
	Intermediate	17.43	-0.169	↓	0.009
	Intolerant	68.53	0.385	↑	0.007
Temperature tolerance	Eurythermal	52.83	-0.582	↓	0.004
	Stenothermal	47.17	0.574	↑	0.004
Tolerance to habitat degradation	Tolerant	46.06	-0.586	↓	0.004
	Intermediate	3.00	N.C.	N.C.	N.C.
	Intolerant	50.94	0.617	↑	0.004
Feeding Habitat	Water column	47.53	-0.270	↓	0.009
	Benthic	52.47	0.262	↑	0.009
Adult trophic guild	Detritivorous	4.77	-0.004	=	0.788
	Herbivorous	0.20	0.008	=	0.369
	Insectivorous	67.73	0.377	↑	0.007
	Omnivorous	22.09	-0.347	↓	0.004
	Parasitic	0.02	0.000	=	0.703
	Piscivorous	2.79	N.C.	N.C.	N.C.
	Planktivorous	2.40	-0.058	=	0.060
Parental care	No protection	74.78	-0.541	↓	0.004
	Protection	25.22	0.533	↑	0.004
Maximum total length	Small	41.16	0.823	↑	0.004
	Intermediate	44.01	-0.803	↓	0.004
	Large	14.83	-0.020	=	0.085
Relative fecundity	Low	27.04	0.528	↑	0.004
	Intermediate	40.78	-0.201	=	0.182
	High	32.09	-0.338	↓	0.016
Egg diameter	Small	68.22	-0.403	↓	0.007
	Large	31.78	0.434	↑	0.004
Lifespan	Short	14.72	0.552	↑	0.004
	Intermediate	75.17	-0.358	↓	0.004
	Long	10.02	-0.204	↓	0.004
Status	Exotic	0.95	0.006	=	0.645
	Native	99.05	-0.006	=	0.645

First, we detected an improvement of water quality and a significant recovery of pollution-sensitive taxa. Second, we identified some group-specific trends in taxonomic and functional richness. Finally, we observed some convergence in the community functional responses to environmental conditions across the three groups.

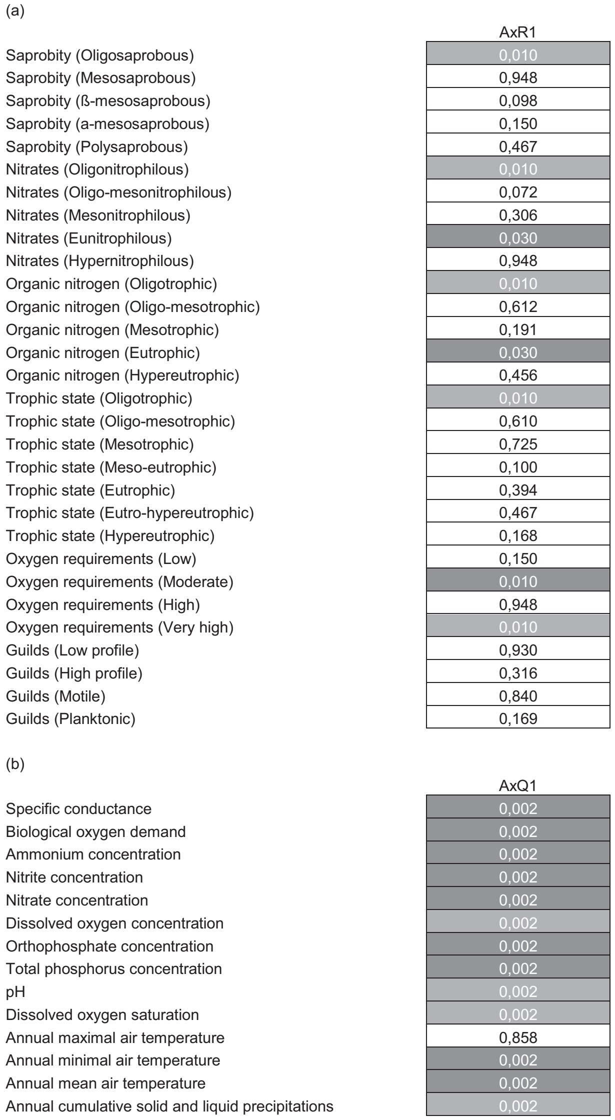
4.1. Recent changes in freshwater environmental conditions and subsequent trends in sensitive vs tolerant taxa across groups

Our results are consistent with an emerging trend of re-oligotrophication of freshwaters (Verbeek et al., 2018), characterized by decreasing nutrient concentrations and biological oxygen demand. This suggests that management strategies to reduce nutrient loads under the European Framework Directive have started to bring positive results. As a consequence, there was an increase of pollution-sensitive taxa and a decrease of eutrophic and pollution-tolerant taxa, supported here by combined RLQ and fourth-corner analyses.

Concerning diatoms, lower nutrient levels, in particular phosphorous, may have limited planktonic taxa abundance. The RLQ analysis supports this view, as planktonic taxa were associated with high nutrients, although the fourth-corner approach fails to find this relationship significant. Among benthic diatom taxa, the species-poor low profile guild, with low nutrient demands, increased in abundance, while the species-rich motile guild, composed of generally eutrophic species, decreased. Similarly, there was a net increase of sensitive macroinvertebrate families (oligotrophic and oligosaprobic) but a net decrease in tolerant macroinvertebrate families (eutrophic and α-mesosaprobic). The re-oligotrophication of the French hydrosystem was also corroborated by the trophic and saprobic preferences of fish communities, as already reported by Dézerald et al. (2020).

Contrary to our expectations, we did not detect climate warming over the study period, although we cannot assume that there was no temporal trend in water temperature: air temperature is a rough approximation of water temperature, which is controlled by multiple factors, including solar radiation, discharge, riparian shade, and groundwater inputs (Johnson et al., 2014). We found no significant change of warm-water or cold-water taxa, however, the trends observed for macroinvertebrate temperature preferences suggested that warm-water specialists tended to increase in abundance, in line with (Floury et al., 2017).

A frequently reported consequence of climate change is the unstability of hydrological conditions, including fluctuations in water flow (Poff et al., 2010). While we did not have national data on these conditions, we noted that many functional traits converged towards resistance and resilience to higher river flow. Specifically, the low profile diatom guild, which increased over the past decades, is clearly favored in high disturbance habitats whereas motile diatoms are disfavored (Passy, 2007). Fish species possessing traits associated with the so-called “periodic strategy” decreased in abundance (Winemiller and Rose, 1992; Winemiller, 2005): periodic strategists tend to delay reproduction to invest in growth and increased fecundity, and are thus characterized by high fecundity, long lifespan, small egg size, and lack of parental care. According to the RLQ results, small egg size is favored by high nutrient levels whereas large egg size and low fecundity are favored by low nutrient levels. Hence traits for diatom and fish, related in the literature to fluctuations in flow, were also clearly related to low nutrient concentrations (Bonada et al., 2007; Erős



(a)

	AxR1
Saprobity (Oligosaprobous)	0,010
Saprobity (Mesosaprobous)	0,948
Saprobity (ß-mesosaprobous)	0,098
Saprobity (a-mesosaprobous)	0,150
Saprobity (Polysaprobous)	0,467
Nitrates (Oligonitrophilous)	0,010
Nitrates (Oligo-mesonitrophilous)	0,072
Nitrates (Mesonitrophilous)	0,306
Nitrates (Eunitrophilous)	0,030
Nitrates (Hypernitrophilous)	0,948
Organic nitrogen (Oligotrophic)	0,010
Organic nitrogen (Oligo-mesotrophic)	0,612
Organic nitrogen (Mesotrophic)	0,191
Organic nitrogen (Eutrophic)	0,030
Organic nitrogen (Hypereutrophic)	0,456
Trophic state (Oligotrophic)	0,010
Trophic state (Oligo-mesotrophic)	0,610
Trophic state (Mesotrophic)	0,725
Trophic state (Meso-eutrophic)	0,100
Trophic state (Eutrophic)	0,394
Trophic state (Eutro-hypereutrophic)	0,467
Trophic state (Hypereutrophic)	0,168
Oxygen requirements (Low)	0,150
Oxygen requirements (Moderate)	0,010
Oxygen requirements (High)	0,948
Oxygen requirements (Very high)	0,010
Guilds (Low profile)	0,930
Guilds (High profile)	0,316
Guilds (Motile)	0,840
Guilds (Planktonic)	0,169

(b)

	AxQ1
Specific conductance	0,002
Biological oxygen demand	0,002
Ammonium concentration	0,002
Nitrite concentration	0,002
Nitrate concentration	0,002
Dissolved oxygen concentration	0,002
Orthophosphate concentration	0,002
Total phosphorus concentration	0,002
pH	0,002
Dissolved oxygen saturation	0,002
Annual maximal air temperature	0,858
Annual minimal air temperature	0,002
Annual mean air temperature	0,002
Annual cumulative solid and liquid precipitations	0,002

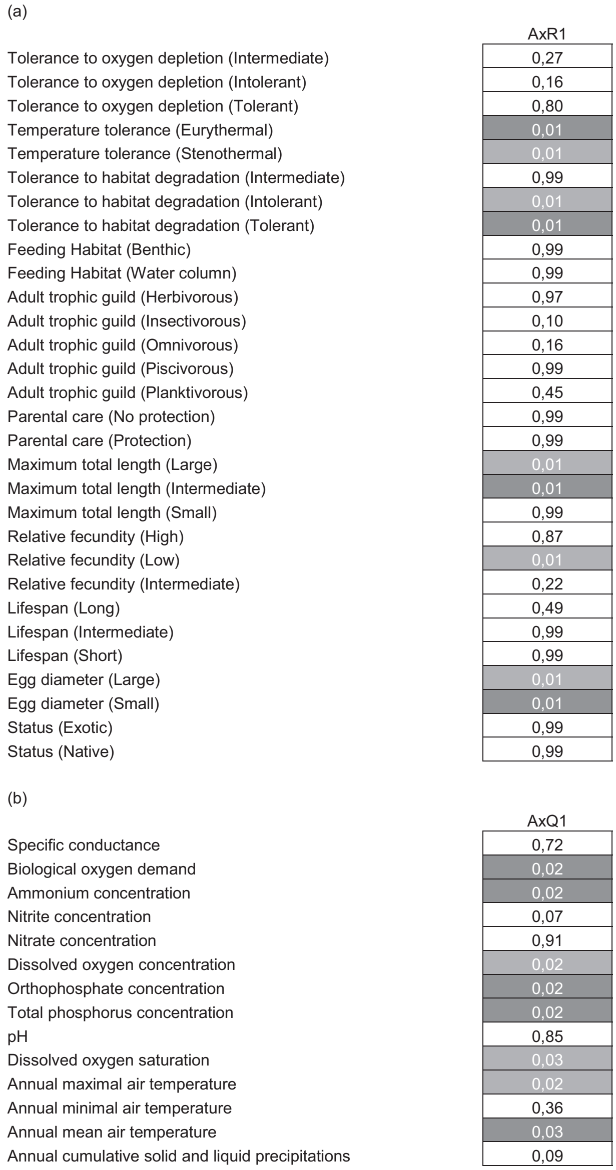
Fig. 3. Combination of fourth-corner and RLQ results for diatoms. (a) Fourth-corner tests between the first RLQ axis for environmental variables (AxR1) and traits. (b) Fourth-corner tests between the first RLQ axis for functional traits (AxQ1) and environmental variables. Significant ($p < 0.05$) positive associations are represented by dark grey cells, and significant negative associations by light grey cells. P-values are given in each cell.

et al., 2012). These results indicate co-tolerance of the studied taxa to both re-oligotrophication and unstability of hydrological conditions (Vinebrooke et al., 2004), favouring traits typical from upstream conditions, adapted to both high hydrologic stress and low nutrient levels.

Increasing trends in proportion of ovoviviparity and small size in macroinvertebrate communities also suggest adaptive strategies to a greater frequency, magnitude or unpredictability of hydrological conditions (Archaimbault et al., 2005; Dolédec and Statzner, 2008; Mondy et al., 2012). However, the fourth-corner analysis results did not reveal any significant relationship between these traits and the trophic/saprobic conditions. This may be due to the great heterogeneity of traits within families, leading to stronger responses of taxonomic metrics to environmental changes compared to traits (Arce et al., 2014).

4.2. General trends of richness differ among groups

Diatom (and to a lesser extent fish) taxonomic richness declined over time, while macroinvertebrate richness increased. Total beta-diversity increased slightly in diatoms, indicating a growing differentiation of assemblages from baseline community composition through time. Considering the paucity of research on stream diatom community dynamics during the last decades (Alahuhta et al., 2019), this study provides novel information on the trends in species and functional richness and composition. In line with models showing a positive relationship between primary producers' richness and nutrient supply (Liess et al., 2009; Passy and Larson, 2019), we report a decrease in diatom richness with the decrease in nutrient levels. As both planktonic and motile guild richness declined, while only low profile guild richness increased, the functional richness also decreased. Prior research demonstrated that nutrient loads control the spatial richness patterns of sensitive vs. tolerant diatom species (Clavel et al., 2011; Soininen et al., 2016; Leboucher et al., 2019), but here we revealed that nutrient levels may also be responsible for temporal diatom richness trends.



(a)

	AxR1
Tolerance to oxygen depletion (Intermediate)	0,27
Tolerance to oxygen depletion (Intolerant)	0,16
Tolerance to oxygen depletion (Tolerant)	0,80
Temperature tolerance (Eurythermal)	0,01
Temperature tolerance (Stenothermal)	0,01
Tolerance to habitat degradation (Intermediate)	0,99
Tolerance to habitat degradation (Intolerant)	0,01
Tolerance to habitat degradation (Tolerant)	0,01
Feeding Habitat (Benthic)	0,99
Feeding Habitat (Water column)	0,99
Adult trophic guild (Herbivorous)	0,97
Adult trophic guild (Insectivorous)	0,10
Adult trophic guild (Omnivorous)	0,16
Adult trophic guild (Piscivorous)	0,99
Adult trophic guild (Planktivorous)	0,45
Parental care (No protection)	0,99
Parental care (Protection)	0,99
Maximum total length (Large)	0,01
Maximum total length (Intermediate)	0,01
Maximum total length (Small)	0,99
Relative fecundity (High)	0,87
Relative fecundity (Low)	0,01
Relative fecundity (Intermediate)	0,22
Lifespan (Long)	0,49
Lifespan (Intermediate)	0,99
Lifespan (Short)	0,99
Egg diameter (Large)	0,01
Egg diameter (Small)	0,01
Status (Exotic)	0,99
Status (Native)	0,99

(b)

	AxQ1
Specific conductance	0,72
Biological oxygen demand	0,02
Ammonium concentration	0,02
Nitrite concentration	0,07
Nitrate concentration	0,91
Dissolved oxygen concentration	0,02
Orthophosphate concentration	0,02
Total phosphorus concentration	0,02
pH	0,85
Dissolved oxygen saturation	0,03
Annual maximal air temperature	0,02
Annual minimal air temperature	0,36
Annual mean air temperature	0,03
Annual cumulative solid and liquid precipitations	0,09

Fig. 4. Combination of fourth-corner and RLQ results for fish. (a) Fourth-corner tests between the first RLQ axis for environmental variables (AxR1) and traits. (b) Fourth-corner tests between the first RLQ axis for functional traits (AxQ1) and environmental variables. Significant ($p < 0.05$) positive associations are represented by dark grey cells, and significant negative associations by light grey cells. P-values are given in each cell.

In contrast to diatoms, the temporal trends of macroinvertebrates showed an increase in taxonomic and functional richness. Nutrient enrichment indeed may have affected stream primary producer and consumer richness in distinct ways. We report here a gain in macroinvertebrate richness concommittent to the decrease in phosphorous concentrations (Evans-White et al., 2009), suggesting macroinvertebrate community recovery may be due to water quality improvement. Our results are also consistent with a meta-analysis of multidecadal biodiversity trends in Europe (Pilotto et al., 2020) and earlier studies in France (Van Looy et al., 2016; Floury et al., 2018), documenting a recent increase in macroinvertebrate taxonomic and functional richness.

Temporal dynamics of fish community richness were generally non-significant. However, it is worth noting that one of the two species significantly increasing in abundance was recently introduced. These results are consistent with an ongoing spatial expansion of non-native species, particularly in France (Daufresne and Boët, 2007; Buisson and Grenouillet, 2009; Hitt and Roberts, 2012; Maire et al., 2019).

4.3. Functional congruences among communities

As stated earlier, we observed a congruence across groups in terms of traits conferring tolerance to nutrient enrichment. However, the re-oligotrophication of freshwaters may also modify the consumers' feeding groups, according to the trophic cascade theory (Carpenter et al., 1985; Brett and Goldman, 1996). Specifically, the temporal shift in diatoms from motile and planktonic to low profile forms may have induced community changes at higher trophic levels. First, dominance of low profile taxa results in thin biofilms, typically favouring macroinvertebrates able to feed on tightly attached diatoms (Tall et al., 2006). Indeed, we observed a significant increase in microphyte consumers (*Glossosomatidae*) and scrapers (*Elmidae*). Second, the boosted diversity of macroinvertebrates, may have underlied the significant increase in insectivorous fish species (*Cottus gobio*) (Wallace and Webster, 1996), associated with oligotrophic conditions. Cross-taxon congruence in terms of co-occurrence and trait makes possible the delineation of functional patterns (Aubin et al., 2013), relevant for biodiversity surveys and conservation planning. Here, the traits favored in diatoms, macroinvertebrates and fish were clearly convergent and represented a “re-oligotrophication” pattern. Our results further indicated shifts in diatoms guilds with correspondent trophic changes in macroinvertebrates and fish, consistent with a trophic cascade. Unfortunately, simultaneous samples of diatoms, macroinvertebrates and fish were collected in fewer than ten sites, which did not allow us to statistically test this possibility. We recommend that future studies dedicated to the temporal monitoring of rivers should consider concurrent collection of several biological groups to better track and understand the global change effects on aquatic diversity.

5. Conclusion

This study of community taxonomic attributes and traits provided novel insights into the recent temporal dynamics of biodiversity in streams. The general decrease of nutrient loads in rivers may have induced the observed recovery of sensitive diatoms, macroinvertebrates and fish. While the temporal trends of richness were clearly different between groups, we noticed a strong cross-taxon congruence, representing a “re-oligotrophication” pattern of traits. Further analyses linking multi-sites and multi-taxa trends to environmental changes will allow better quantifying and understanding the effects of global change on freshwater biodiversity.

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CRediT authorship contribution statement

J. Tison-Rosebery: Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **T. Leboucher:** Conceptualization, Methodology, Software, Formal analysis, Data curation, Writing – original draft. **V. Archaimbault:** Writing – original draft, Writing – review & editing. **J. Belliard:** Writing – original draft, Writing – review & editing. **M. Ferreol:** Data curation. **M. Floury:** Writing – review & editing. **A. Jeliazkov:** Writing – review & editing. **E. Tales:** Writing – original draft, Writing – review & editing. **B. Villeneuve:** Writing – original draft, Writing – review & editing. **S.I. Passy:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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