



# At what scale and extent environmental gradients and climatic changes influence stream invertebrate communities?



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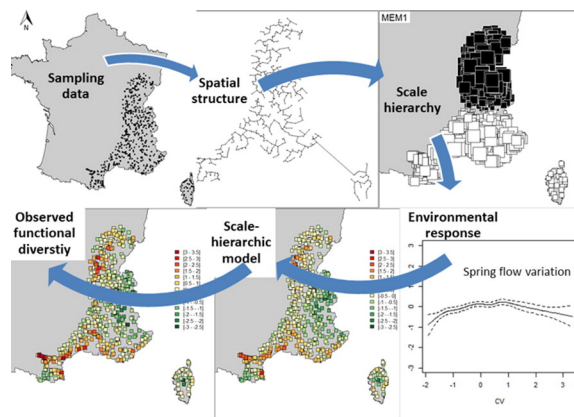
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## HIGHLIGHTS

- Natural environmental gradients structure functional diversity far stronger than stressor gradients.
- Intermediate levels of flow variability maximize functional diversity of stream communities.
- The influence of climatic changes was present at fine subcatchment scale.
- The altitudinal gradient is strongest driver of (meta)community structuring.
- Management needs to embrace analysis and actions at different scale levels.

## GRAPHICAL ABSTRACT



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## ABSTRACT

In a context of increasing landscape modifications and climatic changes, scale hierarchy becomes an ever more crucial issue to integrate in the analysis of drivers and stressors of biological communities, especially in river networks. To cope with this issue, we developed (i) spatial hierarchical models of functional diversity of stream invertebrate communities to assess the relative influence of local- vs. regional-scale factors in structuring community assembly, and (ii) analysis of metacommunity elements to determine the ecological processes behind the structuring. The spatial structuring of benthic invertebrate communities was investigated over 568 sites in South-eastern France. Community structure was mainly driven by the altitudinal gradient and spring flow variation at broad scales, with functional diversity gradually decreasing with elevation and being maximized at intermediate levels of flow variability. According to the 'elements of metacommunity structure' analysis, the prevailing influence of the altitudinal gradient was also supported by a Clementsian structuration of invertebrate communities. Conversely, the influence of observed climatic changes in temperature and rainfall was weak and observed only at fine scales. As a result, natural environmental filters were stronger drivers of the functional diversity of communities than human-induced stressors (e.g. water pollution and hydromorphological alterations). More broadly, our results suggest that management needs to embrace the possibilities of gathering high spatial and taxonomical resolution data when analysing and predicting flow variation and climate change effects in order to preserve and restore functionally diverse communities. Moreover, to develop environmental flow

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schemes or restoration and climate change adaptation strategies for freshwater communities, local and regional processes need to be addressed simultaneously; equally responsible as drivers of community diversity.

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## 1. Introduction

Understanding at which spatial scales environmental factors and human stressors impact biotic communities is essential to design appropriate management measures to preserve biodiversity and adapt to a changing climate (Feld and Hering, 2007; Kail and Wolter, 2013). Connections between large-scale, regional and local processes steer community structure (Pavoine and Bonsall, 2011). This scale dependence is highlighted as crucial when investigating mechanisms of community structure and diversity (Chase and Knight, 2013), especially in relation to environmental heterogeneity (Heino and Grönroos, 2013; Heino et al., 2015a). Still, this scale hierarchy remains complex to integrate in the analysis of drivers and stressors of biological communities, since separation of variables into local (i.e. niche-related) and regional (i.e. dispersal-related) categories is often impossible. Apart from the scale hierarchy problem, large-scale analyses of drivers and stressors of community composition further cope with the problem of biogeography and regional pools driving taxa occurrence (Gotelli et al., 2009). Therefore, analyses of taxonomy-based composition and diversity over large scales have difficulties to reveal true causal relationships with drivers (Leps et al., 2015). Analysis of functional trait composition might bring a solution to this problem by identifying links to driver and stressor mechanisms and unravelling the different spatial-scale effects of ecological processes like environmental filtering (Bonada et al., 2007; Pavoine and Bonsall, 2011; Mouillot et al., 2013). Furthermore, assessing the effect of drivers on different communities encounters difficulties in view of their organisms' different dispersal rates (Logue et al., 2011; Johnson et al., 2013). To this purpose, large-scale study of metacommunity elements can contribute to identify patterns of biotic community structuration, especially in light of global changes taking place (Cadotte, 2006; Heino et al., 2015b). Nonetheless, these global changes might differ strongly in their regional manifestations, both in magnitude and nature of impacts on the physical system as well as in species interactions (Gilman et al., 2010). In this complexity, integrated approaches based on functional traits and geographical information, using techniques of scale-hierarchical modelling and metacommunity models (Leibold et al., 2004; Webb et al., 2010; Göthe et al., 2014), are supposed to be able to account for the different influencing factors (Cadotte, 2006; Brown and Swan, 2010; Dorazio et al., 2010; Erős et al., 2012; Göthe et al., 2013).

River networks and catchments are good examples of highly hierarchical structures for dispersal processes and community assemblages (Campbell Grant et al., 2007; Brown and Swan, 2010). River network properties make these systems unique study systems, yet human impairments are a major global issue, causing discontinuities and so altering metacommunity and biogeographical patterns (Bergerot et al., 2013; Van Looy et al., 2014a), further aggravated by climatic changes (Domisch et al., 2013). Thus, the scale-hierarchical identification of drivers of community diversity is especially challenging for these highly structured environments. Consequently, the combination of metacommunity analysis and spatial hierarchical models is proposed as promising to investigate community diversity and assembly processes in river networks (Campbell Grant et al., 2007; Tonkin et al., 2016).

In this study, we aimed at assessing the relative influence of local- vs. regional-scale factors in structuring benthic invertebrate communities in rivers, keeping in mind the potential cross-scale interactions between climate, geography and stressors. For this purpose, we proposed an analysis using both elements of metacommunity structure and scale-hierarchical analyses of functional diversity to assess the effects of the already observed climatic changes and environmental gradients on

community assembly over 568 sites in streams and rivers from South-eastern France. First, we hypothesized that human-induced stressors should be stronger drivers of community trait composition than the natural environment, both at regional and more local scale levels, consistently with findings based on taxonomic composition and diversity models highlighting water quality and catchment-scale land use as principal drivers (Sundermann et al., 2013; Leps et al., 2015; Villeneuve et al., 2015). Second, we hypothesized that climatic change effects should be expressed at the regional-scale level (Gilman et al., 2010). Finally, we hypothesized that dispersion should outweigh environmental gradients owing to the degree of connectivity within river systems, leading to an absence of boundaries in the metacommunity structure, i.e. a so-called Gleasonian structure (Tonkin et al., 2016).

## 2. Materials and methods

### 2.1. Study area and invertebrate data

We compiled invertebrate data from 568 sites located on streams and rivers from the Rhône basin and Corsica (Fig. 1a). The sites were sampled in 2013 following a common normalised protocol (multi-habitat sampling technique using a hand-net of 25 × 25 cm and 500 µm meshed; norm XP T 90-333 in AFNOR, 2009). Abundance data were gathered for 191 taxa (mostly genera, but 43 taxa were tribes, sub-families or families) and log(x + 1)-transformed. Each taxon was further characterised using 21 life-history traits and 111 sub-categories (Table S1) from Tachet (2010). The selected traits described the potential adaptations of taxa to the environmental characteristics of their habitat (e.g. life-cycle duration) as well as their potential spatial niche (e.g. longitudinal distribution), food requirements and sensitivity to specific stressors (e.g. temperature). The affinity of each taxon for each trait category was fuzzy-coded from '0', meaning 'no affinity', to '3' or '5', meaning 'high affinity' (Chevenet et al., 1994; Usseglio-Polatera et al., 2000). Trait description was mostly available at the species or genus level in Tachet (2010). Therefore, we coded the trait preferences of a given higher-level taxon by averaging the trait category scores over all the species/genera identified in our dataset and belonging to this taxon. Affinities of each taxon for each trait were then transformed into relative use frequency distributions. Finally, the functional diversity (FD) of each of the 568 communities (i.e. samples) was estimated as the dispersion of their taxa in the multi-dimensional space defined by the 111 trait categories. To this end, we first computed a taxon-by-taxon distance matrix from the 21 traits and then measured the functional dispersion in each community weighted by the log-transformed abundances as described by Laliberté and Legendre (2010).

### 2.2. Environmental variables

We collected 31 environmental variables describing altitudinal, hydro-climatic, physico-chemical, land-cover and morphological characteristics of the 568 sites at different spatial scales. Hydro-climatic variables included mean discharge, coefficient of variation of spring flows, long-term trends in spring air temperature and precipitation. The coefficient of variation was calculated for the spring season over the past ten years (i.e. 2003–2013) from gauging stations located near the sites. Daily values of air temperature (°C) and precipitation (mm) were extracted from the Safran model at 8 × 8 km spatial resolution (Vidal et al., 2010). Temperature was extracted from the cells encompassing the sites while precipitation was cumulated over the cells intersecting their upstream catchments. For each site the long-term trends in the

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