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A 34-year survey under phosphorus decline and warming: Consequences on stoichiometry and functional trait composition of freshwater macroinvertebrate communities

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Data availability: The trait databases used in this study are freely available and all modifications made are described in the manuscript. The specific data will be available upon request.

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Abstract

Worldwide, freshwater systems are subjected to increasing temperatures and nutrient changes. Under phosphorus and nitrogen enrichment consumer communities are often thought to shift towards fast-growing and P-rich taxa, supporting the well-known link between growth rate and body stoichiometry. While these traits are also favoured under warming, the temperature effect on stoichiometry is less clear. As recently shown, there is a general link between functional traits and body stoichiometry, which makes the integration of stoichiometric traits a promising tool to help understanding the mechanisms behind taxonomic and functional community responses to nutrient changes and/or warming. Yet, such approaches have been scarcely developed at community level and on a long-term perspective. In this study, we investigated long-term responses in stoichiometry and functional trait composition of macroinvertebrate communities to nutrient changes (decreasing water P; increasing water N:P) and warming over a 34-year period in the Middle Loire River (France), testing the potentially opposing responses to these drivers. Both drivers should cause shifts in species composition, which will alter the overall community stoichiometry and functional composition following assumptions from ecological stoichiometry theory. We found that the macroinvertebrate community shifted towards P-poor taxa, causing significant trends in overall community stoichiometry which indicates long-term changes in the nutrient pool provided by these consumers (*i.e.* decrease in %N and %P, increase in N:P). Further, while the former high-P conditions favoured traits associated to detritus feeding and fast development (*i.e.* small maximum body size, short life duration), recent conditions favoured

predators and slow-developing taxa. These results suggest nutrients to be a more important driver than temperature over this period. By providing a pivotal link between environmental changes and functional trait composition of communities, approaches based on stoichiometric traits offer sound perspectives to investigate ecological relationships between multiple drivers operating at various scales and ecosystem functioning.

Keywords: community, ecological stoichiometry, global warming, nutrient change, stoichiometric traits

Introduction

Climate change and the consequences of human activities are ubiquitous in most ecosystems and freshwaters are often impacted by multiple stressors. Globally, water temperature of streams and lakes has increased and is predicted to rise in the future, often accompanied by drastic changes in flow regime or stratification (Hardenbicker et al., 2017; Michel et al., 2021; van Vliet et al., 2013). Fertilization or fossil fuel burning have dramatically increased nitrogen (N) and phosphorus (P) concentrations in rivers and lakes over the past decades (Battye et al., 2017; Peñuelas et al., 2012). Even where successful nutrient input reduction schemes have led to decline in phosphorus concentrations (Jeppesen et al., 2005), nitrogen levels often remain unaffected by these measures. Along with a faster accumulation of phosphorus rather than nitrogen in freshwaters (Yan et al., 2016), this has also caused a change in the N:P ratio in many systems (Isles et al., 2018; Jeppesen et al., 2005; Peñuelas et al., 2013; Yan et al., 2016).

Apart from toxic effects at rather high increase (Camargo et al., 2005), the effect of nutrient enrichment on consumer communities is mainly indirect, via changes in resource quality and quantity (Evans & Sanderson, 2018; Nessel *et al.*, 2021). In contrast, warming affects

organisms also directly by increasing their metabolic activity and physiological rates thus leading to altered respiration (Hamburger and Dall, 1990), growth (Janssens et al., 2015; Pöckl, 1992; Sutcliffe et al., 1981) or development (Gillooly et al., 2002; Pöckl, 1992). Globally, total invertebrate abundance and biomass tend to increase following nutrient enrichment (Nessel et al., 2021) while overall taxonomic richness, evenness and diversity decrease (Singer and Battin, 2007; Zhang et al., 2019). Declining taxonomic richness was also observed as a response to warming (Daufresne et al., 2009; Latli et al., 2017; O’Gorman et al., 2012; Živić et al., 2014). However, species shifts can occur without affecting diversity indices (McCormick et al., 2004; Nessel et al., 2021). Under increasing nutrient concentrations or temperatures, invertebrate communities tend to shift towards pollution- or temperature-tolerant taxa, with increasing abundances of oligochaets and snails over insects (esp. the orders Ephemeroptera, Plecoptera and Trichoptera) (Friberg et al., 2010; McCormick et al., 2004; Ortiz and Puig, 2007; Theodoropoulos and Karaouzas, 2021; Živić et al., 2014).

Trait-based approaches can help investigating how environmental changes affect the functional structure and composition of communities. For example, feeding groups respond differently to nutrient enrichment, scrapers and collector-gatherers being favoured over shredders and filter/suspension feeders (Demi et al., 2019; McCormick et al., 2004). Life-history traits exhibit shifts towards small and fast-growing/-developing taxa in response to increasing nutrient load (Demi et al., 2019; Singer and Battin, 2007) or temperature (Daufresne et al., 2009; Latli et al., 2017; O’Gorman et al., 2012).

Stoichiometric traits are one kind of biological traits, describing the elemental composition of organisms, *i.e.* the nutrient content (*e.g.* P-content) or ratio (*e.g.* N:P) of an organism’s body tissue. This composition is assumed to represent the organism’s nutrient demand depending on its physiology and biology and is taxon-specific (Frost et al., 2006; Sterner and Elser, 2002). Regulating mechanisms in heterotrophs allow for (general) homeostasis and – although

there is intra-species variation, *e.g.* over ontogeny as demonstrated for aquatic insects (Back and King, 2013) – most aquatic invertebrate species keep a constant body stoichiometry even under changing nutrient conditions (Danger et al., 2013; Evans-White et al., 2005; Persson et al., 2010). As already demonstrated, high phosphorus environments favour taxa with high body P-content (Prater et al., 2015; Singer and Battin, 2007; Teurlinckx et al., 2017), which likely alters the overall nutrient pool provided by an invertebrate community (Prater *et al.*, 2015; Singer & Battin, 2007). Moreover, several studies have demonstrated a strong relationship between stoichiometric traits and other functional traits in macroinvertebrates (Beck, 2021), especially growth rate (Acharya et al., 2004; Elser et al., 2003), development-related traits (Beck et al., 2022) or feeding habits (Cross et al., 2003; Fagan et al., 2002; González et al., 2017, 2011). Fast-growing and fast-developing taxa for example require high amounts of phosphorus to achieve their fast growth rates and thus are expected to express a rather high body P content, commonly referred to as the “Growth Rate Hypothesis” (Acharya et al., 2004; Beck et al., 2021; Elser et al., 2003). The stoichiometric approach thereby is not limited to aquatic invertebrates and works available cover also the terrestrial and marine environments, including various organisms from unicellular microbes and phytoplankton to plants and mammals (recently reviewed by Sardans et al., 2021).

Although temperature probably does not directly interfere with the link between stoichiometric and other functional traits, altered physiological rates and functional traits as a response to warming might indirectly affect organism’s nutrient budget. For example, increased respiration rate under warming can increase the energetic demand of ectotherms requiring increasingly carbon-rich diet (Anderson et al., 2017; Malzahn et al., 2016). Another response could be an increased phosphorus demand due to increased growth rate as observed for a crustacean under moderate temperature increase (Ruiz et al., 2020). Both effects would

antagonistically affect the C:P demand of individuals and consequences at the community level are even less clear.

Several authors already proposed to combine the stoichiometric and metabolic theories (Allen and Gillooly, 2009; Hillebrand et al., 2009; Ott et al., 2014) to better understand the functioning from population to ecosystem level, but observational or experimental evidence is rare. Only few studies have investigated the relationship between environmental nutrient conditions and body stoichiometry at the community scale, or have examined the interacting and probably opposing effects of increasing temperature and nutrient changes beyond planktonic assemblages. The studies available for the aquatic environment remained largely focused on individual taxa or functional groups within communities (*e.g.* Cross et al., 2003; Prater et al., 2015), have been limited to relatively short periods (*e.g.* Singer & Battin, 2007) and/or have faced non-controlled geophysical differences among study sites. The mono-site characteristic of a time series excludes such confounding factors and, due to the long period covered, increases the chance to detect true long-term trends rather than short-term effects.

Based on a long-term dataset, this study aims at investigating how community stoichiometry and functional composition responded to multi-decadal changes in water nutrient concentrations and temperature. We combined stoichiometric and biological trait information available from databases with abundance data collected over a 34-year period at Dampierre-en-Burly, on the upper section of the Middle Loire River (France). Continuous detailed information on water parameters is available, revealing significant changes. Phosphorus concentration decreased following a phosphate input reduction, reaching in the most recent years a range of values revealing the existence of only a moderate impact (in the European Water Framework Directive context; European Council, 2000). Temperature increased (+0.9°C) leading also to a decline in water discharge over this period. These changes caused a shift in the taxonomic and functional composition of the macroinvertebrate community

(Floury et al., 2017, 2013). Therefore, adding a stoichiometric view is attractive in order to investigate its potential to help explaining the observed community changes. The combination of changes in nutrient concentration and temperature at this site allows examining the combined effect of these stressors and shedding light onto the - sometimes contradictory - community responses reported in the literature (Tab. 1) by possibly identifying the main driver.

Our main hypothesis (H1, Tab. 1) is that community %P decreased over time following the water phosphorus concentration (likely going along with increasing community C:P and N:P ratios). This pattern should have been caused by a shift of the community towards P-poor taxa that require lower quantities of phosphorus. Based on the link described by the Growth Rate Hypothesis, we further expect that trait attributes linked to fast growth and development (such as small body size, short life span) will be associated to high body %P, hence disfavoured along P decrease over time. The community should thus shift towards larger taxa with a slower development rate (H2). In case temperature will be the most important driver, we expect taxa expressing fast growth and/or development to be increasingly favoured when temperature increases over the study period (H3). Considering the link towards stoichiometry described above, this temperature increase should also select for P-rich taxa and consequently increase the overall community %P (*i.e.* decrease community C:P and N:P ratios) over the study period (H4). As recent work on macroinvertebrates has demonstrated a general link between stoichiometric and (other) functional traits (Beck, 2021), we expect that the change in the functional composition of the community will be in line with ecological stoichiometry theory.

Tab. 1: Overview of individual and community responses towards phosphorus (P) increase or warming reported in the literature for aquatic macroinvertebrates or zooplankton. The last column gathers the derived hypotheses for our study system (P decrease and warming).

Parameter	Response to P increase		Response to temperature increase		Expected response for the study system (P decrease + temperature increase)
	Reference	Response	Reference	Response	
Mean body size	Davis et al., 2010 Juvigny-Khenafou et al., 2021 Southwood, 1977 Demi et al., 2019 Bourassa & Morin, 1995	↗ ↗ ↘ ↘ →	Latli et al., 2017 O’Gorman et al., 2012 Yvon-Durocher et al., 2011 Daufresne et al., 2009	↘ ↘ ↘ ↘	↗ if nutrient effect dominates (H2) ↘ if temperature effect dominates (H3)
Mean community P-content	Elser et al., 2000 Prater et al., 2015 Singer & Battin, 2007	↗ ↗ ↗	hypothesized by Weal et al., 2010 Bullejos et al., 2014 hypothesized by Cross et al., 2015	↘ ↘ ↗	↘ if nutrient effect dominates (H1) ↗ if temperature effect dominates (H4)
P storage in the community	hypothesized by Cross et al., 2015	↗	hypothesized by Cross et al., 2015	↘	↘

Material & methods

Datasets

Community and environmental data

The study site is located in the upper section of the Middle Loire River in France. Hydro-climatic parameters (temperature, discharge) were monitored at “Dampierre-en-Burly” (47.4°N; 2.3° E) continuously over the 1980-2013 study period, due to a regulatory survey at the *Electricité de France* power plant, located downstream of the study site. Water chemistry information (NO₃, PO₄) was obtained from monthly measurements of the monitoring program of the *Loire-Bretagne Basin Water Authority* at a site located 40 km downstream (“Jargeau”, 47.5° N; 2.1° E). In Dampierre-en-Burly and Jargeau, the Loire is an 8th order river, with a catchment of about 35 500 km², a mean width of 300 m and a mean depth of about 1 m in low flow. Dampierre is at an altitude of 123 m a.s.l., 110 km downstream from the confluence with the Allier River and 550 km from the source. Jargeau is at 109 m a.s.l. A preliminary

climatic, hydrological and chemical study confirmed that the two sites were typical of all other measurement stations in this river reach (Floury et al., 2013, 2012). As a result, these data provided the best homogeneous data coverage available over the study period regarding these parameters and were fully representative for Dampierre-en-Burly.

Invertebrate communities were sampled at Dampierre-en-Burly four times per year (except for 2008 with only three sampling events), providing in total 135 benthic invertebrate community samples between 1980 and 2013. Most sampling events were conducted during summer (June, July, August, September) but the sampling period ranged from April to November.

The invertebrate sampling followed the IQBG protocol (“Indice de Qualité Biologique Globale”; Verneaux et al., 1976) for 1980-1994 and the normalized IBGN field protocol (“Indice Biologique Global Normalisé”: French Norm NF T90-350; AFNOR 1992, 2004) between 1995 and 2013. Both protocols include sub-sampling of different habitats present at the site, but differ in the number of sample units (six vs. eight) and the way to select where the sub-samples are taken. All samplings were performed with a Surber sampler (mesh size : 500 μ m). Abundances were weighted by the sampled area to account for the different surfaces captured by the two protocols (*i.e.* 0.6m² until 1994 and 0.4m² from 1995). Bryozoa, Hydrozoa, Hydrachnidia, Nematoda, Oligochaeta and Porifera have been excluded to avoid identification or quantification bias. Taxonomic resolution of the other groups was harmonized to family level, resulting in a total of 108 taxa included in this study (S1). Although there is variation in trait expression also among finer taxonomic levels, applying the functional trait approach on family level has already allowed suitable results (Dolédéc et al., 2000; Sotomayor et al., 2022). For the period 1980-2008 both data sets have already been used in previous studies (Floury et al., 2017, 2013).

Stoichiometric and biological trait information

Stoichiometric traits were available from a database (Beck et al., 2022) gathering stoichiometric information as mass contents of carbon (%C), nitrogen (%N) and phosphorus (%P) as well as the molar ratios C:N, C:P and N:P. It provides taxon mean values, based mainly on field sampling data but also including values from the literature. In case the stoichiometric information was not available for a taxon, the values from a finer taxonomic level (*i.e.* genus) were used ($n \leq 3$ taxa per individual sample). The data finally covered on average 85% of the communities in terms of abundances.

Eleven biological traits were taken from Tachet et al. (2010), supplemented by two traits (“reproductive cycles”, “molting events”) already used in other works (Beck, 2021; Beck et al., 2021) (Tab. 2). The information is fuzzy coded (Cnevenet et al., 1994): a trait is resolved in different categories, for which each taxon’s affinity is described by scores. These scores range between 0 (= no affinity) and 5 (= high affinity) and have been transformed into relative frequencies within each trait before further analysis. By using this fuzzy coding approach, we rely on potential traits that capture intra-taxon variation. The description of some trait categories was slightly modified, *i.e.* by merging ecologically/functionally similar categories to avoid categories only occupied by a very low number of taxa (S2). The traits and the final categories used in this study can be found in Tab.2.

Data analysis

Trends in community stoichiometry and water parameters

Community stoichiometry was calculated as abundance-weighted mean of individual taxon values. Stoichiometric values (%C, %N, %P, C:N, C:P, N:P) of individual taxa were weighted by the $\log(n_i + 1)$ -transformed abundances (n_i) of taxa. The sum of weighted stoichiometric values was then divided by the sum of weights to obtain the community stoichiometric composition for each sampling event. Thereby, the calculations were based only on those taxa, for which the corresponding stoichiometric information was available. To avoid any bias

when calculating with ratio data, taxon body C:N, C:P and N:P ratios were log-transformed prior to calculations. For each year, the mean of each community stoichiometry variable was calculated ($n = 4$, except for 2008 where $n = 3$).

Water N:P ratio was calculated from NO_3 and PO_4 concentrations on the raw data set, that is for each measurement with both variables available. For the analysis, only water parameter information that was assumed relevant for the macroinvertebrate community (concentrations of NO_3 , PO_4 , water N:P, temperature), was considered. Therefore, available information on the 126-day period before each sampling date was averaged for each invertebrate sampling date. Using the same dataset, such ~4-month period was identified as the optimal proxy for the response time of macroinvertebrate communities to these water parameters at this site (Floury et al., 2013). As for community stoichiometry, the yearly mean of each water parameter was calculated.

To detect possible trends, Mann-Kendall trend tests were applied to each community stoichiometric variable and water parameter. To overcome the problem of autocorrelation in time series data a modified version of the test that removes autocorrelation by Spearman rank correlations (Hamed & Rao, 1978) was used.

Association between water parameters, stoichiometric and biological traits

A RLQ analysis was applied to investigate the co-structure between functional traits (stoichiometric and biological) and water parameters (PO_4 , NO_3 , water N:P, temperature). This extension of the co-inertia analysis (Dolédec and Chessel, 1994) allows to link an environment table (sites x environmental parameters, 'R') to a trait table (traits x taxa, 'Q') via an abundance table (sites x taxa, 'L'), producing a simultaneous ordination of the three tables (Dolédec et al., 1996; Dray et al., 2014, 2003). The dimension of sites in R and L (*i.e.* rows) and of taxa in L and Q (*i.e.* columns) thereby must be the same. Yearly mean

abundances were calculated from the abundance table, so that “year” in our analysis could be treated as “site” from the original design.

First, Correspondence Analysis (CA) was applied to the $\log(n+1)$ -transformed mean abundance array ($=L$). The environmental data array ($=R$) was subjected to Principal Component Analysis (PCA), weighting the rows ($=\text{sites}$) by the row weights provided by the CA. Likewise, the trait array ($=Q$) was subjected to PCA weighting the columns ($=\text{taxa}$) by the columns weights provided by the CA. Water chemistry variables (NO_3 , PO_4 , water N:P) and stoichiometric ratios (C:N, C:P, N:P) were log-transformed prior to the analysis.

Second, the *rlq()* function was applied using the three output objects from the individual analyses described above to perform a double inertia analysis ($'R'$, $'Q'$) linked by a contingency table ($'L'$). The total inertia indicates the link between functional traits and water parameters as mediated by abundances. Its significance was estimated by a permutation test (9999 permutations). We used the two-step procedure suggested by Dray & Legendre (2008) for a better control of type I error.

Differences in body stoichiometry between groups of taxa

Over the study period, Flourey et al. (2013) identified seven groups of macroinvertebrate families that show distinct temporal distributions. They used a cluster analysis on the taxon scores on the first factorial plane obtained from a CA performed on taxa \ln -transformed abundances over the period from 1979-2008. We gathered these groups according to their response curve. Group A contains taxa that were present in the first years of the study and showed decreasing abundances (originally groups 1 and 2 in Flourey et al., 2013). Taxa of group B were present over the whole period showing unimodal or saturating response curves over time (groups 3, 4 and 5). Group C gathers taxa only appearing during the last decade (groups 6 and 7).

We calculated the mean stoichiometric traits (%C, %N, %P, C:N, C:P, N:P) for each group and applied Kruskal-Wallis tests on each stoichiometric variable to test for differences among groups. Pairwise comparisons were applied when significant between-group heterogeneity had been identified (Dunn test, with Bonferroni correction for multiple testing). Non-parametric tests were used because of unequal sample sizes and deviations from homoscedasticity and normality assumptions as judged from graphical inspection.

All the analyses were performed using R (R Development Core Team, 2019, version 3.5.2) and the package *ade4* (Dray and Dufour, 2007).

Tab. 2: Biological traits and their corresponding trait categories.

Functional trait	Categories
Aquatic life stages	egg, larva, nymph, adult
Dispersal	aquatic-active, aquatic-passive, aerial-active, aerial-passive
Feeding habits	deposit feeder, filter-feeder, piercer, parasite, scraper, shredder, swallower/chewer
Food resources	dead animal ($\geq 1\text{mm}$), dead plant ($\geq 1\text{mm}$), detritus ($< 1\text{mm}$), living macrophytes, living microphytes, living microvertebrates, living macroinvertebrates
Life duration	≤ 1 year, > 1 year
Locomotion	attached, burrower, crawler, interstitial, swimmer
Maximum body size	$\leq 0.5\text{cm}$, $> 0.5-1\text{cm}$, $> 1-2\text{cm}$, $> 2-4\text{cm}$, $> 4\text{cm}$
Molting events	0, 1, 2-4, 5-9, 10-14, 15-19, ≥ 20 (= number of molting events)
Resistance forms	eggs/stageblasts, housing/cocoons, diapause/dormancy, none
Respiration	tegument/gill, plastron/spiracle
Reproductive cycles	1, 2, > 2 , > 6 (= number of reproductive cycles per individual)
Reproduction mode	ovoviviparity, isolated eggs, clutches, clutches.vegter (vegetation/terrestrial), asexual reproduction
Voltinism	< 1 , 1, > 1

Results

Trends in community stoichiometry and water parameters

All community stoichiometry variables showed a significant trend over the period 1980-2013. This trend was negative for community %C, %N and %P and positive in community molar ratios (C:N, C:P, N:P) (Fig. 1, Tab.3). From the first decade (1980-1989) to the last decade of the study period (2004-2013), mean yearly community %C decreased from 43.05 to 39.53.

Likewise, community %N and %P decreased from 8.75 to 7.82 and 0.79 to 0.65, respectively. Community C:N increased from 5.87 during the first decade to 6.42 during the last one. Community C:P and N:P changed from 146.94 to 184.93 and 24.53 to 28.50.

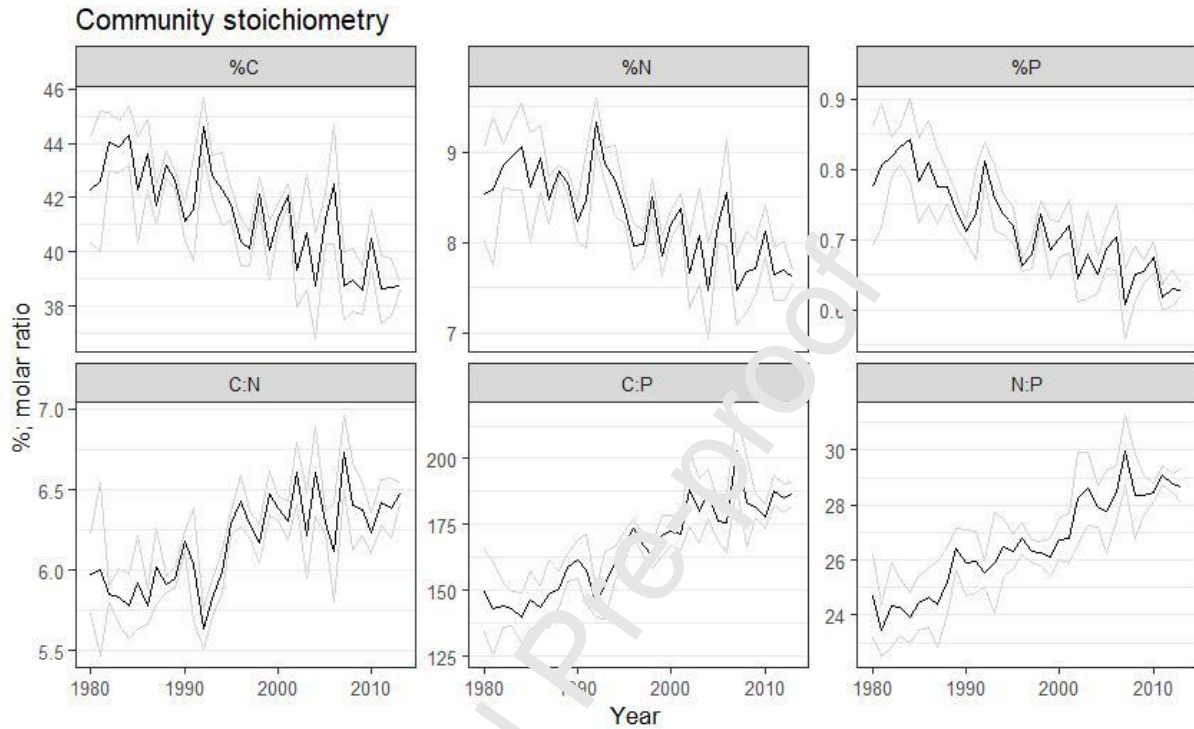


Fig. 1: Community stoichiometry (%C, %N, %P and molar C:N, C:P, N:P) over the study period 1980-2013. The black lines represent yearly mean values; light grey lines the mean \pm the standard deviation. The number of sampling events per year was $n = 4$ for all the years except 2008 with $n = 3$. Please note that ratio values (C:N, C:P, N:P) have been exponentiated in the figure to facilitate interpretation and comparison with other studies, while all analyses have been conducted using log-transformed values.

Water phosphorus concentration decreased significantly over the 34-year period, even though it slightly increased again during the years from 2003 to 2010 (Fig. 2, Tab.3). Compared to the first decade (0.22 mg/ L), the mean concentration during the last decade declined by 63.97% to 0.08 mg/ L.

Water nitrogen concentration fluctuated between years, but with no clear overall trend. Mean concentrations slightly increased from 6.10 to 6.60 mg/ L (+8.19%) between the first and the last decade.

Water N:P ratio increased more than fivefold from 31.52 (first decade) to 174.67 (last decade). From 2002 (when water P was the lowest) to 2004, water N:P drastically increased from 98.73 to a maximum of 377.09 and then decreased to values around 50 in 2009-2011.

Water temperature significantly increased (+29.65%) from 14.37°C (first decade) to 18.63°C (last decade).

Tab. 3: Results of the Mann-Kendall trend tests applied to water parameters and community stoichiometry. Bold lettering indicates statistical significance of Kendall Tau at $\alpha = 0.05$.

	Parameter	Trend	Tau
Water	NO ₃	-	0.11
	PO ₄	↘	-0.61
	N:P	↗	0.57
	Temperature	↗	0.66
Community stoichiometry	%C	↘	-0.60
	%N	↘	-0.56
	%P	↘	-0.70
	C:N	↗	0.56
	C:P	↗	0.76
	N:P	↗	0.79

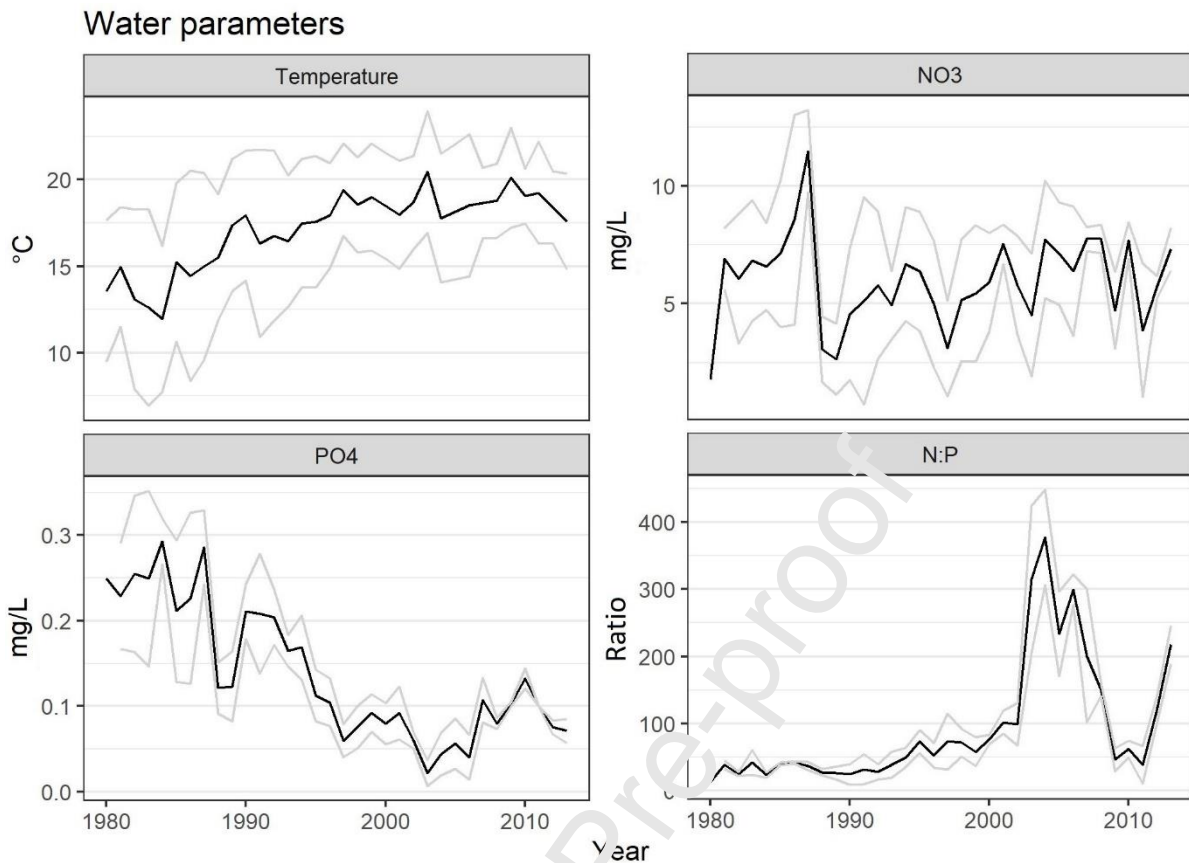


Fig. 2: Water quality parameters (concentration of NO₃ & PO₄ in mg/L and their ratio) and temperature (°C) over the study period 1980-2013. The black lines represent yearly mean values; light grey lines the mean +/- the standard deviation. The number of sampling events per year was n = 4 for all the years except 2008 with n = 3. The calculations were based on mean values over the 126-day period before each faunal sampling date.

Links between water parameters, stoichiometric and biological traits

There was a significant link between water parameters and stoichiometric and biological traits ($p < 0.05$, Tab. 4). Clearly the largest part of co-variation was captured by the first RLQ axis (95.23%, Fig. 3a), which separated water phosphorus concentration ($F1 < 0$) from water N:P and temperature ($F1 > 0$), thus well representing global trends in the annual mean values of water parameters over the study period. Water nitrate concentration, slightly negatively correlated to the first axis, showed a strong correlation to the second axis, which explained only 4.05% of the variance. The following description of the results will focus on trait

category contributions to the definition of the first RLQ axis only. The location of years along the first axis follows a clear trend, supporting an underlying temporal trend (Fig. 3b).

Body %C, %N and %P were all negatively varying along the first axis (Fig. 3c), positively related to water phosphorus concentration (Fig. 3a). Body molar ratios (C:N, C:P, N:P) were varying in the opposite direction, positively linked to water N:P and temperature. All six stoichiometric variables were among the trait categories highest involved in the link between invertebrate traits and environmental parameters as visible from the weighted average factorial scores of sampling events representing these stoichiometric traits along the first axis of the RLQ analysis (Fig. 3c).

The proportion of large-sized invertebrates (> 4 cm) increased along the first RLQ axis and was linked to high water N:P ratio values, while the proportion of small-sized taxa (> 0.5-1 cm) decreased and was related to high water phosphorus concentrations (Fig. 3d). Other size classes exhibited only a slight association with the first RLQ axis but were ordered according to their range of values between these extreme categories (except for the smallest maximum sizes; ≤ 0.5 cm).

Other development-related trait categories highly involved in the link between environmental variables and biological trait and related to high water phosphorus concentrations ($F1 < 0$) included a short life duration (" ≤ 1 year"), polyvoltinism (" >1 generation/year"), one single reproductive cycle per individual ("1 cycle") and a high number of molting events ("10-14", "15-19", " > 20 ") (Fig. 3d). They were associated with aquatic larvae, an aerial, passive dispersal, eggs and statoblasts as resistance stages and deposit (*i.e.* fine detritus) feeding (Fig. 3e+f).

At the opposite side ($F1 > 0$), long-lived (" >1 year"), monovoltin ("1 generation/year") organisms with several reproductive events per individual (mainly two cycles), a direct development ("0 molt") were related to both high water temperature and high values of water

N:P ratios (Fig. 3d). Such organisms exhibited also aquatic adults, living macroinvertebrates (and vertebrates; mainly fish eggs and juveniles) as food, and an aquatic, active dissemination mode (Fig. 3e+f).

Tab. 4: Results of the RLQ analysis linking water chemistry (NO_3 , PO_4 , water N:P) and temperature to species functional (*i.e.* stoichiometric and biological) traits via their abundances over a 34-year period. Total inertia indicates the global link between environment and functional traits, bold lettering indicates significance at $\alpha = 0.05$ (permutation tests with $n=9999$; applying two separate tests to correct for type I error (Dray & Legendre 2008)). The projected inertia along the first three RLQ axes is indicated. The fit of the RLQ analysis compared to the preliminary analyses (*i.e.* inertia/co-inertia) has been quantified by 1) the ratio between eigenvalues from RLQ and PCA for the environment (column Env) and trait (column Traits) tables and 2) the ratio between the correlation between the taxon scores and site scores from the RLQ and CA for the taxon abundance table (column Taxa).

Total Inertia	Projected inertia (%)		Fit of RLQ analysis				
			Env	Traits	Taxa		
1.093	Ax. 1	95.23	Ax. 1	0.98	0.86	Ax. 1	0.53
	Ax. 2	4.05					
	Ax. 3	0.69					

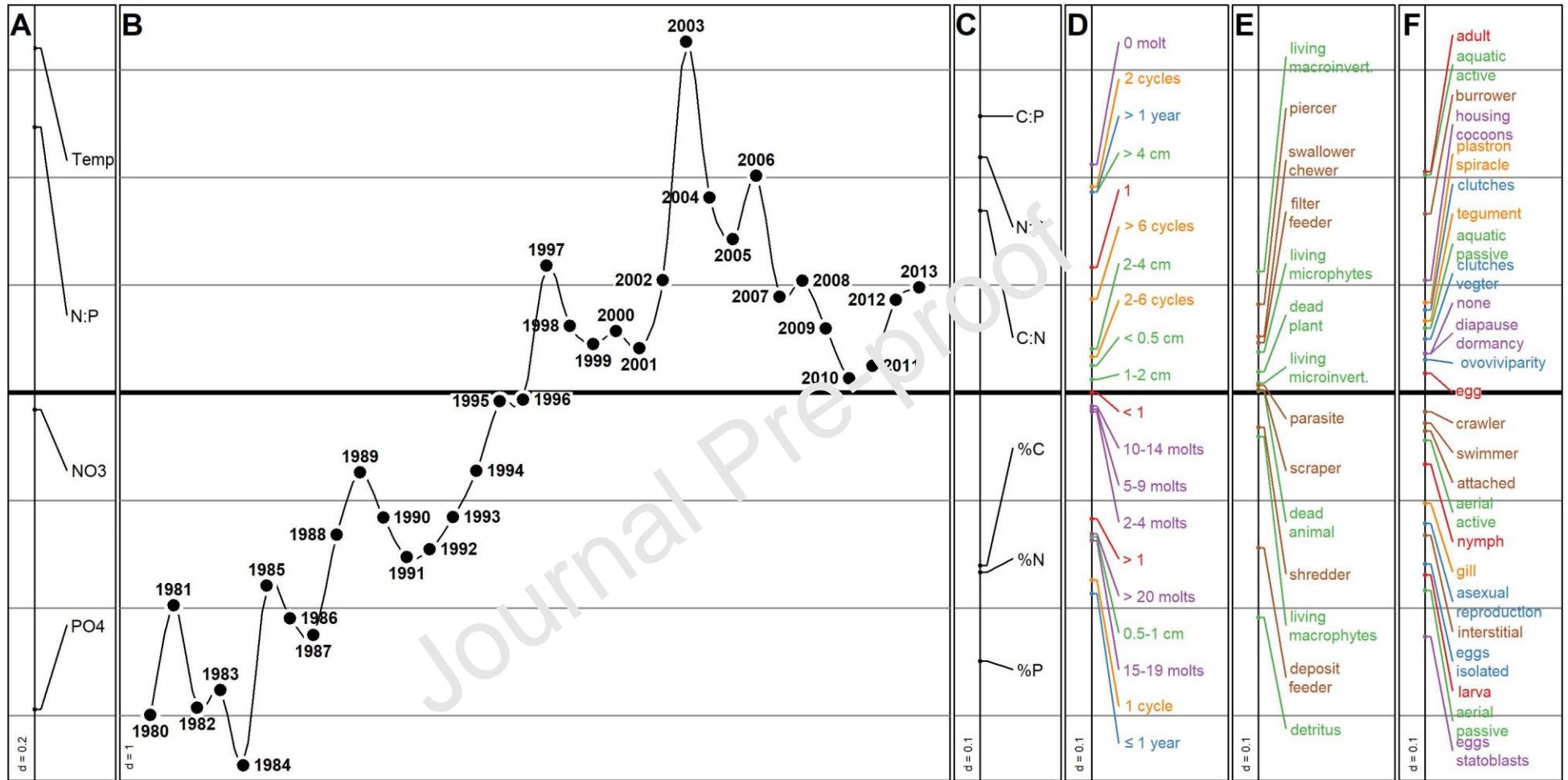


Fig.3 : Canonical weights of a) environmental parameters (water PO₄, NO₃, N:P, temperature) and c-f) biological trait categories along the first RLQ axis. Biological trait categories were all equally part of the analysis and are simply presented group-wise (stoichiometric (c), development (d), feeding (e), other traits (f)) for better readability.

Panel b shows chronologically the location of years along the first RLQ axis.

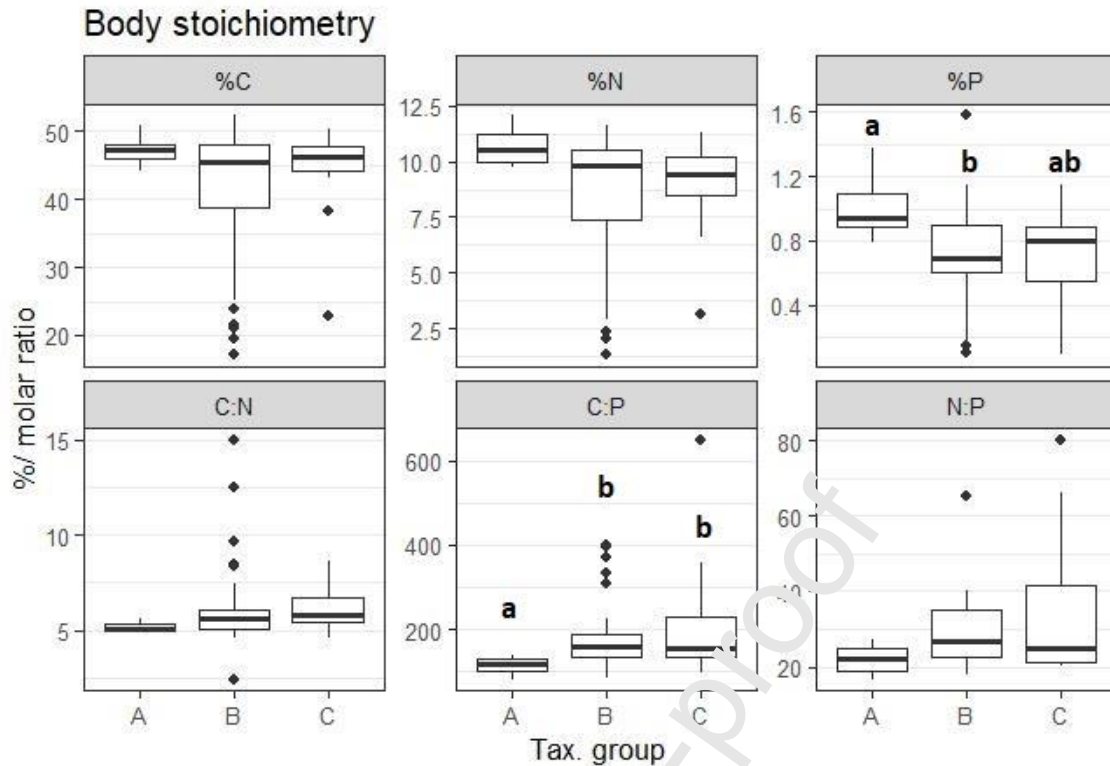


Fig. 4: Body stoichiometry (%C, %N, %P, C:N, C:P, N:P) of macroinvertebrate families belonging to groups with distinct abundance patterns over the study period as defined by Flourey et al. (2013). The horizontal line represents the median, the boxes range from the 25th to the 75th percentile and the whiskers extend to the last values within 1.5 times the inter-quartile range with black dots representing outliers. Different letters indicate significant differences using pairwise Dunn-tests following a significant Kruskal-Wallis test (adjustment of p-values for multiple testing using Bonferroni method). Sample size was n = 6/ 36/ 13 for groups A/ B/ C.

Taxa groups only differed significantly in %P and C:P stoichiometry (Fig. 4). Taxa belonging to group A (decreasing abundance over the study period) had the highest %P among groups, although this difference was only significant compared to group B (Dunn-test with $p < 0.05$). Groups B (present over the whole period) and C (mainly present at the end of the period) did not differ. C:P ratio was significantly lower in taxa of group A than in both other groups, which did not differ ($p > 0.05$). A non-significant trend for highest values of %C and %N in

group A was also observed, while values in groups B and C hardly differed. Body C:N and N:P ratios increased from group A to group B and C, but neither groups differed significantly.

Discussion

The shift in water quality and temperature was significantly linked to community biological and stoichiometric trait profiles, following assumptions based on ecological stoichiometry. Generally, stoichiometric traits were the trait-based metrics most involved in the link between environmental parameters and functional traits of benthic macroinvertebrate assemblages over the study period, taking into account the high scores of sampling events representing these traits along the F1 axis in RLQ analysis.

Trends in community stoichiometry

Phosphorus-related community stoichiometry decreased (%P) or increased (C:P, N:P) significantly over the 34-year study period. It thus followed the decline in water phosphorus concentration (and increase in water N:P ratio), supporting our main hypothesis (H1) and the findings of previous studies (Prater et al., 2015; Singer and Battin, 2007; Teurlinckx et al., 2017). The other community stoichiometric traits also showed significant trends. The likely reason for this is a shift among (major) taxonomic groups that generally differ in their body stoichiometry (Beck et al., 2022; Evans-White et al., 2005; Mehler et al., 2013). The increase in community C:N and C:P went along with increasing proportions of Bivalvia and Gastropoda (S3), two groups that have generally higher C:N and C:P ratios than others (Beck et al., 2022). The proportion of Insecta, which are relatively rich in phosphorus, decreased over the study period, in parallel with the overall community %P and water phosphorus concentration. Families that tended to decrease or even vanished during the first years of the study period, such as Perlodidae, Ephemerellidae or Simuliidae (Floury et al., 2013), had significantly higher %P and lower C:P than those occurring only during the last years (*e.g.* Aeshnidae or Glossosomatidae) or that were present during the whole period (*e.g.* Baetidae or

Rhyacophilidae). The RLQ analysis has further confirmed this selection for phosphorus-rich taxa under high phosphorus conditions.

Links between water parameters, stoichiometric and biological traits

All six stoichiometric traits showed a strong association to the first axis of the RLQ analysis and overall seemed to be more affected by environmental parameters than the other biological traits. The correlations found in other functional traits are in line with our hypotheses based on ecological stoichiometry theory and/or with results already reported in the literature. Taxa with high body %P and expressing traits indicating a fast growth and/or development and often considered as r-strategists (small body size, short life duration, high number of generations) (*e.g.* Southwood, 1977) were positively related to high water phosphorus concentrations and therewith had higher abundances early in the study period. In recent years, the community shifted towards larger, longer-lived taxa with direct development (no molt) and several reproductive events per individual. The recent environmental conditions, notably the reduction in phosphorus load, also selected for taxa with high N:P (and C:N, C:P) ratio. This is in line with the Growth Rate Hypothesis (= GRH, Elser et al., 1996), assuming a high demand for phosphorus and thus higher phosphorus content in the body tissues of fast growing taxa (Acharya et al., 2004; Elser et al., 2003); a link that also seems to hold for development rate (Beck et al., 2021). Other studies already observed a shift towards small-bodied, fast-developing taxa (Demi et al., 2019; Singer and Battin, 2007), and decreasing life duration (Floury et al., 2017) under high nutrient conditions supporting the common assumption in general ecological theory that nutrient enrichment favours r-strategists (Dolédéc et al., 2006; Southwood, 1977). Despite size being a key trait in ecology, there is no consensus about the effect of eutrophication on macroinvertebrate community size structure as observed results go in diverse directions for freshwater (*c.f.* Tab. 1), as well as terrestrial (Mulder and Elser, 2009; Ott et al., 2014) systems. While the lack of an effect can be due to

rather constant taxonomic composition between treatments (Bourassa and Morin, 1995), an increase in mean body size can indicate a response at population level (*i.e.* individuals becoming larger; Davis et al., 2010; Dolédec et al., 2006; Juvigny-Khenafou et al., 2021) and/or a shift in taxonomic composition at community level (Juvigny-Khenafou et al., 2021). The duration (short-term vs. long-term) and strength of the nutrient change might (partly) cause these differing responses. Moreover, the specificities of the study system (*i.e.* the presence or absence of predators or prey refugia) should also be kept in mind when comparing the results.

With decreasing water phosphorus concentration, feeding habits shifted from deposit-feeders and shredders feeding on detritus towards predatory feeding strategies (swallowing/chewing, piercing invertebrates as resource) and filter-feeding. The increase of the latter feeding habit is likely due to the increasing proportion of *Bivalvia* over the study period. A general link between filter-feeding and high C:P and C:N ratios has already been found (Beck, 2021), and was also (partly) related to an effect of phylogeny, since this combination of functional and stoichiometric traits was mainly expressed by molluscan taxa. The same study also reported a positive association between deposit-feeders and shredders towards high body phosphorus content. A decrease in deposit-feeding has already been observed under the same environmental scenario (Floury et al., 2013; Latli et al., 2017), but these works reported either no effect on predators or a decrease (mainly influenced by phytoplankton concentration, a parameter that was not considered in our study), and therewith the opposite to our finding. Generally, the observed predator responses to nutrient enrichment have been divergent (Hulot et al., 2000; McCormick et al., 2004; Wimp et al., 2010; Murphy et al., 2012; Demi et al., 2019) and are most likely not only driven by prey quality but also quantity. Predatory feeding behaviour has already been linked to body nitrogen content (Fagan et al., 2002; Cross et al., 2003; Beck, 2021), but not to phosphorus. Although in our study this link was among the

strongest links over the feeding-related traits, feeding traits overall contributed only little to the link between traits and environmental parameters.

Like community stoichiometry, part of the observed trait patterns was clearly driven by trait syndromes, *i.e.* groups of traits that originate from phylogenetic constraints, and shifts among larger taxonomic groups, especially the increase of Mollusca with notably the bivalve *Corbicula* (see Floury et al., 2013). However, some of these observations can also be explained by ecological stoichiometry theory. For example, the decreasing affinity for aerial, active dispersal could either be due to a generally rather high nitrogen content of Insecta (Beck et al., 2022), the only group expressing this trait, or due to a higher investment into nitrogen-rich muscle tissue necessary for flight. This makes it impossible to disentangle causes and effects among stoichiometric traits, other biological traits and taxonomy. In case of community stoichiometry however, the observed decrease in community phosphorus content remained when only analysing the insect community and therewith reducing the effect of taxonomy (S. 4).

Nutrients vs. temperature as drivers of the community response

The strong negative relationship between phosphorus concentration and coordinates of sampled years along the first axis of the RLQ analysis, and the position of high PO_4 concentrations opposite to high water N:P and temperature values clearly represent the major trends in environmental parameters. They suggest a stronger driving effect of phosphorus concentration and temperature on the functional trait composition of invertebrate assemblages than nitrogen concentration, which fluctuated among years but did not show a continuous trend over the study period. The observed changes in stoichiometric and biological traits support our hypotheses H1 and H2 expected under P decrease to the detriment of hypotheses H3 and H4 expected under temperature increase. Thus, it seems that the P-decrease had a higher impact on the stoichiometric composition of invertebrate assemblages than the

temperature increase. As a result, temperature does not seem to be the most important driver of invertebrate traits in the Loire River at Dampierre-en-Burly over the study period. Flourey et al. (2013) already suggested that water quality (esp. phosphorus concentration) was a more important driver on life-history traits than hydro-climatic parameters (temperature, discharge). Overall, the positive effect of phosphorus decline likely buffered the effect of increasing temperature (Flourey et al., 2013). This might explain, why – despite an improvement of water quality – we observed the decrease or the disappearance of several pollution-sensitive families of Ephemeroptera (e.g. Heptageniidae) and Plecoptera (e.g. Perlodidae and Perlidae). Other sensitive taxa appeared during the last decade (e.g. the trichopterans Glossosomatidae and Philopotamidae or the ephemeropteran Leptophlebiidae). In other multiple-stressor experiments the effect of nutrients on taxa or trait groups was only minor compared to those of temperature or physical habitat changes (sediment deposition, flow velocity), but affected body sizes and community size-structure (Juvigny-Khenafou et al., 2021; Piggott et al., 2015). Other works have suggested also an effect of increased predation risk (due to exogenous species whose settlement has been facilitated by new environmental conditions) rather than a direct effect of temperature or water quality on invertebrate traits related to life history (Lattin et al., 2017).

Although our initial hypotheses regarding temperature (H3, H4) were not supported, the observed patterns could nevertheless (also) be explained by concepts within the ecological stoichiometry theory framework. Increased respiration rates under high temperatures (Hamburger and Dall, 1990) or a reduced quality of autotrophic resources (Domis et al., 2014; Yvon-Durocher et al., 2017) could have favoured taxa of high body C:P and C:N ratios and their corresponding functional traits (as discussed above). As shown for the freshwater crustacean *Daphnia*, the relationship between nutrient requirements (C:P) and temperature seems to be U-shaped (Ruiz et al., 2020), suggesting lower nutrient and higher carbon

requirements (high C:P) at high temperature increase. For a leptophlebiid mayfly, Moody et al. (2017) showed that the GRH did not hold under temperature variation *i.e.* that an increase in body P content under warming was not caused by a temperature-induced increase in growth rate.

It is likely, that the 2003 heat wave in France caused the high involvement of temperature in our study, and it therefore would be interesting to further disentangle the effect of nutrients vs. temperature events, especially considering long-term effects of the latter. A scenario with increasing temperature but stable nutrient concentrations could provide information about temperature as a driver of (stoichiometric) trait composition. Since this study was done using field data from uncontrolled conditions, we surely cannot exclude that other stressors (*e.g.* hydromorphological alterations, episodic contaminations) altered the community composition, especially since often multiple anthropogenic factors act simultaneously in large rivers. Notably, transport facilities and rather moderate inputs of pesticides and other micro-pollutants (episodically detected during the study period) might have had an influence on this section of the Middle Loire (Loire-Bretagne Basin Water Authority, 2019).

Invasive species can also cause major changes for macroinvertebrate assemblages and the whole ecosystem, for example reducing phytoplankton availability and planktonic production (Floury et al., 2013; Pignour et al., 2014) and thus altering the food web structure (Latli et al., 2017) and O₂ budget (Bachmann and Usseglio-Polatera, 1999) as in the case of the bivalve *Corbicula* in West-European streams. In our case, *Corbicula* likely largely drove the increase in certain functional trait categories (*e.g.* filter-feeding, aquatic adult large body size) in the more recent decade. However, as pointed out throughout the discussion, the observed patterns both in community stoichiometry and functional trait composition are largely in line with ecological stoichiometry theory. It would thus be interesting to further investigate the role of

stoichiometry in the establishment of invasive species, as this has the potential to improve our mechanistic understanding of invasion success (González et al., 2010).

Outlook

The main advantage of stoichiometric traits is their ultimate link to elements that allows understanding shifts in taxonomical and functional community structure (as demonstrated in this work), but could also help answering nutrient-related questions beyond community level. In an ecological context, community stoichiometry can be used as a descriptor of the nutrient pool provided by the community. Serving as food for higher trophic levels, releasing nutrients into the water via excretion (Elser & Urabe, 1999; Vanni *et al.*, 2002; Liess & Hillebrand, 2006) or providing energy and nutrient flows from the aquatic to the terrestrial system *via* emergence of insects (Martin-Creuzburg *et al.*, 2017; Raitif *et al.*, 2018), macroinvertebrates are important contributors to nutrient cycling in many freshwaters. Any shift in this nutrient pool thus can cause effects within and beyond community level, for example by providing lower quality prey or reduced nutrient release (Elser & Urabe, 1999; Vanni *et al.*, 2002; McManamay *et al.*, 2011; but see also Vanni & McIntyre, 2016) due to taxa exhibiting low C:P and C:N.

Integrating biomass information would allow quantifying nutrient stocks or exports. A first estimation using this dataset suggests that although community %P decreased, the overall amount of phosphorus storage increased (in line with a general increase in overall biomass, S5). Although the estimated phosphorus export by emerging insects increased, this element seemed to remain in the system for a longer period as suggested by the sharp decline in relative phosphorus export. This indicates that the change in community (trait) structure, also affects the nutrient pool structure of the community and it would be interesting to investigate whether there is a general response primarily towards changing nutrient conditions and/or

towards community stoichiometric trait structure. Additionally, investigating whether the link between stoichiometric/biological traits and environment nutrient levels holds for other systems (*e.g.* soil, lakes) or over a spatial – rather than temporal – nutrient gradient could underline the potential of stoichiometric traits in a wider range of ecological contexts.

Conclusion

We demonstrated that over a 34-year period community (phosphorus) stoichiometry followed the decrease in water phosphorus concentration, which thus directly affected the nutrient pool provided by the community *via* a shift towards P-poor taxa. Shifts regarding functional traits were also in line with assumptions based on ecological stoichiometry theory. Recent communities consisted of larger-bodied taxa with traits indicating slow growth/development, predatory and filter-feeding habits rather than deposit-feeding or shredding. This suggests that nutrients rather than temperature were the main driver of invertebrate community trait composition over the study period. As such, our results have underlined the potential of integrating stoichiometric traits into (trait-based) analyses to better understand the mechanisms behind functional community responses towards nutrient-related stressors. Integrating variables such as biomass could further help quantifying nutrient stocks and fluxes under global stressors.

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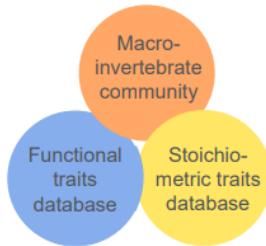


A 34-year survey under phosphorus decline and warming:
Consequences on stoichiometry and functional trait composition
of freshwater macroinvertebrate communities



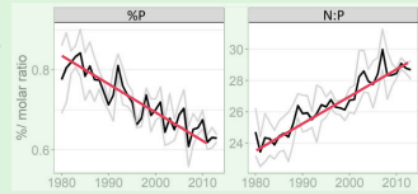
Does theory from Ecological Stoichiometry Theory (EST) hold on community level and over the long-term?

30 years of phosphorus decline and warming

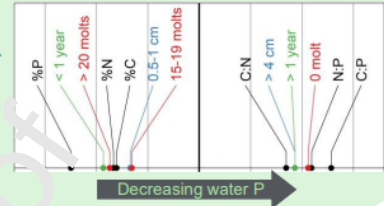


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Altered community stoichiometry
→ altered nutrient pool provided by consumers
→ %C, %N, %P, molar C:N, C:P, N:P



Functional trait shifts in line with EST
→ P rich, fast-growing, fast-developing taxa under high P



→ Stoichiometric traits have the potential to help explaining functional shifts in community composition and consequences for nutrient cycling

Graphical Abstract

Highlights

- Warming and nutrient changes cause taxonomic and functional community shifts
- Stoichiometric traits are linked to functional traits and environmental nutrients
- 34 years of P decline favored P-poor taxa and increased community C:P and N:P ratios
- A changing nutrient pool likely affects nutrient storage or export from the stream
- Temporal shifts in functional traits were in line with ecological stoichiometry theory

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