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

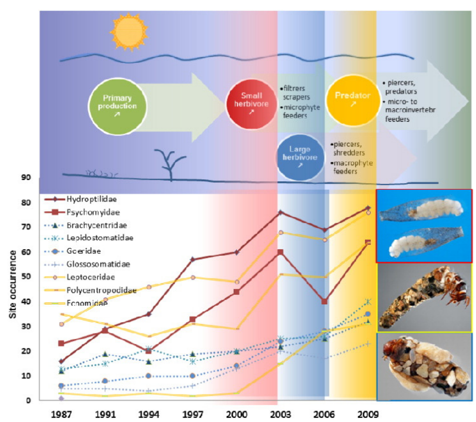
Kris Van Looy *, Mathieu Floury, Martial Ferréol, Marta Prieto-Montes, Yves Souchon

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



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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.

* 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).

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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

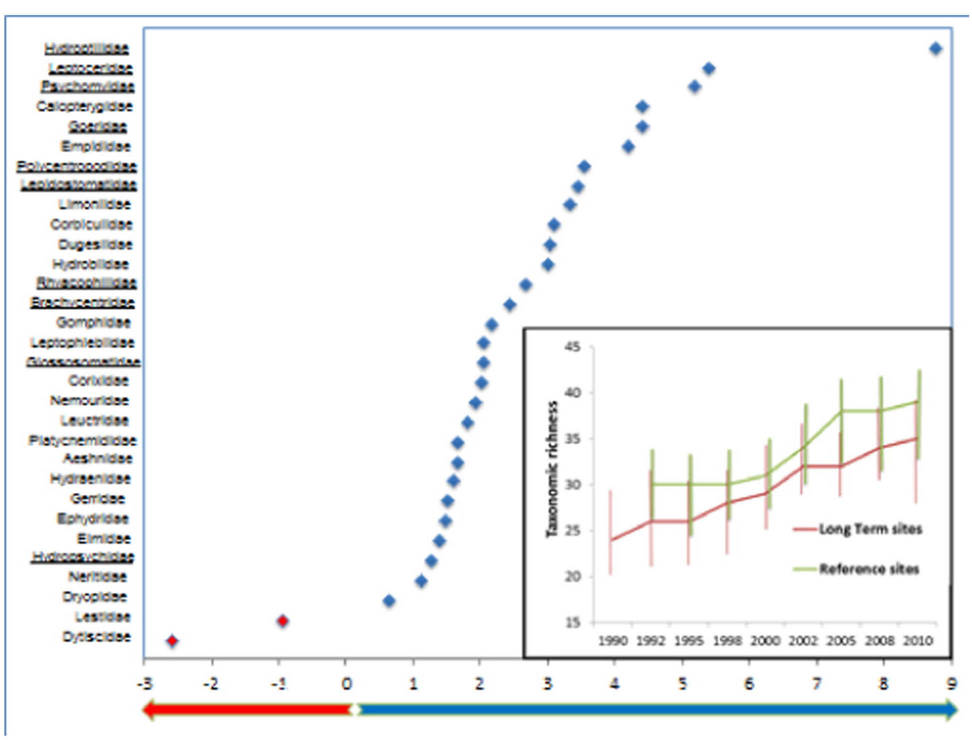

Fig. 1. Significant winners and losers and richness increase over the time series.