

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/303094564>

Long-term changes in temperate stream invertebrate communities reveal a synchronous trophic amplification at the turn of the millennium

Article in *Science of The Total Environment* · September 2016

DOI: 10.1016/j.scitotenv.2016.04.193

CITATIONS

9

READS

324

5 authors, including:



Kris van looy

OVAM flemish agency for sustainable management of material and soils

70 PUBLICATIONS 868 CITATIONS

[SEE PROFILE](#)



Mathieu Floury

National Research Institute of Science and Technology for Environment and Agric...

11 PUBLICATIONS 140 CITATIONS

[SEE PROFILE](#)



Martial Ferréol

National Research Institute of Science and Technology for Environment and Agric...

28 PUBLICATIONS 546 CITATIONS

[SEE PROFILE](#)



Yves Souchon

French National Research Institute for Agriculture and Environment

103 PUBLICATIONS 1,871 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Ecosystem resilience; measuring sustainability and capacity to restore [View project](#)



Climate change and aquatic ecosystems [View project](#)



Long-term changes in temperate stream invertebrate communities reveal a synchronous trophic amplification at the turn of the millennium



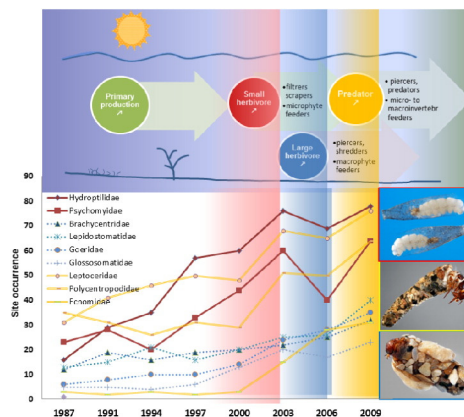
Kris Van Looy*, Mathieu Floury, Martial Ferréol, Marta Prieto-Montes, Yves Souchon

Irstea, National Research Institute of Science and Technology for Environment and Agriculture, UR MALY, River Hydro-ecology Lab, 5 rue de la Doua, Lyon-Villeurbanne, France

HIGHLIGHTS

- French stream invertebrate communities exhibited strong changes over the last decades
- Climate change and water quality improvement mutually influenced the community trends
- Several lines of evidence show the 1997–2003 community shift being a trophic amplification
- This trophic amplification mechanism has supported a strong diversity increase
- As such, it could have wider implications by reinforcing community recovery

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 4 April 2016
Received in revised form 29 April 2016
Accepted 29 April 2016
Available online xxx

Editor: D. Barcelo

Keywords:

Aquatic macroinvertebrates
Large scale
Time series
Climate change
Shift
Response diversity

ABSTRACT

The positive effects of water quality improvement on stream biodiversity in the temperate regions are expected to be at risk with the projected climatic changes. However, the processes and mechanisms behind the predicted threats remain uncertain. From long-term series of benthic invertebrate samples from temperate rivers and streams in France, we analyzed diversity and composition shifts over time in relation to geographic elements and human stressors. Mechanisms for community changes were investigated with a trait-based analysis for the entire dataset and for a selected caddisfly community module. We observed a 42% increase in the taxonomic richness of stream invertebrate communities over the last 25 years. A gradual trend induced by water quality improvement was distinguished from a more abrupt climate change-induced shift in communities around the year 2000. Trophic amplification – the intensification of trophic interactions and pathways through the food web – was identified as the mechanism behind the strong community shift. Four lines of evidence for this trophic amplification are highlighted: (i) higher dissolved oxygen concentrations indicated a shift in primary production, (ii) the trait-based analysis of entire communities showed a bottom-up food web amplification, (iii) the trait-based analysis of the community module evidenced feeding strategy shifts and increased food web interactions, and (iv) the abundance analysis of the community module showed a productivity increase. These results lend credit to persistent investments in water quality for improving stream biodiversity, and contrary to expectation, climate change impacts seem so far to have reinforced these positive effects.

© 2016 Elsevier B.V. All rights reserved.

* Corresponding author at: Irstea, National Research Institute of Science and Technology for Environment and Agriculture, UR MALY, River hydro-ecology unit, 5 rue de la Doua CS70077, 69100 Villeurbanne Cedex, France.

E-mail addresses: Kris.van-looy@irstea.fr (K. Van Looy), Mathieu.floury@irstea.fr (M. Floury), Martial.ferreol@irstea.fr (M. Ferréol), Marta.Prieto-Montes@irstea.fr (M. Prieto-Montes), Yves.souchon@irstea.fr (Y. Souchon).

1. Introduction

Given the uncertainties of actual predictions, real-world observations combined with more evidence-focused approaches to climate change impacts are required (Fordham, 2015). Predictive frameworks for climatic changes are now being developed that identify strong risks of species loss in aquatic ecosystems, especially of benthic invertebrates over temperate regions (Bonada et al., 2007; Poff et al., 2012). Forecasts and extrapolations of climate change for stream macroinvertebrates over Europe predict a substantial decrease in the numbers of climatically suitable areas for most species (Domisch et al., 2013). Comparable exercises predict a significant decrease in the diversity of fish communities (Buisson et al., 2013; Comte & Grenouillet, 2013; Logez & Pont, 2013). Conversely, water quality management in this temperate region over the past decades has successfully contributed to a recovery of the biological quality thought to be at risk under further climatic changes (Durance & Ormerod, 2009). Warming temperatures and flow changes can aggravate environmental risks for pollution sensitive species (Verberk et al. 2016), hence a confounding factor in detecting trends is the distinction between responses to water quality improvement programs and those to climate change.

Improved mechanistic understanding of climate change interaction with other stressors is urgently required for effective adaptation to minimize warming impacts. Temperature increase for France is reported to have reached 1 °C over the last three decades for air temperature measurements, a high value compared with global averages (Fig. S1). For water temperature an even higher average increase of 2 °C over the same period is reported (Daufresne & Boët, 2007; Floury et al., 2012). Trends of increasing winter flows and decreasing summer flows have also been recorded over the region in the last three decades (Stahl et al., 2010; Giuntoli et al., 2013). Up to now, stream invertebrate community changes in Western European studies have been documented as gradual (Langford et al., 2009), and their recovery through water quality improvement is assumed to have so far outweighed the impact of climate change, as observed for English streams (Vaughan & Ormerod, 2012). Mechanisms of change in relation to climate changes correspond not only to temperature preferences, but also to responses to the

described hydrological and climate regime disturbances, in terms of food web fragmentation (Woodward et al., 2010), greenhouse gas forcing (Parmesan et al., 2013) and trophic ecosystem shifts (Beaugrand et al., 2014). The trophic amplification of climate change is described as a productivity increase along one or more trophic pathways (Kirby & Beaugrand, 2009, Chust et al., 2014). The use of taxonomic composition alone may not suffice to detect such processes of functional community change; we therefore applied a trait-based approach to assessing responses in stream communities based on the biological trait profile of a community (Webb et al., 2010).

Our main objective was to determine the prevailing mechanisms of change in river benthic invertebrate communities, in the light of actual co-occurring processes of water purification and climate warming. In particular, we hypothesized following Vaughan & Ormerod that (i) the two processes worked antagonistically, and (ii) recovery resulting from water quality improvement still outweighed the climatic change-induced effects on invertebrate communities. To test these hypotheses, we gathered a long-term dataset of annually sampled stream and river sites in France, spanning the last three decades and over 1000 km in longitude and latitude (Fig. S2). We tested the responses to environmental and climatic changes in taxonomic composition and in trait profiles to detect the mechanisms behind the changes. Water purification effects should be observed in a gradual increase in pollution-sensitive species. Climate change effects are expected in trait profiles of temperature tolerance and trophic groups, in increased productivity and food web interactions.

2. Materials and methods

2.1. Invertebrate dataset construction

In collaboration with experienced hydrobiologists of the regional services for stream and river monitoring we compiled a long-term (LT) dataset spanning 25 years (1987–2012) from monitoring sites throughout France sampled annually for aquatic invertebrates with confidence in procedure and operators through time (most sites sampled by same operator throughout). 91 sites matched these criteria

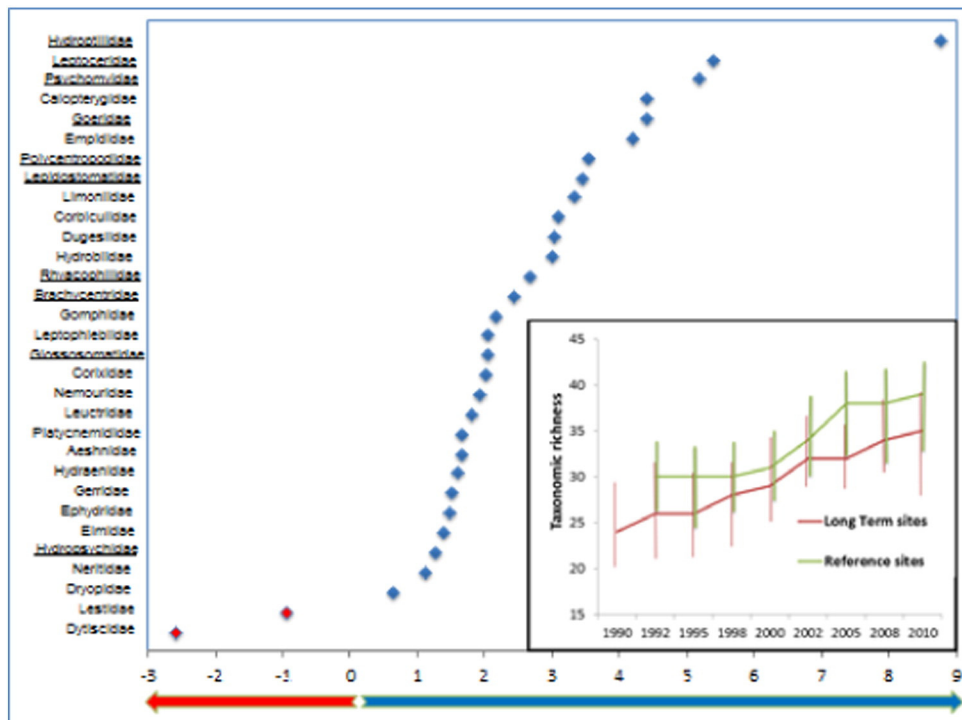


Fig. 1. Significant winners and losers and richness increase over the time series.

(Fig. S1). The sites ranged from streams to large rivers (annual mean discharges in the range 9–192 m³/s) spanning over 1000 km and with an altitude range of 8–977 m above sea level. In addition to the 91 selected sites (the ‘national case’), two large rivers (Doubs and Gave de Pau) provided consistent 35-year monitoring results with seven sites distributed throughout the river length for each river. These datasets (‘regional cases’) were retained to check for scale-dependence of detected trends and reveal any differences between regional and national-scale shifts. Finally a distinct set of undisturbed reference condition sites – assessed based on catchment land use and water quality criteria – was assembled comprising 51 annually sampled sites. As the French reference monitoring network started only in 1992, this reference dataset is shorter in time than the other two long-term datasets. The spatial spread of both monitoring networks was chosen to represent the variety of river types and catchment areas. The reference condition sites allowed us to cross-check general trends against those associated with no immediate human impacts, i.e. to separate direct human-induced effects from climatic change-induced trends (Vaughan & Ormerod, 2012). For robustness of the data analyses of the different datasets and in the light of the single annual biota sampling, we constructed eight 3-year periods of analysis (middle years of periods are presented in Fig. 1) to avoid accidental gaps in the series (<8%) and to dampen meteorological irregularities. For each period one sample per site was retained for the LT series analysis. Per period, the samples of the most representative year – selected for most sampled and absence of climatological anomalies – were primarily selected.

The sampling protocol for all the sites consisted in sampling a reach ten times the stream width, for which a number of unitary samples were collected with a Surber sampler with mesh size 500 µm and area 0.05 m². Eight samples representative of the reach’s mesohabitats – categorized by both substrate type and water velocity – were considered. For the sampled reach the substrates (sand, gravel, bryophytes, etc.) were recorded over the reach in percentage cover. This information was used in the ordinations as habitat diversity (number of substrate types) and type (dominant type).

All the invertebrates in the samples were identified, but the level of taxonomic resolution varied with time period and region. We therefore retained the most consistent level available: the family level. This level has been shown to be the most robust when analyzing macroinvertebrate diversity changes at large spatial scales because biogeographical differences in species pools limit the detection of general patterns at finer levels of taxonomic resolution (Heino, 2014). We are aware of the low taxonomic resolution in addressing our questions, but can rely on other work that shows that for larger spatial scale datasets, the taxonomic level does not change the observed community change patterns and relationships with environmental elements (Heino, 2014; Jähnig et al., 2009; Mueller et al., 2013). We also assessed sensitivity to taxonomic resolution by verifying the community composition gradient in ordination at genus level for the first and last period, for which we had data at this finer taxonomic level. Likewise, we looked in detail at the species level for the periods when this information was available to check for consistency in the results and conclusions.

2.2. Environmental data

For water quality parameters corresponding to human pressure, we used monthly measured ammonium, nitrites, nitrates and orthophosphates according to national standards (Villeneuve et al., 2015). For climate change parameters, unfortunately direct measurements of change in temperature, carbon dioxide (bicarbonates) and light intensity for the sites over the time series are not available (irregular in timing) for the analysis. Therefore, we look at dissolved oxygen content as this is generally used as measure for aquatic primary productivity (Odum, 1956). Mean values of concentrations were calculated on the monthly water samples for a time span of 11 months before and 1 month after the biological sampling.

Catchment disturbance and water pollution (based on the chemical water quality) were used as the environmental factors representing the main stressors to river biodiversity. The human disturbance of the sites is described with the land use in the catchment. Naturalness of the upstream catchment (percentage cover) was calculated for each site based on CORINE Land cover data (for the year 2006) with the first order classification, which distinguishes near-natural land use of forests and extensively used grasslands. Altitude and river size (with proxy Strahler order) were entered into the analysis as geographical parameters, to complete the environmental gradient of river conditions potentially explaining macroinvertebrate community structuring. At the sample site level, type and diversity of substrates were retained as habitat variables.

2.3. Trend detection

To identify trends, patterns of taxonomic richness change for both the 91 LT sites and the 51 reference sites were first investigated by averaging the taxonomic richness over the sites per time period. We used a linear regression for occurrence frequency over the eight time periods to identify significantly changing taxa distributions, and selected the significant trends ($p < 0.05$), with control of the residual correlation and visual control of occurrence graphs. We used regression slope as an estimation of strength of trend (Fig. 1). This resulting value is comparable to the odds ratio for describing taxon trends (e.g. Chessman, 2009), and detects the same strongly changing taxa, but this approach is better adapted to data with many sporadic and fluctuating occurrences. Trends in water quality parameters were tested by ANOVA over the time periods for the different sets of sites.

To characterize general trends in community composition, a within-class correspondence analysis (WCA) was run on the LT sites and the regional cases. This test performs a particular case of an orthogonal principal component analysis, in which a single factor acts as covariate (Lebreton et al., 1991). The aim of this ordination was to perform a correspondence analysis that summarizes biological trends, while masking site influence (seen as the class effect to be removed). For the community analyses all abundances were log + 1 transformed, and rare taxa, occurring at <5% relative abundance of the whole study dataset, were removed.

The link between environmental data and the biological compositional changes through time were then characterized for the LT sites with partial canonical correspondence analysis (pCCA). The aim of this ordination was to summarize biological trends according to environmental data, just like a standard CCA, while co-varying out site influence. As with the WCA, geographical distance between study sites was expected to be one of the most strongly prevailing gradients, and was considered again as a class effect to be removed. Water quality parameters and the selected geographical, human disturbance and local habitat variables were included, and relationships between environmental parameters and invertebrate trends were tested in the pCCA for the purpose of estimating the percentage of total inertia explained by environmental parameters.

To determine the mechanisms of responses in stream communities, we assessed the trait profiles of communities, as biological traits can indicate functional relationships between biota and environmental characteristics (Dolédéc & Stutzner, 2008). We calculated community traits by implementing a fuzzy coding approach using the affinity of each taxon for trait modalities (Usseglio-Polatera et al., 2000). The biological traits (Supporting Information Table S1) relate to the life history of organisms (e.g. size, number of reproductive cycles) or features that confer resilience or resistance beyond that provided by life history traits (e.g. attachment), as well as more general biological and physiological features (e.g. feeding groups, respiration).

Trait-based indicators were constructed to identify the impact of climate change and water quality improvement; using traits of temperature tolerance and pollution sensitivity respectively. Trait modalities

were ranked from highly sensitive (psychrophilic for temperature and very sensitive for pollution) to tolerant (thermophilic and eurythermic for temperature and very tolerant for pollution). Relative frequencies of tolerance categories were expressed on a scale ranging from 0 (not present at the site) to 1 (100% individuals belonging to this category). Tolerance indicator values ranged from 0 to 1, with 1 corresponding to maximum resistance or tolerance to warming and pollution. To detect river type specific trends, a distinction in river sizes was applied for first- and second-order streams, medium-sized rivers (Strahler order 3–4) and large rivers (orders 5–6).

To analyze the entire set of community traits and properties of sites through time, a fourth-corner analysis approach was used (Dray et al., 2013) that distinguishes significant differences in trait composition over time. This method tests the associations between individual traits and predictor variables weighted by species abundances. Here we used time as single variable to analyze trait compositional changes over the sample sites, with the successive time periods investigated in terms of disjunctive variables. In the analysis we used as input matrices the taxon trait matrix, the sample species abundances and the sample time periods. Fourth-corner outputs are statistical parameters to be incorporated into causal ecological models describing the mechanisms determining the observed correlations, rather than modelling technique outputs. Results are Pearson correlation coefficients for each pair between trait modalities and periods. Their significances were tested respectively by a permutation of both rows (samples) and columns (taxa). For the eight time periods, trait modalities that were significantly positively or negatively ($p < 0.05$) associated with a period were detected.

2.4. 'Community module' analysis

To make the analysis of community changes conclusive, given that measures of spatial and temporal variation can vary when the size of the species pool varies (Chase & Myers, 2011), we analyzed the changes for a 'constant' species pool in a determined community module in the sense of Gilman et al. (2010). This group selection allows to look how large-scale processes influence biodiversity and community assembly. To counter the generally assumed homogenization caused by global change (Olden & Poff, 2004; Poff et al., 2012), the community assembly has to show a response diversity that is only weakly spatially structured – not fully governed by geographical and environmental gradients (Ruokolainen et al., 2009; Chase, 2010). Using partial Mantel tests, we tested for this absence of spatial and environmental structuring.

As community module we selected the *Trichoptera* families in which we saw the most marked changes, but which showed fairly continuous presence over time. The high diversity of life strategies in caddisflies – covering the full extent of the food web occupied by the invertebrate fauna – has already prompted scientists to use this order in studies to gain a better understanding of the effects of climatic changes on aquatic ecosystems (Hering et al., 2009). The selected community module consisted of the 12 most frequent families of the *Trichoptera* order, for which sites were selected with at least 6 out of 12 families present, and with continuous presence before and after the year 2000, thereby ensuring temporal continuity. 79 out of the 91 LT sites had data that met the module selection criteria. Spatial β diversity was measured for abundance data as Bray-Curtis dissimilarities between sites for the different periods. Shifts in the spatial variation were investigated with ANOVA. To test whether a general thermal regime shift occurred, or else a spatial structuring in the presence of environmental forcing, the Mantel test of similarity between communities over the spatial gradient can be conclusive for this dataset. Partial Mantel tests for the environmental factors and the geographical distance allow us to decouple pure spatial from environmental structuring, and look for differentiation over time (Anderson et al., 2011). We also looked at the trait changes for the community module in time to confirm the trait-based analysis. To look for overall productivity changes we calculated overall

abundance of the community module for the different periods, based on the logarithmic site abundance values for the selected caddisfly taxa (for the 79 sites). All testing was done with R statistical packages.

3. Results

3.1. Long-term trends in invertebrate communities

We found a strong continuous diversity increase in the LT sites, the mean taxonomic richness rising by 42% over 25 years (Fig. 1). For the community composition, in the WCA ordination 55% of the total inertia was retained with co-varying out site effect. The first axis, corresponding to the temporal change, explains 26% of the variance. Two distinct trend periods were detected (Fig. 2). The first covered the period 1980–2000, and showed a gradual albeit slow increase in pollution-sensitive taxa such as *Perlidae*, *Ephemerebellidae*, *Blephariceridae* and *Heptageniidae*. A shift in the trend occurred around the year 2000 (Fig. 2), with stronger compositional changes taking place thereafter. For this second period the change was toward more mobile and tolerant taxa such as *Hydroptilidae*, *Coenagrionidae*, *Gyrinidae* and *Empididae*. Taxa with the strongest increasing trends ('winners') over the long-term time series (Fig. 1, see also ordination result in Supplementary Table S2) belonged to the *Diptera*, *Odonata* and especially the *Trichoptera*, with more than half (9 out of 17 taxa with regression slope > 2) of the strongly increasing taxa in this order. Only two taxa exhibited decreasing trends ('losers'), which were associated with lentic environments. The invasive taxa *Corbiculidae* and *Hydrobiidae* also belonged to the winners. Finally, neither excluding the invasive taxa from the dataset, nor performing the ordination on presence/absence of data (rather than abundance of data) modified the observed patterns.

Stream invertebrate families with significant trends in the long-term time series are presented by the regression slope values for occurrence frequency over the sites in time (*Trichoptera* families are underlined). The inset graph shows the evolution of taxonomic diversity (average richness and SD) for the long-term time series and the undisturbed reference sites.

We checked the above trends against the changes in the set of reference condition sites. For the 51 reference sites, the period before 2000 showed constant diversity, unlike the recent period (after 2000), which showed a 23% increase in taxonomic richness (Fig. 1). The new millennium trend was the same as for the LT set. While water quality showed significant trends ($p < 0.01$) for the LT sites, with diminishing concentrations of orthophosphates (average decrease over all sites – 0.09 mg/l, Supporting Information Fig. S3), ammonium (– 0.05 mg/l) and nitrites (– 0.05 mg/l), in the reference sites no tendency was present in any of the water quality parameters (at $p < 0.1$). Dissolved oxygen showed significant trend taking place only from 1997 onwards (Fig. S3); in air temperature recordings we observed an earlier shift, with a significant warming since 1990 (Fig. S2).

In the partial-CCA ordination, the first two axes explained 71% of the variability in chemical water quality. Consequently, the two trend periods can be significantly associated with patterns of change in the chemical water quality. The first periods 1–4 were closely correlated with the nutrients (mostly to orthophosphates), while periods 5–8 were correlated with dissolved oxygen. However, only 3.2% of the biological variation can be specifically attributed to these water quality changes, whereas substrate composition alone explained 8.5% of the biological variation. For the trait-based indicators, significant changes were observed for pollution sensitivity; no overall trend in temperature tolerance was present (Fig. 3). For the pollution sensitivity, the significant changes covered the entire period and all the river sizes. For temperature tolerance, a trend was present only in the small streams, and was not indicative of the predicted climate-induced changes to more thermophilic and eurythermic taxa.

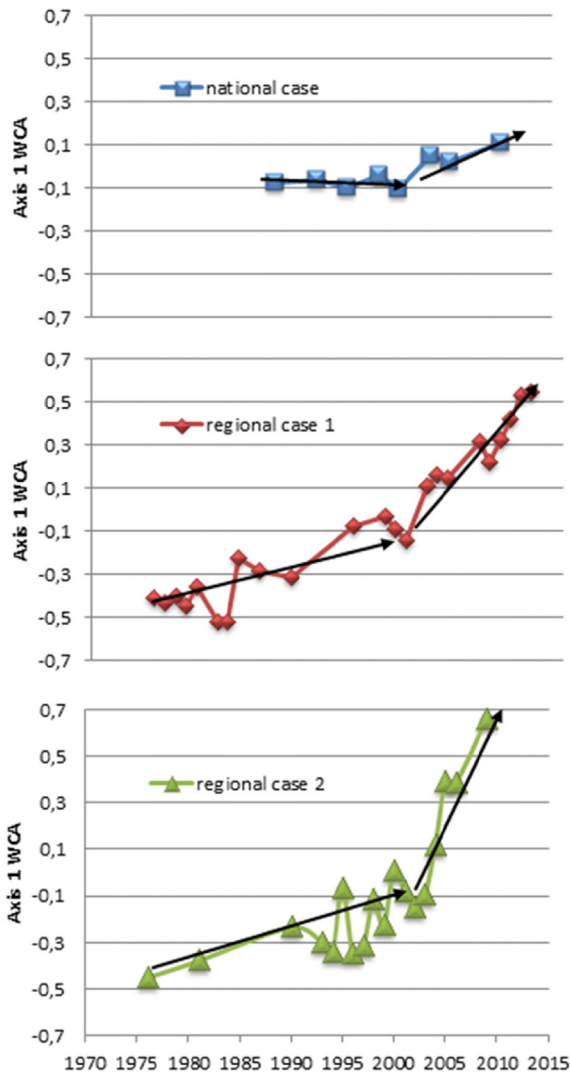


Fig. 2. Community changes in time for the national and two regional scale cases. The ordination values of the first temporal WCA axis are shown for the long-term time series and the two regional cases. The ecosystem shift around the year 2000 is marked. Strong community changes are present for the most recent decade.

3.2. Bottom-up trophic amplification

The fourth corner analysis revealed significant community trait changes around 2000 for the trait categories of functional feeding groups and food resources. Significant functional group increases occur gradually higher up the food web with time (Fig. 4a), starting with filter feeders associated with the period 1997–1999 ($p = 0.006$). The first years of the new millennium (2000–2002) were significantly associated with microphyte scrapers ($p = 0.004$), followed by piercer herbivores (piercers 2003–2005 $p = 0.03$, macrophyte feeders 2003–2010 $p = 0.001$), which were significantly associated with the 2003–2005 period, in turn followed by a period of predator increase ($p = 0.02$). This trophic amplification process was significantly identified in the community module (Fig. 4b), with a strong increase in small filterer and biofilm-feeding taxa (*Hydroptilidae*, *Psychomyiidae*) from a presence in 20% of the LT sites to an omnipresence of >75% occupation of sites, followed by a more gradual increase in larger herbivores (mixed group feeding on detritus, algae and macrophytes), and finally a faster increasing group consisting of medium-sized predatory *Polycentropodidae*, *Leptoceridae*, *Ecnomidae* and *Rhyacophilidae*, which showed a retarded response, but with a strong, rapid increase a few

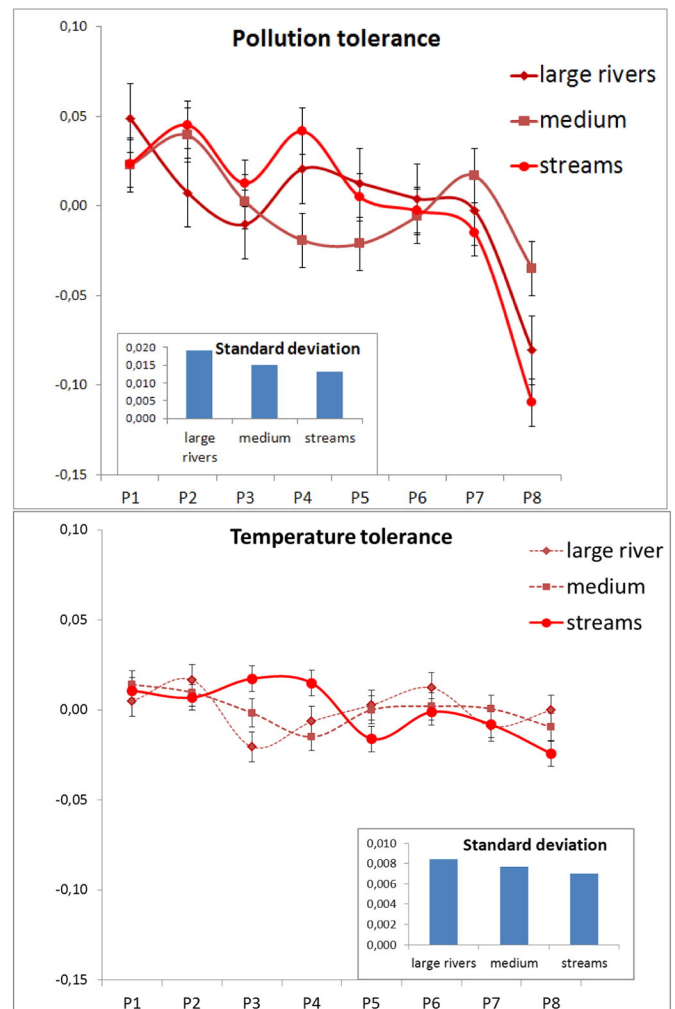


Fig. 3. Trait-based pollution and temperature tolerance indicator trends. Centered weighted scores for the temperature and pollution tolerance trait indicators over time periods for large, medium and small rivers. Significant changes are indicated by solid lines.

years after the first group, which consisted of prey species. Further evidence for the productivity increase and trophic amplification was found in the community module abundance shifts. Summed abundances for the community module not only significantly increased, but even rose 3-fold between period 1 (187) and period 8 (539) (see Fig. 5). This site abundance increase nevertheless did not result from a dominance or homogenization process, as the community module showed an increase in β diversity over time, and no invasive taxa were present, a sign of boosting of regional pools. Response diversity led to the high dissimilarity in the caddisfly community module (mean dissimilarity 0.47), resulting in strong spatial differentiation in abundances and dominance (Fig. 5). The Mantel tests showed that the dissimilarity was not correlated with geographic distance or environmental gradients (same counts for the overall LT dataset, see Supporting Information).

4. Discussion

As our objective was to determine how far long-term changes in the macroinvertebrate assemblages could be attributed to water quality changes versus climatic warming, we first differentiated responses to water chemistry and responses to temperature. Despite the persisting risks for water quality (Malaj et al., 2014), the improvement effects were clearly identified in the recovery of pollution-sensitive taxa. On the other hand, the climate change effect was not present in our trait-based indicator of thermal tolerance of the assemblages, and the

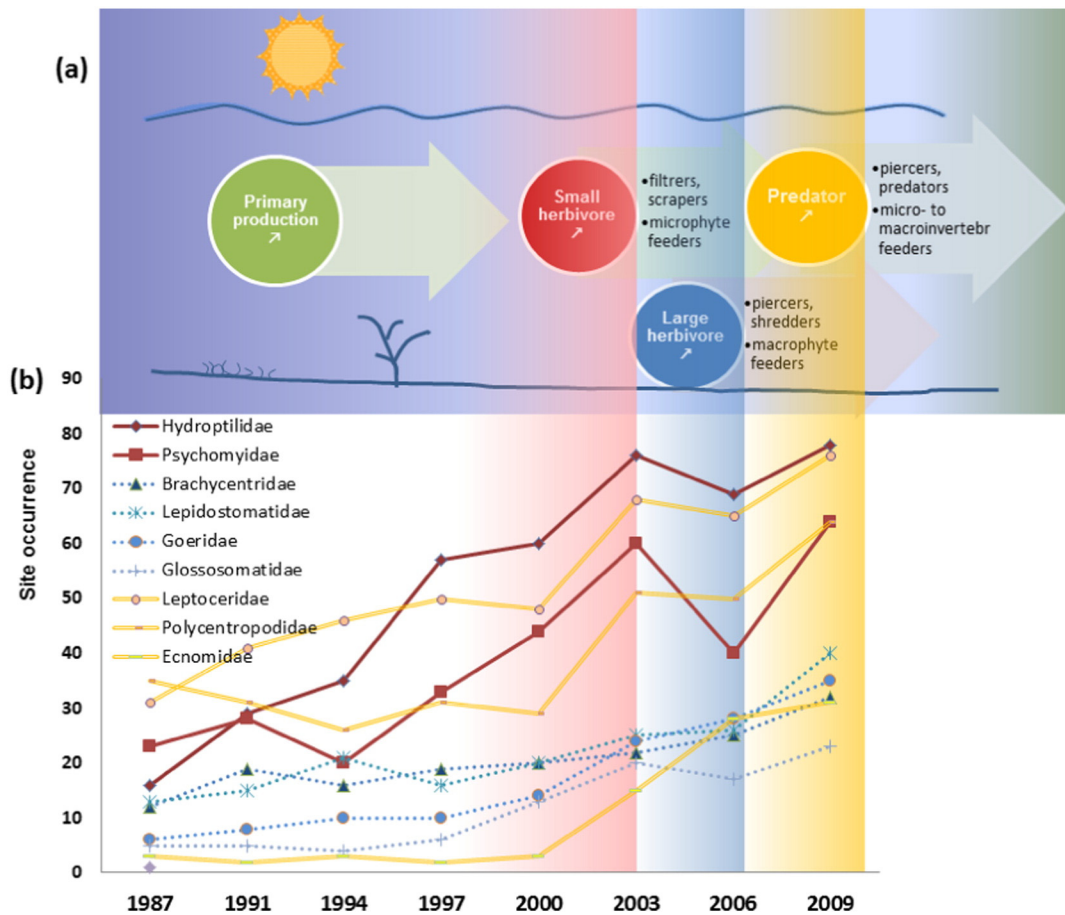


Fig. 4. (a) Observed bottom-up food web amplification with significant community trait changes for feeding groups and habits in time, showing gradual increase of trophic levels with time. (b) Frequency of caddisfly families over the long-term series (presence of taxa over 91 sites; on first axis the center year of period). Three groups can be distinguished: (1) the first steeply responding group of the smallest caddisfly families mainly filter feeding on algae (red solid lines), (2) a large herbivore group displaying a gradual increase (blue dotted lines), and (3) the last responding strongly expanding group of medium sized predatory taxa (orange dashed lines).

opposite was even observed. The gradual trend over the whole period to more pollution-sensitive taxa outweighed a thermal response signal, as pollution sensitive taxa are often psychrophilic.

Hence in this single response analysis the water quality improvement still seems to outweigh climate change effects. The fact that no change in temperature tolerance was observed, even under the recorded strong temperature increase, may also be due to low responsiveness of this trait. Most invertebrate families in European rivers have large geographical ranges within and beyond the Palaearctic, which implies high thermal tolerance. Furthermore, there is a strong variance in temperature requirements among invertebrate species within families (Hildrew & Edington, 1979). Hence observation of warming effects might be more likely at the species level than at broader taxonomic or functional levels (Bonada et al., 2007), although several studies have detected significant trends based on family-level data (Chessman, 2009; Duranc & Ormerod, 2009).

Nevertheless, we observed a strong climate change-induced trend breaking into the gradual water quality improvement trend. While Vaughan and Ormerod (2012) were unable to identify the share of climate change in community changes in a context of water quality improvement of English streams, we can confidently attribute the shift occurring in the communities studied to climate change. The shift is identified as independent of the water quality changes by (i) a control set of reference condition sites, and (ii) a correspondence analysis performed between biotic and water quality variations.

The mechanism for the observed shift is trophic amplification. Four lines of evidence for this trophic amplification are highlighted: (i) the shift in dissolved oxygen indicates an increased primary production,

(ii) the trait-based analysis of entire communities showed a bottom-up food web amplification, (iii) the trait-based analysis of the community module evidenced feeding strategy shifts and increased food web interactions, and (iv) the abundance analysis of the community module showed a productivity increase. The sequential trophic group increase and preponderance in time reflected the ecosystem response of a bottom-up food web increase starting with small filtering and biofilm-feeding taxa, followed by the larger-sized taxa higher up in the food web. The caddisfly functional groups were boosted not only in frequency of occurrence (up to 90% of the sites), showing the generality of the trend over France, but also in overall abundances. The amplification doubled taxonomic richness and tripled abundances. This mechanism of magnification up the food web corresponds to the trophic amplification described in the introduction. It is associated with a strong increase in both richness and abundance of the taxa, thus involving an intensification and multiplication of pathways through the food web. Increasing productivity attributed to climate change has already been documented in France for marine (Beaugrand et al., 2014) and forest ecosystems (Bontemps et al., 2012), showing synchronous shifts occurring at the turn of the millennium. The reported climatic change-induced shifts for the French marine environment, also occurring between 1997 and 2003, were also attributed to a trophic amplification (Goberville et al., 2014). At the origin of the ecosystem shift we assume a productivity increase to generate the trophic amplification. Climate change is documented to increase primary production of streams, as higher temperatures and carbon dioxide result in higher bacterial and photosynthetic activity (Wrona et al., 2006; Finlay, 2011). This increased primary production we observed in the dissolved oxygen

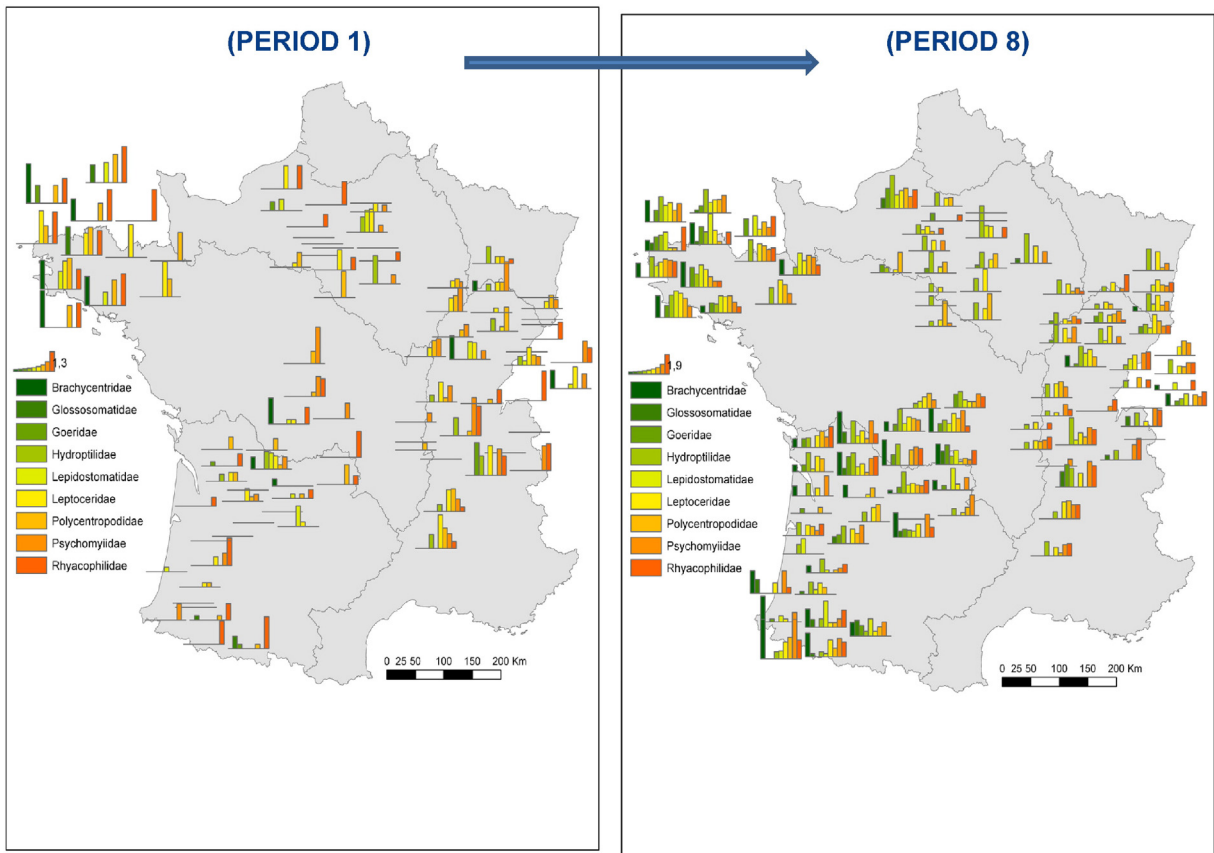


Fig. 5. The site sample abundances for the first period (1987–1990) and the most recent period (2008–2011) of the selected taxon group of frequent caddisfly families. Strong increases in both abundances and richness are seen (note in the figure that the logarithmic scale for the two periods is different; for the first period logarithmic abundance scaled 1.3 corresponds to 1.9 in right-hand figure). The recent period shows highly diverse communities with high abundances of caddisflies showing both locally and regionally strong evenness.

increase, as oxygen production is an approved measure of stream productivity (Odum, 1956; Kevern & Ball, 1965). Recent evidence also shows that warming can in some cases enhance the diversity of phytoplankton communities, increasing productivity (Yvon-Durocher et al., 2015). These mechanisms still need further investigation for their spatial distribution and geographic context. The observed trophic amplification is in line with the suggested absence of competitive exclusion for stream invertebrates (Death, 2002), enabling higher diversity with increasing productivity (Tonkin et al., 2013). The mechanism of trophic amplification governing the richness increase is comprehensible as more species can co-exist thanks to more resources in the absence of competitive limitation. Especially, its synchronized manifestation over such a large spatial scale and within such a short time frame is an extraordinary phenomenon. To the question of why such a trend in biodiversity increase had not been noted before, or only in part (Dornelas et al., 2014), we can reply that analyses of large-scale long-term trends are still scant. To our knowledge, there are no reports of three-decade, continuously sampled sites of stream communities over a spatial scale as large as the dataset we have analyzed. Nevertheless, the observed trend may not be ubiquitous. We believe that water quality improvement played a trigger role in the synchronicity of the observed diversity increase. Growth and dispersion over the river network are enabled once water quality reaches a basic quality level, as already documented for English chalk streams (Durance & Ormerod, 2007). Hence although the spatial pattern of strong water quality improvements did not correspond to the strongest shifts in communities, the general improvement determined for the chemical parameters obviously contributes to the observed increase in biological diversity. One further factor that potentially enabled this trend was the broad geographical variety of the French territories studied, with many preserved headwaters and stream

sections. Finally, streams and rivers, more than terrestrial and lentic ecosystems, are characterized by strong natural perturbations, and their communities are very well-adapted to changing conditions.

For our temperate-region rivers, the risk remains that too much productivity and temperature increase may induce negative responses. Cold water species obviously do not benefit as much as eurythermal species in our observations. Also, expected changes to flow regimes might degrade conditions. For instance, for Arctic freshwater ecosystems, the projected increase in productivity with climatic changes is accompanied by profound hydroregime changes, strongly confounding biotic responses (Wrona et al., 2006). Projected climate-induced intensification of floods and droughts might cause species loss in time. The recent period does include extreme hydro-climatic events in the region studied that have impacted strongly on communities at the local scale (Daufresne & Boët, 2007; Floury et al., 2013), but with no evidence of impact in the large-scale long-term trends. Given estimations that temperate ecosystems are those that will experience the least biodiversity change (Sala et al., 2000), we conclude, based on the strong changes observed in our study, that uncertainties in the current predictions of global change are many times larger than often presumed (see also Heino et al., 2009).

Climate change effects are obviously not restricted to shifts forced by thermal preferences. The need to move toward understanding the complex interactions between ecological impacts of climate change is topical (Parmesan et al., 2013; Hipsev et al., 2015). With some other authors (e.g. Woodward et al., 2010; Parmesan et al., 2013), we suggest that new concepts for more functional climate change analysis are needed, oriented to increasing and adapting productivity and mobility. At present, most studies use distribution-climate models and invoke a lack of adaptability to environmental changes (Heino et al., 2009; Poff

et al., 2012). In our data, however, we clearly observe an increase in diversity that is not limited to a small group of species appearing everywhere, but a more powerful expression of regional species pools and a productivity increase that strengthens food web interactions. The persistent investments in water quality have thus had positive effects on biodiversity, and have been reinforced by climate change effects up to the present time. Our results argue for concerted regional efforts to improve water quality and species dispersal, and reinforce regional species pools and their resilience to further climate change.

Acknowledgments

We thank the Regional Directories' Environmental Agencies (DREAL) for their collaboration in harmonizing invertebrate sampling data series for this study, and the devoted macro-invertebrate biologists for the quality and continuity of the sampling network. Thierry Tormos and Ricardo N. Simon improved figures and wording. Jani Heino and Catherine Leigh offered valuable comments and suggestions. Photo credits: Fabrice Parais.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.scitotenv.2016.04.193>.

References

- Anderson, M.J., TO, Crist, Chase, J.M., et al., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28.
- Beaugrand, G., Goberville, E., Luczak, C., Kirby, R.R., 2014. Marine biological shifts and climate. *Proc. R. Soc. B Biol. Sci.* 281, 20133350.
- Bonada, N., Dolédec, S., Statzner, B., 2007. Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implication for future climatic scenarios. *Glob. Chang. Biol.* 13, 1658–1671.
- Bontemps, J.-D., Herve, J.-C., Duplat, P., Dhôte, J.-F., 2012. Shifts in the height-related competitiveness of tree species following recent climate warming and implications for tree community composition: the case of common beech and sessile oak as predominant broadleaved species in Europe. *Oikos* 121, 1287–1299.
- Buisson L, Grenouillet G, Villéger et al. (2013) Toward a loss of functional diversity in stream fish assemblages under climate change. *Glob. Chang. Biol.*, 19, 387–400.
- Chase, J.M., 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328, 1388–1391.
- Chase, J.M., Myers, J.A., 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philos. Trans. R. Soc., B* 366, 2351–2363.
- Chessman, B.C., 2009. Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. *Glob. Chang. Biol.* 15, 2791–2802.
- Chust, G., Allen, J.L., Bopp, L., et al., 2014. Biomass changes and trophic amplification of plankton in a warmer ocean. *Glob. Chang. Biol.* 20, 2124–2139.
- Comte, L., Grenouillet, G., 2013. Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography* 36, 1236–1246.
- Daufresne, M., Boët, P., 2007. Climate change impacts on structure and diversity of fish communities in rivers. *Glob. Chang. Biol.* 13, 2467–2478.
- Death, R.G., 2002. Predicting invertebrate diversity from disturbance regimes in forest streams. *Oikos* 97, 18–30.
- Dolédec, S., Statzner, B., 2008. Invertebrate traits for the biomonitoring of large European rivers: an assessment of specific types of human impact. *Freshw. Biol.* 53, 617–634.
- Domisch, S., Araújo, M.B., Bonada, N., Pauls, S.U., Jähnig, S.C., Haase, P., 2013. Modelling distribution in European stream macroinvertebrates under future climates. *Glob. Chang. Biol.* 19, 752–762.
- Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., Magurran, A.E., 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344, 296–299.
- Dray, S., Choler, P., Dolédec, S., et al., 2013. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95, 14–21.
- Durance, I., Ormerod, S.J., 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. *Glob. Chang. Biol.* 13, 942–957.
- Durance, I., Ormerod, S.J., 2009. Trends in water quality and discharge confound long-term warming effects on river macroinvertebrates. *Freshw. Biol.* 54, 388–405.
- Finlay, J.C., 2011. Stream size and human influences on ecosystem production in river networks. *Ecosphere* 2, 87.
- Floury, M., Delattre, C., Ormerod, S.J., Souchon, Y., 2012. Global versus local change effects on a large European river. *Sci. Total Environ.* 441, 220–229.
- Floury, M., Usseglio-Polatera, P., Ferreol, M., Delattre, C., Souchon, Y., 2013. Global climate change in large European rivers: long-term effects on macroinvertebrate communities and potential local confounding factors. *Glob. Chang. Biol.* 19, 1085–1099.
- Fordham, D.A., 2015. Mesocosms reveal ecological surprises from climate change. *PLoS Biol.* 13 (12), e1002323.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. *Trends Ecol. Evol.* 25, 325–331.
- Giuntoli, I., Renard, B., Vidal, J.P., Bard, A., 2013. Low flows in France and their relationship to large-scale climate indices. *J. Hydrol.* 482, 105–118.
- Goberville, E., Beaugrand, G., Edwards, M., 2014. Synchronous response of marine plankton ecosystems to climate in the Northeast Atlantic and the North Sea. *J. Mar. Syst.* 129, 189–202.
- Heino, J., 2014. Taxonomic surrogacy, numerical resolution and responses of stream macroinvertebrate communities to ecological gradients: are the inferences transferable among regions? *Ecol. Indic.* 36, 186–194.
- Heino, J., Virkkala, R., Toivonen, H., 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biol. Rev.* 84, 39–54.
- Hering, D., Schmidt-Kloiber, A., Murphy, J., et al., 2009. Potential impact of climate change on aquatic insects: a sensitivity analysis of European caddisflies (*Trichoptera*) based on distribution patterns and ecological preferences. *Aquat. Sci.* 71, 3–14.
- Hildrew, A.G., Edington, J.M., 1979. Factors facilitating the coexistence of Hydropsychid caddis larvae (*Trichoptera*) in the same river system. *J. Anim. Ecol.* 48, 557–576.
- Hipsey, M.R., Hamilton, D.P., Hanson, P.C., et al., 2015. Predicting the resilience and recovery of aquatic systems: a framework for model evolution within environmental observatories. *Water Resour. Res.* 51, 7023–7043.
- Jähnig, S.C., Brunzel, S., Gacek, S., Lorenz, A.W., Hering, D., 2009. Effects of re-braiding measures on hydromorphology, floodplain vegetation, ground beetles and benthic invertebrates in mountain rivers. *J. Appl. Ecol.* 46, 406–416.
- Kevern, N.R., Ball, R.C., 1965. Primary productivity and energy relationships in artificial streams. *Limnol. Oceanogr.* 10, 74–87.
- Kirby, R.R., Beaugrand, G., 2009. Trophic amplification of climate warming. *Proc. R. Soc. Lond. B: Biol. Sci.* 276, 4095–4103.
- Langford, T.E.L., Shaw, P.J., Ferguson, A.J.D., Howard, S.R., 2009. Long-term recovery of macroinvertebrate biota in grossly polluted streams: re-colonisation as a constraint to ecological quality. *Ecol. Indic.* 9, 1064–1077.
- Lebreton, J.D., Sabatier, R., Banco, G., Bacou, A.M., 1991. Principal component and correspondence analysis with respect to instrumental variables: an overview of their role in studies of structure-activity and species-environment relationships. In: Devillers, J., Karcher, W. (Eds.), *Applied Multivariate Analysis in SAR and Environmental Studies*. Kluwer, Dordrecht, pp. 85–114.
- Logez, M., Pont, D., 2013. Global warming and potential shift in reference conditions: the case of functional fish-based metrics. *Hydrobiologia* 704, 417–436.
- Malaj, E., von der Ohe, P.C., Grote, M., et al., 2014. Organic chemicals jeopardize the health of freshwater ecosystems on the continental scale. *Proc. Natl. Acad. Sci.* 111, 9549–9554.
- Mueller, M., Pander, J., Geist, J., 2013. Taxonomic sufficiency in freshwater ecosystems: effects of taxonomic resolution, functional traits, and data transformation. *Freshw. Sci.* 32, 762–778.
- Odum, H.T., 1956. Primary production in flowing water. *Limnol. Oceanogr.* 1, 102–117.
- Olden, J.D., Poff, L.N., 2004. Clarifying biotic homogenisation. *Trends Ecol. Evol.* 19, 282–283.
- Parnesan, C., Burrows, M.T., Duarte, C.M., et al., 2013. Beyond climate change attribution in conservation and ecological research. *Ecol. Lett.* 16, 58–71.
- Poff NL, Olden JD, Strayer DS (2012) Climate change and freshwater extinction risk. In: *Saving a Million Species: Extinction Risk from Climate Change* (ed. by L. Hannah), pp. 309–336 Island Press.
- Ruokolainen, L., Ranta, E., Kaitala, V., Fowler, M.S., 2009. When can we distinguish between neutral and non-neutral processes in community dynamics under ecological drift? *Ecol. Lett.* 12, 909–919.
- Sala, O.E., Chapin, F.S., Armesto, J.J., et al., 2000. Biodiversity - global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Stahl, K., Hisdal, H., Hannaford, J., et al., 2010. Streamflow trends in Europe: evidence from a dataset of near-natural catchments. *Hydrol. Earth Syst. Sci.* 14, 2367–2382.
- Tonkin, J.D., Death, R.G., Barquin, J., 2013. Productivity-diversity relationships for stream invertebrates differ geographically. *Aquat. Ecol.* 47, 109–121.
- Usseglio-Polatera, P., Bournaud, M., Richoux, P., Tachet, H., 2000. Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshw. Biol.* 43, 175–205.
- Vaughan, I.P., Ormerod, S.J., 2012. Large-scale, long-term trends in British river macroinvertebrates. *Glob. Chang. Biol.* 18, 2184–2194.
- Verberk, W.C.E.P., Durance, I., Vaughan, I.P., Ormerod, S.J., 2016. Field and laboratory studies reveal interacting effects of stream oxygenation and warming on aquatic ectotherms. *Glob. Chang. Biol.* 22, 1769–1778.
- Villeneuve, B., Souchon, Y., Usseglio-Polatera, P., Ferréol, M., Valette, L., 2015. Can we predict biological condition of stream ecosystems? A multi-stressors approach linking three biological indices to physico-chemistry, hydromorphology and land use. *Ecol. Indic.* 48, 88–98.
- Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.L., Poff, L.N., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecol. Lett.* 13, 267–283.
- Woodward, G., Perkins, D.M., Brown, L.E., 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. *Philos. Trans. R. Soc., B* 365, 2093–2106.
- Wrona, F.J., Prowse, T.D., Reist, J.D., Hobbie, J.E., Levesque, L.M., Vincent, W.F., 2006. Climate change effects on aquatic biota, ecosystem structure and function. *Ambio* 35, 359–369.
- Yvon-Durocher, G., Allen, A.P., Cellamare, M., Dossena, M., Gaston, K.J., Leitao, M., Montoya, J.M., Reuman, D.C., Woodward, G., Trimmen, M., 2015. Five years of experimental warming increases the biodiversity and productivity of phytoplankton. *PLoS Biol.* 13, e1002324.