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Research

Climatic and trophic processes drive long-term changes in functional diversity of freshwater invertebrate communities

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When investigating the fields of biogeography and macroecology, climate- and productivity-related variables are frequently identified as the strongest correlates of species-diversity patterns. These variables have been usually merged under the climate/productivity hypothesis and describe the direct and indirect actions of climate on species. Being among the most vulnerable ecosystems to climate change, streams and rivers are expected to be influenced both by climatic and trophic (i.e. productivity-related) factors. We propose here to distinguish the relative influence of the two processes on large-scale, long-term changes in the functional diversity of freshwater invertebrate communities over two decades in France. To this end, we designed two functional indices using invertebrate traits to surrogate the respective mechanisms: climate vulnerability and feeding specialisation. Using geographically weighted regression (GWR) models, we showed that trends in both indices, along with the initial regional species-pools, have significantly contributed to the overall long-term increase in functional diversity of invertebrate communities. In addition, we highlighted a strong geographical differentiation in the contribution patterns with the climate vulnerability effect decreasing with latitude and the feeding specialisation effect being higher in headwaters than in large rivers. Finally, taking into account this non-stationarity in the ecological processes and responses using GWR models allowed explaining about 75% of the long-term changes in the community diversity. Consequently, this study offers sound perspectives in predicting the future patterns of trends in functional diversity of communities under different scenarios of environmental changes, like climate and/or land-use.

Introduction

One of the main purposes in ecology is to understand the drivers of biodiversity gradients (Willig et al. 2003, Field et al. 2009). A multitude of biogeographic hypotheses have been proposed to explain diversity patterns that are now widely merged into three broad mechanisms: spatial heterogeneity, climate/productivity and history (Oberdorff et al. 2011, Tisseuil et al. 2013, Eme et al. 2015). Figuring out the underlying drivers of diversity as well as the forms of their relationships can still be controversial (Currie et al. 2004, Field et al. 2009, Whittaker 2010). Nonetheless, climatic

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and productivity-related factors are frequently identified as the strongest correlates of species-richness gradients (Chase and Leibold 2002, Field et al. 2009, Chase 2010, Langenheder et al. 2012). According to the climate/productivity hypothesis, these variables describe the action of climate on species, either directly by influencing physiological processes, or indirectly by controlling resource productivity or biomass (Hawkins et al. 2003, Brown et al. 2004, Currie et al. 2004, Field et al. 2009, Eme et al. 2015). On the one hand, direct effects of climatic warming can involve fatal alterations of biological processes like growth, reproduction, foraging, immune competence, behaviour and competitiveness (Pörtner and Farrell 2008). These impacts on individuals then have repercussions on higher levels of organisation thereby contributing to the global loss in biodiversity (Parmesan and Yohe 2003, Walther 2010). On the other hand, a less-investigated indirect effect of warming is the trophic amplification process by which a significant increase in biological diversity arises from a productivity enhancement (Kirby and Beaugrand 2009).

Streams and rivers are among the most vulnerable ecosystems to climate change (Sala et al. 2000). As such, they are likely to experience the different types of climate-induced effects. For instance, deleterious effects of climate warming on stream communities have already been reported for a decade (Durance and Ormerod 2007, Buisson et al. 2008). Conversely, recent studies in freshwaters have also highlighted a trophic amplification mechanism responding to temperature increase in phytoplankton (Yvon-Durocher et al. 2015) and invertebrate (Van Looy et al. 2016) communities. In both cases, observations suggest that the first consequence of climate change would be an increase in diversity because 1) most cool-water and warm-water species are promoted by newly suitable (i.e. warmer) conditions while cold-water species decrease but represent a very small minority (Buisson et al. 2008) and/or 2) the bottom-up propagation of the amplification signal through the food web raises an intensification and a multiplication of its trophic pathways (Van Looy et al. 2016).

Usually, climate- and productivity-related variables have been combined under the climate/productivity hypothesis because both types have often been modelled using climatic proxies (Hawkins et al. 2003, Field et al. 2009). Moreover, taxonomy-based indices can be inefficient to unambiguously disentangle such processes with functional relevance to the understanding of community dynamics (Webb et al. 2010). The present study aimed at distinguishing the relative influence of the two mechanisms on functional diversity (FD) of invertebrate communities over two decades in French streams and rivers. To this end, we used two trait-based indices to represent distinctly the two climate-driven mechanisms: climate vulnerability (CV) and feeding specialisation (FS). First, we tested for their relevance as proxies using a set of multi-scale predictors expected to have significant effects on these processes. Second, we performed geographically weighted regression (GWR) models 1) to assess the relative contributions of the two proxies, along with the regional species-pool (i.e. γ-diversity), to long-term changes in functional diversity of invertebrate communities and 2) to search for geographic non-stationarity in the contribution of the three components.

More specifically, we tested six hypotheses: 1) CV should follow a general decrease over the past two decades due to the expansion of thermo-tolerant taxa (Durance and Ormerod 2007, Floury et al. 2013), 2) meanwhile, FS should exhibit a general increase related to trophic amplification as specialist taxa are believed to benefit from higher resource availability (Vázquez and Simberloff 2002, Mondy and Usseglio-Polatera 2014), 3) consequently, both biotic trends should have significantly contributed to a general long-term rise in functional diversity of invertebrate communities, 4) geographically, we expected an increasing contribution of CV along a north-south gradient according to the predicted northwards colonisation/migration by Mediterranean species (Bonada et al. 2007), 5) likewise, we predicted a greater influence of FS in headwaters than in large rivers since more complex trophic networks of downstream reaches are less likely to be further densified (Woodward et al. 2016), and 6) the regional species-pool should have also influenced long-term changes in functional diversity of local communities, either jointly with the climate/productivity changes via species sorting processes, or separately via dispersal-driven mechanisms (Leibold et al. 2004).

Material and methods

Functional trait-based indices

We compiled long-term data series from 305 sites located on French streams and rivers. In average, sites were sampled fifteen to sixteen times over twenty years within the period 1992–2013 for benthic macroinvertebrates following a common normalised protocol (multi-habitat sampling; norm XP T90-333 in AFNOR 2009). We focused on Ephemeroptera, Plecoptera, Trichoptera, Coleoptera and Odonata (EPTCO) orders for which we gathered presence–absence data on 278 taxa collected among 4734 samples (mostly genera, but 50 taxa were tribes, sub-families or families). Each taxon was characterised using 13 autecological traits and 70 categories (Supplementary material Appendix 1 Box A1, Table A1) from Tachet et al. (2010). These traits were selected to define two functional indices measuring the climate vulnerability (Hering et al. 2009, Conti et al. 2014) and the degree of feeding specialisation (Mondy and Usseglio-Polatera 2014) of each taxon (Supplementary material Appendix 1 Box A2, Fig. A1, A2). Community weighted means of the two indices were then calculated for each of the 4734 site-by-date samples by averaging the individual scores of occurring taxa. In addition, the overall functional diversity of each of the 4374 communities (i.e. site-by-date samples) was estimated as the dispersion (i.e. spread) of their taxa in the multi-dimensional space defined by the 70 trait categories. To this end, we first computed a taxon-by-taxon distance matrix from the 13 species traits and then measured the functional dispersion in each community as described by Laliberté and Legendre (2010).

Finally, we estimated the long-term changes in the three functional indices at each sampling site as areas between smoothed time series and initial index values averaged over the first ten years (i.e. 1992–2001; Supplementary material Appendix 1 Box A3, Fig. A3). Hereafter, 'CV', 'FS' and 'FD' refer to these values of long-term changes in climate vulnerability, feeding specialisation and functional diversity, respectively (Fig. 1). To account for the contribution of regional species-pools to diversity changes, functional indices were complemented by an estimator of the initial γ-diversity (hereafter 'γ_0'; Fig. 1) at each site defined as the overall taxonomic richness of the site and its five nearest neighbours over the first ten years (i.e. 1992–2001).

Environmental predictors

We collected environmental data from predictors expected to drive patterns of CV, FS and γ_0 either due to their long-term changes or their geographical differentiation. A first set of 5 'temporal' predictors was compiled to assess long-term changes in climate and water quality. Daily values of air temperature and precipitations were extracted from the Safran meteorological system at 8 × 8 km spatial resolution (Vidal et al. 2010). For each sampling site, temperature was extracted from the cell encompassing the site while precipitations were

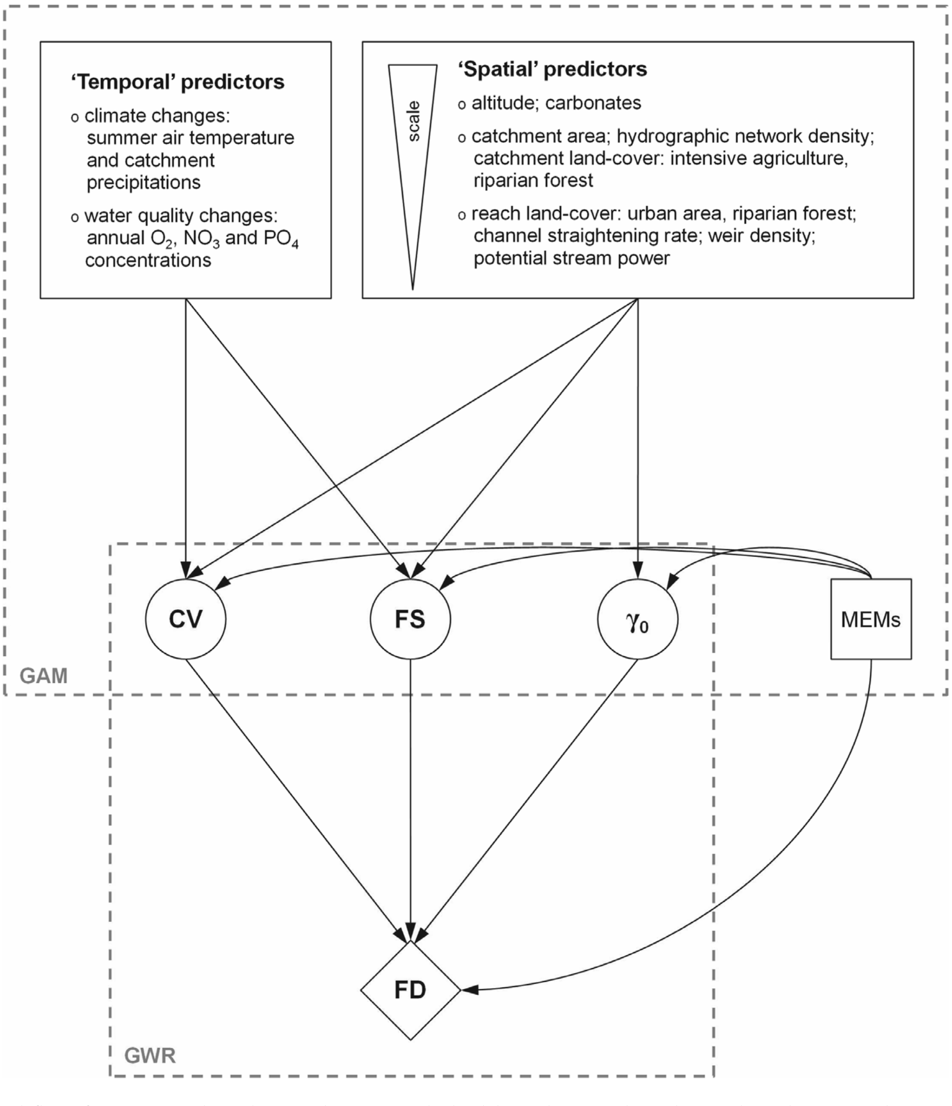

Figure 1. Overall workflow for statistical analyses. The upper dashed box depicts the relationships between the environmental variables (i.e. temporal and spatial predictors and MEMs) and the three indices [i.e. changes in climate vulnerability (CV), changes in feeding specialisation (FS) and initial γ-diversity (γ_0)], assessed with GAM models. The lower dashed box depicts the relationships between the three indices (i.e. CV, FS and γ_0) and the changes in functional diversity (FD), assessed with GWR models. See Material and methods for further details on variable definition and model computation.

cumulated over the cells intersecting the upstream catchment of the site. Preliminary analyses highlighted strong correlations between annual and seasonal means for both variables, thus we focused on summer values since they were expected to be the most limiting for organisms. In addition to climate variables, monthly concentrations of dissolved oxygen, nitrates and phosphates were extracted at each sampling site from <www.data.eaufrance.fr>. First, we calculated the mean annual summer temperature and cumulated precipitations and the mean annual concentrations of oxygen, nitrates and phosphates for the 305 sites along their respective sampled periods. Then, we estimated the long-term trends in the five parameters (Fig. 1) using the slopes of the linear regressions onto years (i.e. their mean rates of change over the entire period).

A second set of 11 'spatial' predictors was compiled to represent the landscape and habitat heterogeneity of the 305 sites at different spatial scales (Fig. 1; Table 1). Altitude and carbonates were considered as regional descriptors while catchment and reach scales were described by different geographical (area), hydrological (river network density), land-cover (e.g. riparian forest) and hydromorphological (e.g. straightening) variables (Table 1). We verified that variables were weakly correlated ($|r| < 0.32$) within each spatial scale.

Finally, we performed an eigenfunction spatial analysis based on Moran's eigenvector maps (MEMs) to account for spatial structures among the sampling sites not captured by the different predictor sets (Dray et al. 2006, Griffith and Peres-Neto 2006). The MEM variables (i.e. eigenfunctions) were obtained from a spectral decomposition of the truncated distance matrix based on Euclidean distances among the 305 sites. Only MEMs with significant positive eigenvalues were retained in further analyses (Borcard and Legendre 2002). These variables can be used as environmental predictors of spatial variation in biological indices since spatial patterns may be a consequence of environmental autocorrelation, dispersal limitation or historical effects on community composition (Dray et al. 2012, Peres-Neto et al. 2012).

Statistical analyses

First, we $\arcsin(\sqrt{x})$-transformed percentage and proportion data and we $\log10(x)$- or $\log10(x + 1)$-transformed the other variables when needed to satisfy the normality assumption. All variables were then standardised.

In a first step (upper box in Fig. 1), we aimed at 1) assessing the effects of long-term trends in climate and water quality drivers (i.e. 'temporal' predictors) on CV and FS, 2) taking into account whether these temporal effects could have been mediated by multi-scale spatial drivers arranged along a 'top-down' hierarchical organization (i.e. 'spatial' predictors), and 3) accounting for spatial autocorrelation and/or additional drivers potentially not addressed in our dataset (i.e. using MEMs). For this purpose, we first assessed the effect of the temporal predictors on CV and FS by testing all the possible combinations of variables in generalised additive models (GAMs). For each combination, covariates were modelled with regression splines to account for non-linear relationships and we retained the model that maximised the adjusted R^2 as the best model. Then, we defined similarly the best GAMs using successively regional-scale, catchment-scale, reach-scale and MEMs variables as explanatory variables and residuals of the 'previous' model as response variable. Finally, we merged the five successive best models in a final additive model. The same approach was used for γ_0 using the regional-scale model as the first model.

In a second step, we investigated the relative effects of CV, FS and γ_0 on FD using geographically weighted regression (GWR) models (lower box in Fig. 1). GWR enabled to account for potential non-stationarity in the contribution spatial patterns of the three components by estimating independent regression parameters (i.e. coefficients and R^2 values) for each sampling site (Eme et al. 2015). This approach relies

Table 1. Details on the variables used to describe the different spatial scales.

Spatial scale	Type of variable	Variable	Details
Regional	Biogeochemical	Carbonates	Calcium concentration[1] averaged over 1992–2013
	Geographical	Altitude	Measured at the sampling site
Catchment	Geographical	Area	Upstream catchment surface
	Hydrological	Hydrographic network density	Calculated over the upstream catchment
	Land-cover	Intensive agriculture	Proportion (%) of the upstream catchment[2]
	Land-cover	Riparian forest	Mean proportion (%) of the upstream 30-m riparian buffer[3], i.e. averaged over the upstream stretches and tributaries
Reach	Land-cover	Urban area	Proportion (%) of the 100-m riparian buffer[2]
	Land-cover	Riparian forest	Proportion (%) of the 30-m riparian buffer[3]
	Morphological	Channel straightening rate	Proportion of straight units over the stretch
	Morphological	Weir density	Number of weirs/stretch length
	Hydro-morphological	Potential stream power	$\rho g Q_{99} S_v$[4]

[1] these data were extracted at <www.data.eaufrance.fr>.

[2] these data were extracted from the Corine Land Cover GIS layer (EEA 2007).

[3] these data were extracted from the BD TOPO® GIS layer.

[4] where ρ is the water density, g is the gravitational acceleration, Q_{99} is the 99th percentile of daily discharges and S_v is the valley slope.

on the attribution of decreasing weights (using a Gaussian function) to the neighbouring sites within a given bandwidth according to their growing geographical distance to the focal site (Brunsdon et al. 1996). The number of neighbours was optimised by searching between 7 and 30% of all sites with the Golden Section Search (Svenning et al. 2009). Finally, variance partitioning based on partial GWR models was performed to assess the relative contribution of the three indices (Eme et al. 2015). Residuals of the global GWR model were adjusted against the MEMs variables to check for a potential influence of spatial autocorrelation and/or additional drivers.

All analyses except GWR models were run in R statistical software (R Core Team). FCA, GAMs, integral calculation and MEMs were computed using respectively the ade4 (Dray and Dufour 2007), mgcv (Wood 2006), tis (Hallman 2013) and PCNM (Legendre et al. 2013) R packages. GWR and partial GWR models were performed using GWR4 software (Nakaya et al. 2009).

Results

Functional trait-based index responses to environmental predictors

Overall, the average long-term change in climate vulnerability (CV) of invertebrate communities was slightly greater than zero (mean = 0.1 ± 0.4). However, CV was highly variable across France with 171 sites exhibiting positive values, mainly in the north-western and eastern regions, and 134 sites exhibiting negative values, mainly in the middle and the south-eastern regions (Fig. 2a). Long-term changes in feeding specialisation (FS) were more homogeneous in direction with 214 sites exhibiting positive values (mean = 0.3 ± 0.5), but were also spatially variable with the strongest values observed in the central region (Fig. 2b). Similarly, the initial γ-diversity (γ_0) showed various spatial patterns with regional species-pools ranging from

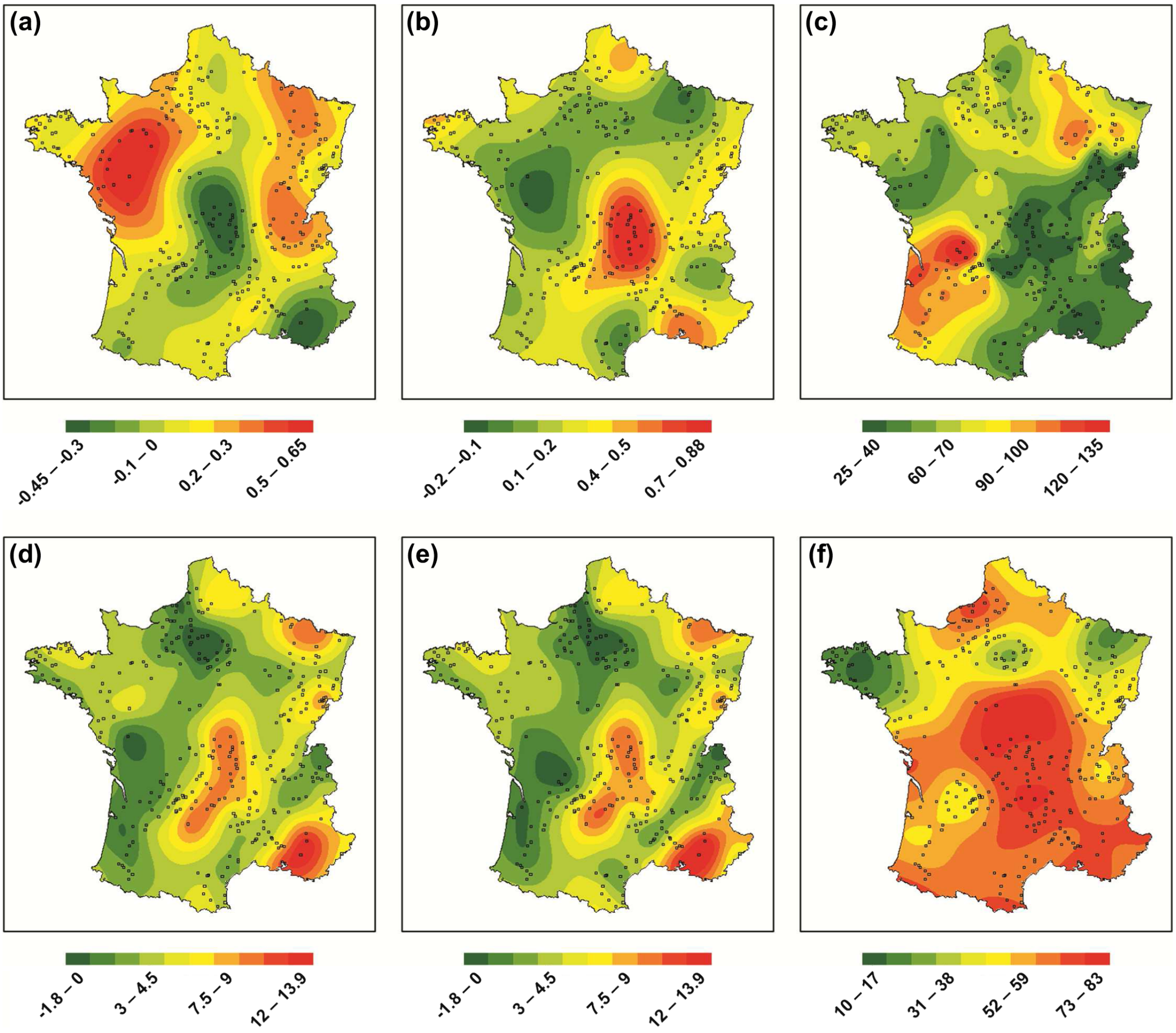

Figure 2. (a–d) Smoothed maps of observed patterns for the four indices over France (see Material and methods for details on index definitions): (a) changes in climate vulnerability (CV); (b) changes in feeding specialisation (FS); (c) initial γ-diversity (γ_0); (d) changes in functional diversity (FD). (e–f) Smoothed maps of GWR results: (e) FD predicted by the final model; (f) R^2 values. Points indicate the site locations.

25 – roughly in the south-eastern quarter – to 135 taxa – in the southwestern region (Fig. 2c).

The modelling approach based on successive GAMs was quite efficient in capturing these variations with final additive models explaining around 50% of the variance in CV and FS and more than 80% of the variance in γ_0 (Table 2). Temporal and catchment-scale predictors along with MEMs exhibited the greatest contributions ($>10\%$) to CV and FS variations (Table 2). For instance, CV showed significant responses to changes in temperature and catchment area (Fig. 3a), while FS showed significant responses to changes in both temperature and phosphate concentration (Fig. 3b). If MEMs were by far the strongest predictors of γ_0, regional- (e.g. altitude) and catchment-scale (e.g. urban land-cover) variables had also a significant influence (Fig. 3c; Table 2).

Index contributions to changes in functional diversity

The three indices significantly contributed to the general increase ($\text{mean} = 4.2 \pm 4.2$) in functional diversity (FD) of invertebrate communities over France, as observed for 266 of the 305 sites. Overall, CV and FS exhibited similar contributions of about 24% to FD variations, while γ_0 had a slightly lower influence of about 17% (Table 3). Subsequently, the final model integrating the residual effect of MEMs (ca 10%) explained almost 75% of the variance in FD (Fig. 2d–e). The cumulated contribution was quite homogeneous over France, except for Brittany, Paris Basin and Moselle valley (Fig. 2f). Moreover, the local regression parameters of GWR models enabled to verify the consistency of the overall relationships: FD was negatively related to CV and γ_0 at about 99 and 92% of the 305 sites, respectively, whereas FD was positively related to FS at about 87% of the sites (Supplementary material Appendix 2 Table A2).

Locally, CV and FS provided spatially varying contributions to FD, ranging from 0 to 43% (Fig. 4a–b; Table 3). The spatial contribution pattern of CV was highly related to latitude ($\text{p-value} < 0.001$) with contribution increasing from north to south (Fig. 4d). The FS contribution pattern was significantly structured across a river size gradient ($\text{p-value} < 0.001$) with greater proportions of variance explained in small streams than in large rivers (Fig. 4e). Finally, γ_0 exhibited a more homogeneous contribution pattern ranging from 1 to 24% (Fig. 4c; Table 3).

Discussion

Overall, we observed 1) a general long-term increase in functional diversity (FD) of invertebrate communities over France, 2) a significant contribution (ca 24%) of long-term changes in climate vulnerability (CV) to FD, and 3) a negative relationship between CV and FD. These results supported our third hypothesis stating that a decrease in climate vulnerability would have significantly contributed to a general long-term rise in functional diversity of invertebrate communities. Although they could be somewhat counter-intuitive, such 'positive' effects of climate-induced changes have already been demonstrated for different species (Araújo et al. 2006). In France, Buisson et al. (2008) suggested that the global positive impact of climate change on stream fish assemblages could be due to the prevalence of cool- and warm-water species in temperate systems, which are further promoted by newly suitable (i.e. warmer) conditions. Consistently, we highlighted a greater influence of CV in the south where the proportion of climate-sensitive taxa decreased the most, albeit not everywhere, as expected following our fourth hypothesis. These results supported the assumption of a colonisation and migration pattern by Mediterranean species sustaining the diversity increase in southern France, in agreement with the species range shifts predicted by several studies (Bonada et al. 2007, Domisch et al. 2013, Conti et al. 2014). As regards to our first hypothesis, nonetheless, we did not observe a generalised decrease in the climate vulnerability of invertebrate communities. More than half of the studied sites exhibited the contrary trend, that is, an increasing proportion of climate-sensitive taxa over the past two decades. According to the first modelling step, these sites would have consistently been exempted or partially preserved from warming, which seemed to occur more likely in small catchments (Fig. 3a). By hosting taxa that are threatened by warming, such locations provide biological refuges whose identification and protection are of priority for species conservation under future climate change (Keppel et al. 2012).

Consistently with our second hypothesis, the predicted increase in the feeding specialisation (FS) of communities was more generalised over France with more than 70% of the sites involved. Moreover, we highlighted negative and hump-shaped responses of FS across gradients of changes in phosphate concentration and temperature, respectively (Fig. 3b). As a result, low FS values corresponded to strong phosphate decreases, which were associated to changes from hypertrophic to eutrophic conditions, thus less prone to generate significant responses in specialisation of communities. Conversely, the highest increases in specialisation over the past twenty years occurred under weak changes in phosphates and moderate warmings. Such a response pattern would typically correspond to a trophic amplification process by which a moderate temperature increase enhances productivity and promotes specialists of different resource

Table 2. Summary results of the final additive models: percentage of variance in the three indices explained by the different sets of predictors (temporal, spatial and MEMs).

	Variance explained (%)					
		Spatial predictors				
Response variable	Temporal predictors	Regional	Catchment	Reach	MEMs	Total
CV	17.4	4.1	12.7	5.6	10.4	50.2
FS	14.3	2.0	10.1	7.1	14.8	48.3
γ_0	–	14.0	15.4	4.5	49.1	83.0

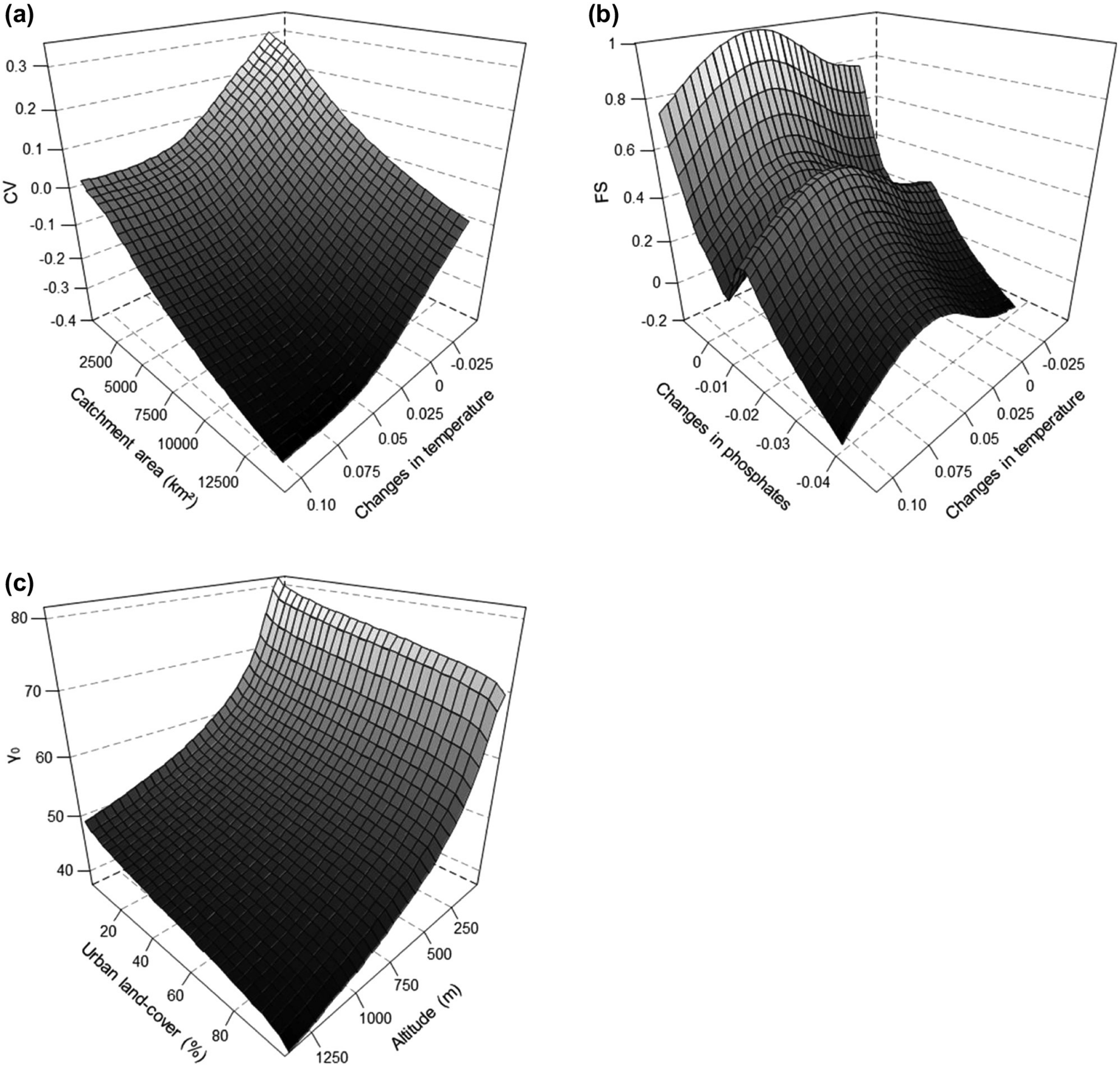

Figure 3. Examples of index responses to environmental predictors assessed with GAMs: (a) changes in climate vulnerability (CV) modelled across gradients of catchment area and changes in temperature; (b) changes in feeding specialisation (FS) modelled across gradients of changes in phosphate concentration and temperature; (c) initial γ-diversity (γ_0) modelled across gradients of urban land-cover and altitude.

Table 3. Summary results of the GWR models. Global coefficients denote the percentage of variance in functional diversity (FD) explained by the three indices and MEMs. Local extremes ('min', 'max') and standard deviations ('SD') were calculated from the independent regression parameters estimated at the 305 sites.

Coefficients		Variance explained (%)				
		CV	FS	γ_0	MEMs	Total
Global		23.8	23.4	16.7	10.5	74.4
Local	min	0*	5.2	1.2	–	–
	max	42.7	40.9	23.5	–	–
	SD	9.9	8.2	4.9	–	–

*negative values arising from the partial GWR approach were considered as null.

types (Yvon-Durocher et al. 2015, Van Looy et al. 2016). Furthermore, FS positively contributed to the increase in functional diversity of communities, in the same extent than CV (ca 24%), in agreement with our third hypothesis. More specifically, the spatial contribution pattern gave evidence for a greater influence of specialisation in small streams than in large rivers as predicted under our fifth hypothesis. These findings supported the assumption that trophic amplification and bottom-up regulation is more likely to occur in less-complex food webs, like those encountered in headwaters for instance (Woodward et al. 2016). Higher habitat heterogeneity has been acknowledged to inflate species richness through increased specialisation (Ohlemüller et al. 2008, Eme et al. 2015). Therefore, considering food resources as a component

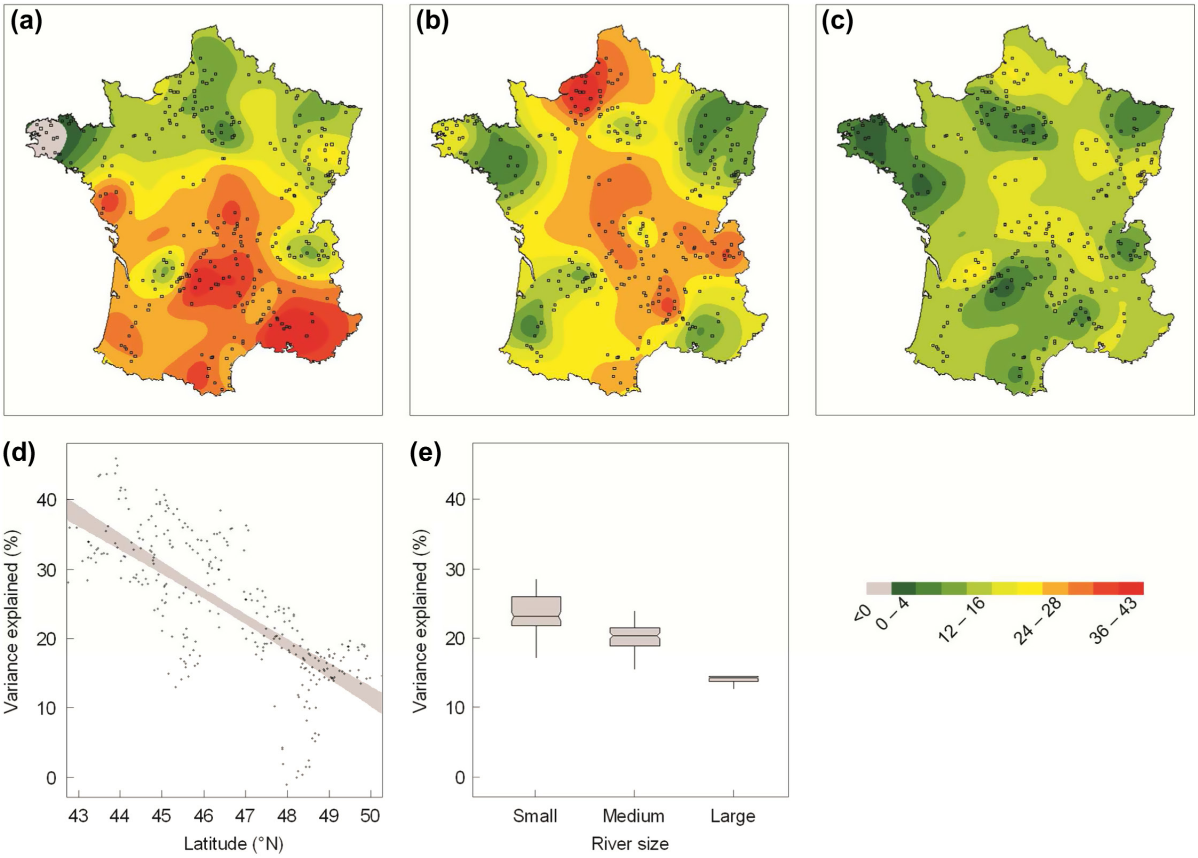

Figure 4. (a–c) Smoothed maps of contribution to changes in functional diversity (FD) assessed with GWR models: percentage of variance explained by (a) changes in climate vulnerability (CV); (b) changes in feeding specialisation (FS); (c) initial γ-diversity (γ_0). Points indicate the site locations. (d) Relationship between CV contribution and latitude (black dots). The grey area represents the 95%-confidence interval of a linear regression model. (e) Relationship between FS contribution and river size (small = 1st–2nd Strahler order, medium = 3rd–5th order, large = 6th order and more). As the sites were unequally distributed across the river size gradient, the boxplots were computed by randomly sampling 50 sites (with replacement) of each size.

of habitat sensu lato, higher resource heterogeneity would be more likely to enhance the diversity in these communities. As such, trophic amplification processes could be involved in partial mitigation of the deleterious warming effects on biodiversity in headwaters, which are particularly sensitive to climate change (Durance and Ormerod 2007, Buisson et al. 2008), especially at high elevations where cold-adapted species are already at the edge of their geographical distribution range (Domisch et al. 2013).

While the long-term changes in functional diversity were strongly driven by the climate/productivity mechanisms represented by CV and FS, they were also influenced by the regional species-pools, as emphasised by the significant contribution of γ_0 (ca 17%), thus supporting our sixth hypothesis. Overall, the functional diversity increase was less pronounced in regions with higher initial richness. The spatial contribution pattern of γ_0 revealed that this relationship was almost equally important over France. Basically, this result can be explained by the fact that the more diverse were the communities, the fewer were the available niches and, thus, the narrower was the margin for a potential functional diversity increase. More broadly, this response pattern can also be related to the spatial insurance hypothesis, which states that diversity acts as insurance for ecosystem functioning against environmental changes, especially at large spatial and temporal scales (Loreau et al. 2003, Shanafelt et al. 2015). These spatial insurance effects rely on spatial exchanges among local systems (Loreau et al. 2003), thereby depending on dispersal processes that are essential to community persistence within heterogeneous landscapes (Tonkin et al. 2014). As a result, more diverse assemblages are expected to be more stable since different species will have various responses to environmental fluctuations that compensate each other, hence stabilising community productivity in time (Loreau et al. 2003). Furthermore, it is worth noting that the lowest temporal variations in functional diversity of invertebrate communities were also related to weak changes in feeding specialisation. In other words, functional diversity was more stable at the sites where specialists did not significantly increase. This observation may have involved differential responses among communities depending on their dominant initial feeding strategy, since a greater insurance potential is expected for communities made up of generalists (Matias et al. 2013). Thereby, invertebrate assemblages mainly composed of feeding generalists would have been already 'stable' by the end of the 1990s, making them (nearly) unchanged in response to climatic and trophic changes afterwards. Conversely, specialist assemblages would have reached (or will reach) this stable state several years later. Following this assumption, we could now expect equivalent insurance potentials given that 1) the diversity–productivity relationship is steeper for specialist communities (Gravel et al. 2011) and 2) generalist and specialist communities tend to be similarly productive at higher levels of diversity (Matias et al. 2013).

Nonetheless, – whatever the ecological strategies involved (e.g. specialists vs generalists) – the counterpart of the spatial insurance is a buffering effect of biotic interaction processes which can lead to a homogenisation of the regional ecosystems and its subsequent risks of biodiversity loss (Olden et al. 2004, Shanafelt et al. 2015, Wang and Loreau 2016). Up to now, however, there is no evidence for a homogenisation pattern emerging at the scale of France thanks to the geographical differentiation of the functional processes involved in the maintenance of species diversity. Conversely, the large-scale rise in diversity even provides a greater resilience capacity to invertebrate communities against disturbances (Mori et al. 2013, Isbell et al. 2015). Similarly, for example, the regional zooplankton biodiversity has been shown to partially dampen the effects of temperature warming on ecosystem productivity (Thompson and Shurin 2012).

Beyond these present trends, one could also wonder how invertebrate communities will further respond to future changes. Even though the decrease in climate vulnerability has sustained a gain in diversity for now, the growing number of colonizing tolerant taxa could, in return, foster species losses by competitive exclusions (Buisson et al. 2008). Moreover, the most sensitive taxa still present up to now are expected to gradually disappear owing to distribution range contractions due to rising temperatures (Domisch et al. 2013). Similarly, the positive effect of the trophic amplification on diversity – as being based on moderate warmings – could be drastically dampened or suppressed by even-warmer temperatures. Finally, the spatial insurance effects are also expected to be less effective in maintaining community diversity in the face of global changes like climate change due to increasing synchrony among ecosystems (Shanafelt et al. 2015).

Under these threats to biodiversity, we argue that the present study can provide insights for practical conservation. Overall, our findings provided a strong support to the relevance of the functional indices built for this study, which allowed explaining about 75% of the long-term changes in the functional diversity of invertebrate communities over the last two decades in France. As such, they reinforced the great interest of using species traits and/or trait-based composite metrics to investigate specific issues like large-scale, long-term drivers of functional diversity of communities. In addition, we emphasised the importance of taking into account the spatial non-stationarity of ecological processes and responses when carrying out such investigations. As a consequence, we were able to highlight both direct and indirect effects of climate change on running water ecosystem functioning and whether these processes differed spatially, offering wider perspectives in a better identification of 1) geographical areas and/or stream types that need a priority protection, and 2) potential mitigation options that could be considered.

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Supplementary material (Appendix ECOG-02701 at <www.ecography.org/appendix/ecog-02701>). Appendix 1–2.