

Toward a loss of functional diversity in stream fish assemblages under climate change

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Abstract

The assessment of climate change impacts on biodiversity has so far been biased toward the taxonomic identification of the species likely either to benefit from climate modifications or to experience overall declines. There have still been few studies intended to correlate the characteristics of species to their sensitivity to climate change, even though it is now recognized that functional trait-based approaches are promising tools for addressing challenges related to global changes. In this study, two functional indices (originality and uniqueness) were first measured for 35 fish species occurring in French streams. They were then combined to projections of range shifts in response to climate change derived from species distribution models. We set out to investigate: (1) the relationship between the degrees of originality and uniqueness of fish species, and their projected response to future climate change; and (2) the consequences of individual responses of species for the functional diversity of fish assemblages. After accounting for phylogenetic relatedness among species, we have demonstrated that the two indices used measure two complementary facets of the position of fish species in a functional space. We have also rejected the hypothesis that the most original and/or less redundant species would necessarily experience the greatest declines in habitat suitability as a result of climate change. However, individual species range shifts could lead simultaneously both to a severe decline in the functional diversity of fish assemblages, and to an increase in the functional similarity among assemblages, supporting the hypothesis that disturbance favors communities with combination of common traits and biotic homogenization as well. Our findings therefore emphasize the importance of going beyond the simple taxonomic description of diversity to provide a better assessment of the likely future effects of environmental changes on biodiversity, thus helping to design more effective conservation and management measures.

Keywords: assemblages, climate change, functional traits, range shifts, species distribution models, stream fish

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Introduction

Climate change has been identified as one of the major drivers of biodiversity changes in the coming decades (Sala *et al.*, 2000). It is now evident that species from many taxonomic groups have responded to the recent climate modifications by shifting their ranges or becoming extinct locally (Parmesan & Yohe, 2003; Root *et al.*, 2003; Hickling *et al.*, 2006). These individual responses may result in substantial changes at the assemblage level (Stralberg *et al.*, 2009; Bertrand *et al.*, 2011). To date, the assessment of the impacts of climate change on biodiversity has been biased toward identifying individual species that are either benefiting from climate change or experiencing overall declines ('winners' vs.

'losers'; Hamer, 2010; Domisch *et al.*, 2011; Rosset & Oertli, 2011), without attempting to identify the biological attributes that could explain these responses. Beyond the taxonomic nomenclature of the species involved, it could be interesting to identify common features that could explain the sensitivity of particular organisms to climate disturbances. Moreover, understanding how the responses of individual species could modify the structure and composition of communities beyond the species level (Cadotte *et al.*, 2011) is an issue that has been rarely investigated. It has only recently begun to be explored with regard to the phylogenetic (Thuiller *et al.*, 2011) and functional (Thuiller *et al.*, 2006; Buisson & Grenouillet, 2009) diversity of assemblages.

It is now clearly recognized that it is crucial to include functional traits (i.e. biological attributes influencing the organism's performance, Violle *et al.*, 2007)

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in community ecology (McGill *et al.*, 2006). Indeed, metrics derived from these functional traits seem to offer relevant tools for detecting changes in the diversity and structure of communities going beyond measurements of the taxonomic alpha diversity (e.g. species richness) that do not account for the biological identity of organisms. For instance, functional diversity, which represents the diversity of biological traits present in a species assemblage (Petchey & Gaston, 2006), has been used to determine how diversity may be affected by environmental stress or disturbance (Suding *et al.*, 2008). Dramatic losses of functional diversity have been reported for several taxonomic groups, including the effects of logging on tropical anuran communities (Ernst *et al.*, 2006) or the consequences of habitat changes on birds and mammals (Flynn *et al.*, 2009), fish (Olden *et al.*, 2006; Villéger *et al.*, 2010) and dung beetles (Barragan *et al.*, 2011) communities. However, it is worth noting that the literature focusing on such functional changes has been limited to empirical observations of the effects of habitat alterations (e.g. agricultural intensification). As far as we are aware, there is a paucity of studies that have attempted to explore the future modifications of functional diversity under global changes (e.g. climate change, biological invasions).

Functional diversity is a multifaceted component of biodiversity that can be quantified within a multidimensional space derived from a set of functional traits (Villéger *et al.*, 2008; Mouchet *et al.*, 2010). In this study, we used the position of species functional niche relative to the other species to describe two overlooked facets of functional diversity. First, we consider functional originality which characterizes the position of a species in the functional space relative to a global pool of species (Bellwood *et al.*, 2006; Villéger *et al.*, 2010). Functional originality thus indicates the average rarity of all the biological features of each species (Pavoine *et al.*, 2005; Mouillot *et al.*, 2008). However, this measure does not account for the uniqueness of the species functional traits. Indeed, two species may share a combination of attributes very original compared with the other species of the pool. Thus, in addition to the originality index, the degree of uniqueness may be viewed as a complementary facet of the biological identity of species. Functional uniqueness is roughly the opposite of functional redundancy, which has been shown to be a determining factor in the stability of ecosystems (Walker, 1995; Naeem, 1998; Fonseca & Ganade, 2001). From the position of the functional niche measured at the species level, average specific values can also be derived at the community level, as it has been developed for other ecological metrics (e.g. community specialization index: Julliard *et al.*, 2006). This makes it

possible to quantify how the functional structure of communities can respond to environmental disturbances.

In this context, both these functional metrics have been combined with projections of species range shifts derived from species distribution models to forecast the impact of climate change on the functional facets of biodiversity. Stream fish have been investigated here for several reasons. First, they inhabit freshwater habitats that are confronted by a variety of threats (e.g. habitat degradation, water extraction, pollution, overfishing, Vörösmarty *et al.*, 2010), but those related to climate-induced stress have been recognized as being some of the main challenges for future conservation (Sala *et al.*, 2000; Heino *et al.*, 2009; Strayer & Dudgeon, 2010). Second, stream fish have been shown to be highly sensitive to climate change (e.g. temperature warming, water discharge reduction). Several fish species have already shifted their ranges (Booth *et al.*, 2011; Almodóvar *et al.*, 2012), and potential shifts in response to future climate change have also been projected (Eaton & Scheller, 1996; Buisson *et al.*, 2008; Lyons *et al.*, 2010).

Therefore, using projections of range shifts in response to climate change for fish species in French streams (Buisson & Grenouillet, 2009), our detailed objectives were: (1) to find out whether the most original and/or less redundant species were also the ones most affected by climate disturbances, and (2) to investigate the consequences of individual responses of species to climate change on the functional diversity of fish assemblages.

Materials and methods

Fish data

Fish data were provided by the French National Agency for Water and Aquatic Environment (Onema), the national organization in charge of the protection and conservation of freshwater ecosystems in France. Fish data collected by standardized electrofishing in 1110 stream reaches (about 100 m long) evenly distributed within 83 French river basins were extracted from this database. The stream reaches were selected owing to their reference status (i.e. least impacted by anthropogenic disturbances; Oberdorff *et al.*, 2002) to avoid results biased by non-climatic disturbances. They covered all types of streams found in France, ranging from small headwater to large lowland rivers. Two electrofishing methods have been used depending on depth and width: smaller rivers have been sampled by wading (mostly two-pass removal) and larger ones by boat. Fish assemblages present in these stream reaches were described in terms of the presence-absence of the 35 most common fish species in the dataset for statistical reasons (Buisson & Grenouillet, 2009; see Table S1 for a list of species).

Environmental data

Ten environmental variables influencing the spatial distribution of fish (Matthews, 1998) were used to characterize the 1110 sites. Six of these variables described the physical habitat: the surface area of the drainage basin above the sampling site (km²), distance from the headwater source (km), mean stream width (m), mean water depth (m), river slope (‰), and elevation (m). To eliminate the colinearity between the surface area of the drainage basin and the distance from the headwater source, a principal component analysis (PCA) was used. The first axis of the PCA, accounting for 93.2% of the total variability, was kept as a synthetic variable (G) describing the upstream–downstream gradient (Buisson & Grenouillet, 2009). Four climatic variables were extracted from the CRU CL 2.0 (Climatic Research Unit Climatology 2.0 ver.) dataset (New *et al.*, 2002) at a resolution of 10' × 10', and averaged for the period 1961–1990 to describe the current climate at the stream reach scale: mean air temperature of the coldest and the warmest months (°C), mean annual air temperature (°C), and mean annual rainfall (mm). Air temperature was used as a proxy for stream temperature as it is known that air and water temperatures are strongly positively correlated in streams (Caissie, 2006). The mean annual rainfall gives an idea of the amount of flowing waters and acts consequently on the microhabitat structure available for organisms.

Two scenarios (A1Fi and B2) illustrating contrasting greenhouse gas emission levels predicted for the end of the 21st century were used in this study to assess the potential effects of future climate change scenarios on fish assemblages. Future projections were averaged for a 30-year period ending in 2080. They were both derived from the general circulation model HadCM3 (Hadley Centre for Climate Prediction and Research's General Circulation Model; Gordon *et al.*, 2000).

Ensemble modeling of fish species distribution

Fish distribution data were related to the set of environmental variables using species distribution models (Elith & Leathwick, 2009), making it possible to predict the current suitability of each study site for each individual fish species. Seven different statistical methods (generalized linear models, generalized additive models, multivariate adaptive regression splines, random forests, boosted regression trees, linear discriminant analysis, and classification tree analysis) have been used to account for the algorithmic variability between predictions (see Buisson & Grenouillet, 2009 for details concerning the modeling procedure). The models were calibrated on the current dataset and were then used to generate projections of the potentially suitable habitat in 2080 according to both the A1Fi and B2 scenarios. Model outputs (i.e. the probability of occurrence of each species) obtained across the seven different statistical methods were averaged for both the current and future periods, and used to assess the suitability of each stream reach (Araujo & New, 2007). An unlimited dispersal scenario assuming that fish species could reach all sites becoming climatically suitable in the future was used. To avoid the bias arising from the transformation of probabilities

of occurrence into binary outputs (Nenzen & Araujo, 2011), all the analyses conducted in this study were based on the probabilities of occurrence of the species.

The average change in the probability of occurrence in response to climate change across the 1110 stream reaches was then calculated for each species. Although the response of a fish species may vary depending on the geographical area (Buisson & Grenouillet, 2009), this approach makes it possible to evaluate the potential effects of climate modifications at the regional scale (i.e. for the whole of France). Species described as 'winners' were defined as species that could benefit from climate change (i.e. those whose mean probability of occurrence could increase as a result of climate change) and 'losers' were defined as species for which climate change could be detrimental (i.e. those whose mean probability of occurrence could decrease in response to climate change).

To quantify changes in the composition of fish assemblages in response to climate change (species turnover), we calculated the Bray-Curtis dissimilarity between the current and future species composition (in terms of probability of occurrence) of each of the 1110 fish assemblages (Stralberg *et al.*, 2009). This dissimilarity metric ranged from 0 (no change in the probabilities of occurrence between current and future periods) to 1 (extreme changes in the probabilities of occurrence, i.e. high turnover in species composition).

Defining functional originality and uniqueness indices for fish species

Each fish species was functionally described in terms of three main biological functions using 13 traits (Olden *et al.*, 2006; Villéger *et al.*, 2010): food acquisition (feeding habitat, trophic guild, and life habitat), locomotion (mean body length, body shape, swimming factor, rheophily, and migration type), and reproduction (relative fecundity, spawning time, life span, parental care, and reproduction habitat) (see Table S1 for more details). These 13 traits were selected as they are among the most commonly used in studies applying a functional approach to fish communities (e.g. Winemiller & Rose, 1992; Lamouroux *et al.*, 2002), they are not redundant and they are easily available for all 35 studied species. In addition, the number of traits for each function was balanced allowing giving an equal weight to each function when describing functional niche. Trait values for the 35 fish species were taken from the literature (Kottelat & Freyhof, 2007; Froese & Pauly, 2012), expert knowledge, and derived from pictures for body shape and swimming factor (Table S1). As most traits were discrete, the potential intraspecific variation in life-history traits (Blanck & Lamouroux, 2007) at the scale of France was neglected, and functional traits were assumed to be constant throughout France.

A multidimensional functional space was then constructed using these 13 functional traits. Gower's distance was computed for each pair of species. This distance allows mixing variables of different natures while giving them equal weight. Following Villéger *et al.* (2008), this functional distance matrix was then used to compute a Principal Coordinate Analysis (PCoA) (Gower, 1966; Legendre & Legendre, 1998).

The first four axes of the PCoA, accounting for 66.4% of the total variability, were selected. The orthogonal axes provided by the PCoA could be seen as synthetic functional traits summarizing a fish functional niche. Fish species coordinates in the four-dimensional space defined by the PCoA were used to calculate two indices: functional originality and functional uniqueness.

The functional originality of each species was defined as the Euclidean distance to the average position of the species pool, which was here the center of the four-dimensional space (Bellwood *et al.*, 2006; Villéger *et al.*, 2010). This index thus indicated the position of each fish species within the functional space derived from the 13 biological traits across the 35 species, relative to a hypothetical average species (in terms of functional traits). The higher this index, the greater the functional difference between the species investigated and the hypothetical average species (Fig. 1).

The functional uniqueness of each species was defined as the Euclidean distance to the nearest neighbor in the functional space. This index thus assessed the proximity of each fish species to its nearest neighbor in the functional space. Functional uniqueness was high when a species had unique traits values combinations compared with each species of the pool (i.e. low redundancy), and was low when a species had a close neighbor in the functional space (i.e. these two species are functionally redundant) (Fig. 1).

The raw values of the functional originality and uniqueness indices were standardized by dividing them by the respective

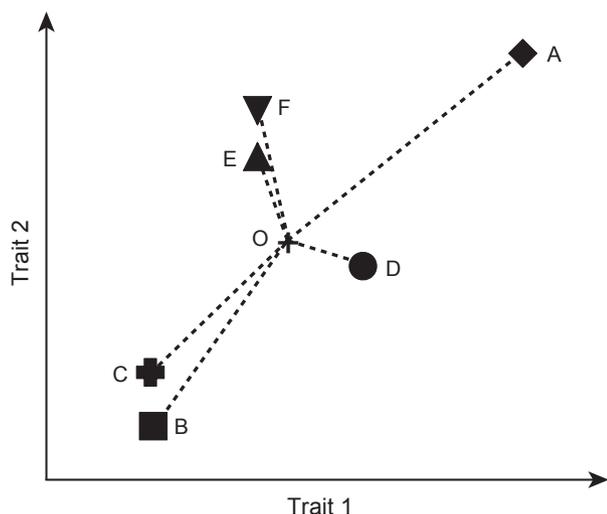


Fig. 1 Theoretical study case showing species with contrasting functional originality and functional uniqueness. Six species (A–F) are plotted in a two-dimensional functional space (for graphical convenience). Point O (black cross) indicates the center of gravity of this species pool (i.e. the hypothetical average species). Species A is functionally original (remote from O) and unique (functionally different from other species). Species B and C are also original, but they are functionally redundant (i.e. close to each other in the functional space). Similarly, species D is not original (close to O) and is also unique, whereas species E and F are not original, but functionally redundant.

maximum value observed among the 35 fish species. Both these indices were calculated for each fish species relative to the pool of species studied. Values remained thus unchanged whatever the other fish species co-occurring in the stream reaches.

Phylogenetic relatedness in functional originality and uniqueness

We tested the phylogenetic signal in the originality and uniqueness indices using the *K* statistic as implemented in the *picante* package (Kembel *et al.*, 2010) in the R statistical environment (R Development Core Team, 2011). This statistical test compares the observed phylogenetic signal in each functional index to the expected phylogenetic signal under a Brownian motion model of evolution (Blomberg *et al.*, 2003). *K* values of 1 correspond to a Brownian motion process, *K* values greater than 1 indicate strong phylogenetic conservatism, whereas *K* values closer to zero correspond to a random or convergent pattern of evolution. The statistical significance of the phylogenetic signal was evaluated by comparing observed patterns of the variance of phylogenetically independent contrasts to a null model of shuffling species labels across the tips of the phylogeny (Blomberg *et al.*, 2003). The phylogenetic tree used was extracted from Grenouillet *et al.* (2011).

As closely related species often share similar characteristics, species cannot be considered to be independent points in comparative analyses. The relationship between functional originality and uniqueness was thus tested after accounting for phylogenetic relatedness among fish species, using Generalized Estimation Equations (GEEs, Paradis & Claude, 2002) as implemented in the *ape* package (Paradis *et al.*, 2004). This approach takes into account the phylogenetic relatedness among fish species by constructing a species-to-species correlation matrix derived from the phylogenetic tree. Unlike the standard independent contrasts method, GEE explicitly incorporates the correlation matrix into the framework of a Generalized Linear Model (GLM), without assuming a significant phylogenetic signal in the studied response.

To test the relationship between the degree of originality/uniqueness of species and their responses to climate change, GEEs relating the average change in probability of occurrence of each species across the 1110 stream reaches under each climate change scenario (response variable) to each functional index (explanatory variable) were also used, making it possible to control for phylogeny (Paradis & Claude, 2002).

Assessing changes in the functional originality and uniqueness of fish assemblages in response to climate change

The mean functional originality and uniqueness of each of the 1110 fish assemblages were calculated by averaging species index values weighted by species probabilities of occurrence under the present and projected future climate conditions.

Projected future values of originality and uniqueness for each assemblage were compared with current values using *t*-tests and Fisher tests for paired samples to test the equalities of both the means and the variance. Pearson's correlation

coefficient was used to measure the magnitude of the relationship between projected changes in functional originality and functional uniqueness.

Hierarchical models to test for the determinants of the projected functional changes

Due to their spatial and hierarchical nature, river systems can be viewed as interacting systems of biological and physical components, from the basin scale to successively smaller scales (Frissell *et al.*, 1986). Accordingly, a challenge in stream ecology is to analyze patterns and processes into hierarchical levels of organizations. In that context, hierarchical – or multi-level – regression models appear as appropriate tools, providing variance partitioning among covariates that operate at various spatial scales (Gelman & Hill, 2006). Therefore, hierarchical linear models were devised to test for local- and regional-scale drivers of changes in both the functional originality and uniqueness of fish assemblages, using the *lme4* package (Bates *et al.*, 2011). For each functional change, the full model was a varying intercept, varying slope, two-level, hierarchical linear model with error terms that were Gaussian. Intercepts and slopes could vary according to each river basin (Gelman & Hill, 2006). Three local-scale predictors were fitted to the functional changes: two local-scale abiotic covariates describing the spatial position of the sites (i.e. elevation (log transformed) and the position along the upstream–downstream gradient), and one biotic covariate quantifying the projected species turnover of each fish assemblage under climate change scenarios (derived from Bray–Curtis dissimilarity). At the regional (i.e. river basin) scale, two predictors (i.e. mean latitude and mean longitude of the river basin) were used to test for broad-scale geographic patterns in functional changes.

For both projected changes in functional originality and functional uniqueness, we fitted the full model (i.e. three local-scale predictors and two regional-scale predictors), and we tested for interactions among the three local- and two regional-scale predictors (i.e. six two-term interactions). The most parsimonious model for supporting the data was selected after a stepwise selection procedure based on the Akaike Information Criterion (Gelman & Hill, 2006). To compare the relative strength of local- vs. regional-scale predictors in driving functional changes, all the predictors were transformed to z-scores to standardize the slope coefficients.

Results

Relationship between the functional indices and potential species' responses to future climate change

The functional originality and uniqueness indices revealed a marked variability between species (Fig. 2, Table S2). For instance, the most original species (*Anguilla anguilla*) was located more than five times further to the center of the functional space than the least original species (*Rutilus rutilus*). Similarly, the distance between the species having the most unique combina-

tion of traits (*Cottus gobio*) and its nearest neighbor (*Ameiurus melas*) was five times greater than the distance between the two most redundant species (*Chondrostoma nasus* and *Parachondrostoma toxostoma*). There was a strong phylogenetic signal (i.e. conservatism) of both originality ($K = 0.17$, $P = 0.001$) and uniqueness ($K = 0.65$, $P = 0.002$) among fish species. For instance, it appeared that cyprinid species were consistent in displaying relatively low functional originality (Fig. 2, Table S2). In addition, when accounting for phylogenetic relatedness, the relationship between functional originality and uniqueness measured at the species level was not significant ($F = 1.33$, $P = 0.41$), indicating that these two indices measured two complementary facets of the fish functional niche.

Among the 35 fish species studied, the mean probability of occurrence across the 1110 stream reaches was projected to decrease according to the A1Fi climate change scenario for eight species (in order of decreasing magnitude of change in the mean probability of occurrence: *Salmo trutta*, *C. gobio*, *Lampetra planeri*, *Pungitius laevis*, *Perca fluviatilis*, *Phoxinus phoxinus*, *Abramis brama*, *Gymnocephalus cernuus*), whereas the other 27 species could find habitat more environmentally suitable in the future (Fig. 3a and b, Table S2). Results were quite similar for the B2 scenario, but 5 and 30 species were 'losers' and 'winners', respectively (Fig. 3c and d, Table S2).

Overall, for both climate change scenarios, there was no significant relationship between the projected response of fish species to climate change (i.e. change in probability of occurrence) and their level of functional originality (A1Fi: $F = 8.07$, $P = 0.16$; B2: $F = 1.81$, $P = 0.36$; Fig. 3a and c) and uniqueness (A1Fi: $F = 8.35$, $P = 0.15$; B2: $F = 7.15$, $P = 0.17$; Fig. 3b and d) after controlling for phylogeny, thus rejecting the hypotheses that the most original and less redundant species would be most adversely affected by climate change. For instance, of the two most original species one was a 'loser' (*C. gobio*) and the other a 'winner' (*A. anguilla*). It should also be pointed out that the greatest 'loser' (*S. trutta*) had a low uniqueness index, indicating a high degree of functional redundancy with at least another species. Nevertheless, the species that were projected to strongly increase their mean probability of occurrence were all among the least unique species (*Telestes souffia*, *P. toxostoma*, *Squalius cephalus*), and the two species that displayed the most unique set of functional traits were both 'losers' (*C. gobio* and *L. planeri*).

Potential effects of climate change on functional indices measured at the fish assemblage level

According to both the A1Fi and B2 scenarios, the response of individual fish species to future climate

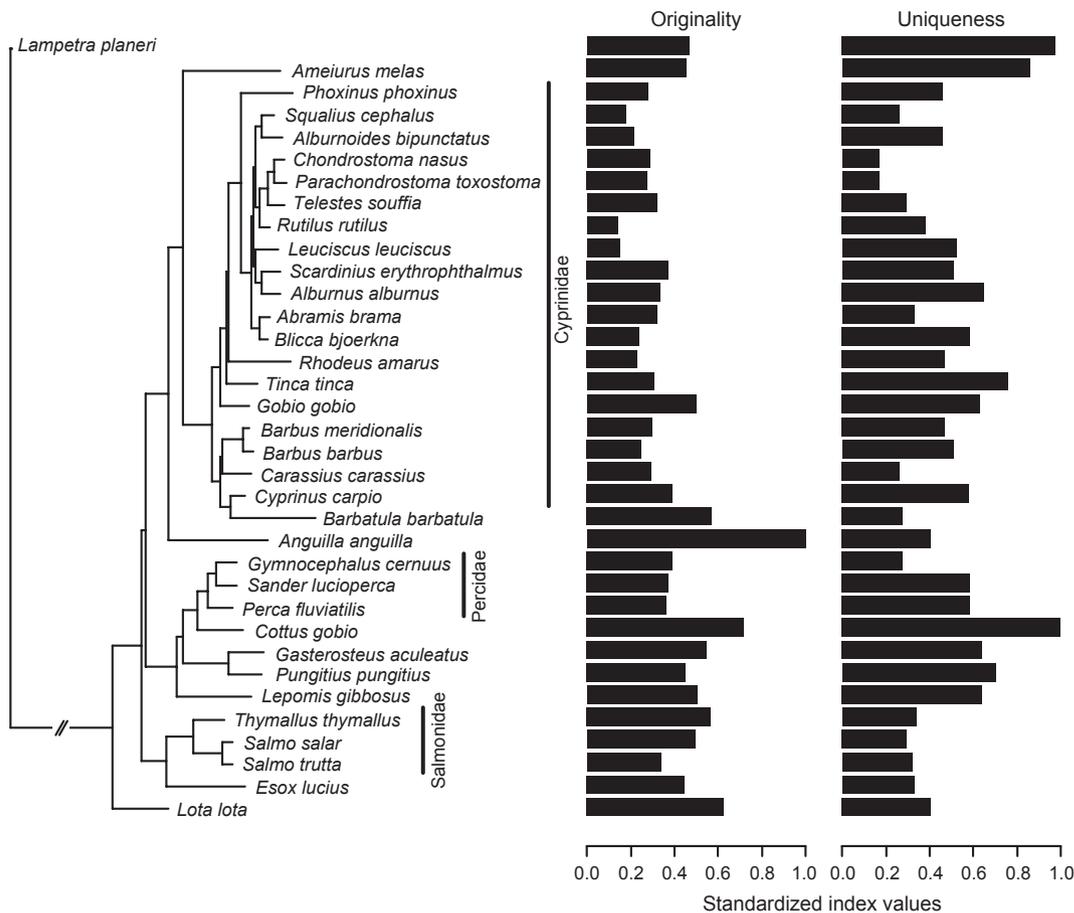


Fig. 2 Phylogeny of the 35 fish species studied. Species names are those for which molecular sequences were used and follow the classification of Maitland (2000). Note that some of them have been changed after Kottelat & Freyhof (2007). The most common fish families are shown. The relationship between species identity and the values of the two functional indices (originality and uniqueness) is indicated. Both functional indices exhibit significant phylogenetic signals (see text for details).

change could lead to a decrease in the mean originality of fish assemblages compared with current assemblages (A1Fi: $t = 30.2$, $P < 0.001$; B2: $t = 34.9$, $P < 0.001$; Fig. 4a). In addition, the originality index of projected future assemblages displayed less variability for both climate change scenarios compared with the current assemblages (A1Fi: $F = 2.1$, $P < 0.001$; B2: $F = 1.5$, $P < 0.001$; Fig. 4a).

A similar trend was found for the functional uniqueness index of fish assemblages that could decrease with increasing climate change (A1Fi vs. current: $t = 51.7$, $P < 0.001$; B2 vs. current: $t = 41.6$, $P < 0.001$; A1Fi vs. B2: $t = -36.4$, $P < 0.001$; Fig. 4b), and become less variable in the future than at present (A1Fi: $F = 3.3$, $P < 0.001$; B2: $F = 1.6$, $P < 0.001$; Fig. 4b).

The potential changes in functional originality and uniqueness measured at the assemblage level were significantly positively correlated for both scenarios ($r = 0.63$, $P < 0.001$, Fig. 5). For instance, both the functional originality and uniqueness could decrease in

more than 80% of fish assemblages. Nevertheless, opposite changes in these two indices could also occur as 13.7% and 8.6% of fish assemblages could experience a decline in their degree of uniqueness, but an increase in originality according to the A1Fi and B2 scenarios, respectively (Fig. 5).

Identification of the main drivers of changes in functional indices

The best hierarchical models to explain changes in functional originality and uniqueness in response to climate change included both local- and regional-scale predictors as well as the interactions between them (Table 1). Among the local-scale predictors, projected species turnover was selected in all the models and correlated negatively with functional changes. The functional originality and uniqueness of fish assemblages decreased more markedly with increasing changes in the species composition of fish assemblages (Fig. 6e

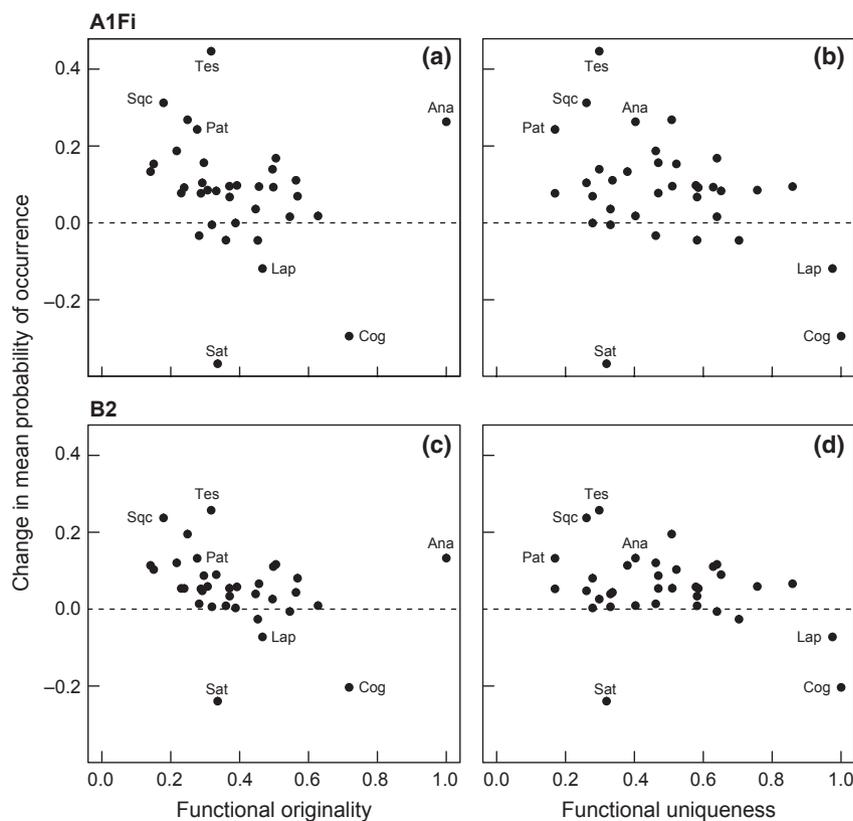


Fig. 3 Relationships between functional indices and projected changes in the probability of occurrence of each of the 35 fish species under A1Fi and B2 climate change scenarios: change in probability of occurrence vs. functional (a, c) originality and (b, d) uniqueness. Species codes (only shown for species cited in the text): Ana, *Anguilla anguilla*; Cog, *Cottus gobio*; Lap, *Lampetra planeri*; Pat, *Parachondrostoma toxostoma*; Sat, *Salmo trutta*; Sqc, *Squalius cephalus*; Tes, *Telestes souffia*.

and f). Moreover, functional changes were also determined by local descriptors of the spatial position of the sites, as elevation and position along the stream gradient were positively correlated with changes in originality and uniqueness, respectively (Table 1). Loss of originality was more pronounced at low elevations (Fig. 6c); whereas a greater decline in the degree of uniqueness was projected upstream (Fig. 6b). Both functional changes showed broad-scale geographical patterns as basin longitude correlated positively with these changes, whereas basin latitude correlated negatively (except for changes in functional originality in the B2 climate change scenario). These results revealed that functional changes were more pronounced in the western than the eastern river basins (Fig. 6g and h), and also more pronounced in northern than in southern river basins (Fig. 6i and j).

Discussion

As far as we are aware, this study is the first to investigate the functional consequences of future climate change at both species and assemblage levels using two

indices to describe the biological identity of species and the functional diversity of assemblages. Among the pool of species studied, we have demonstrated that the two functional facets assessed (i.e. originality and uniqueness) were not correlated at the species level. Being functionally distant from the hypothetical average species was therefore not incompatible with the existence of a close functional neighbor, at least given the set of biological traits considered here to measure functional originality and uniqueness. This finding reveals that these functional metrics are complementary facets of the species functional niche, and seem to be relevant for comparing the functional identity of a particular species to that of a pool of species.

Overall, we have identified a small number of species that are very original or low redundant relative to the pool of 35 fish species. This was probably due to the predominance of cyprinid species in French streams (54% of the species studied). Indeed, cyprinids are strongly dominant at the European scale (Reyjol *et al.*, 2007). Consequently, all these species are close to the hypothetical average species in the defined functional space and also roughly similar to each other (although

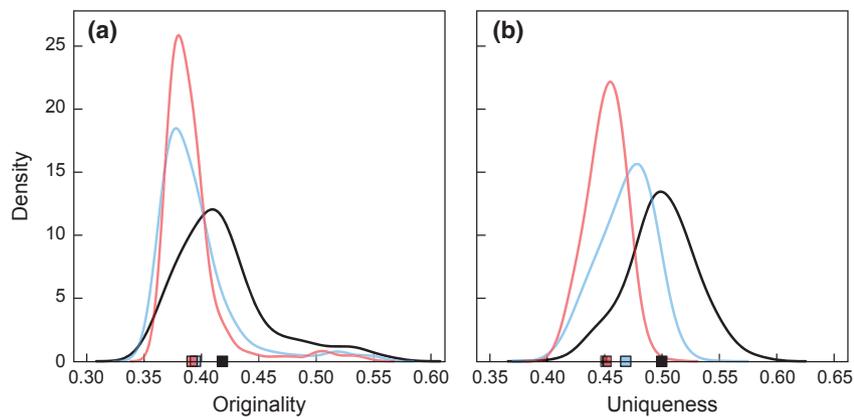


Fig. 4 Probability density functions for (a) functional originality, and (b) functional uniqueness, based on the 1110 fish assemblages for current (black), future B2 (blue), and future A1Fi (red) scenarios. Squares represent the mean functional (a) originality and (b) uniqueness across the 1110 fish assemblages.

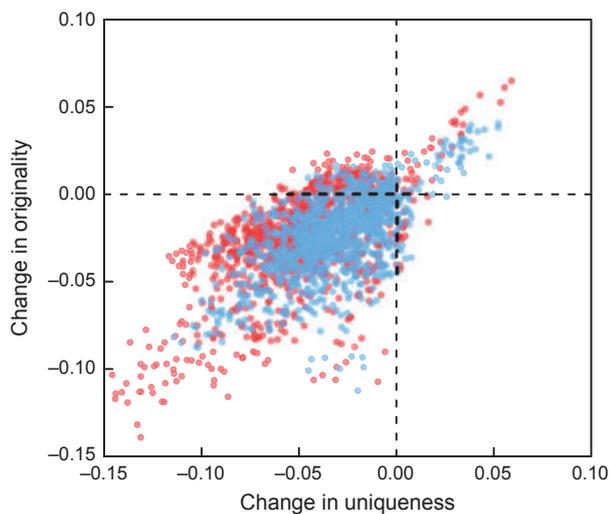


Fig. 5 Projected changes in functional originality according to projected changes in uniqueness for the 1110 fish assemblages under B2 (blue) and A1Fi (red) climate change scenarios. Negative values indicate a projected decrease in the functional index between current and future periods, whereas positive values indicate a projected increase.

some species may have unique strategies for single traits). In contrast, the species identified as being the most original and with the highest degree of uniqueness belonged to other fish families (e.g. Anguillidae, Cottidae) that consist of relatively few species. For instance, *A. anguilla*, despite being tolerant to a wide variety of habitats (Adam *et al.*, 2008), has morphological attributes and a breeding behavior much different from cyprinid species, explaining its high level of functional originality compared with the pool of 35 species. The significant phylogenetic conservatism found for originality and uniqueness supports this pattern.

However, it should be kept in mind that these indices are measured relative to the species pool and so the values found here are not meaningful outside the context of this study (Mouillot *et al.*, 2008). For instance, we assumed that the pool of 35 fish species would remain stable during climate change, and that no additional species could appear in French streams. However, it is known that climate change could promote the expansion of non-native species and make it more likely for them to become established (Rahel & Olden, 2008). These non-native species may have functional features that differ from those of native and currently established non-native species (e.g. larger body size, Blanchet *et al.*, 2010) and thus, including these species could modify the range of functional traits and subsequently the values of the originality and uniqueness indices.

The primary goal of this study was to test the potential link between the functional identity of fish species and their projected responses to climate change. After controlling for phylogenetic relatedness, we have demonstrated that species that are likely to experience the greatest declines in habitat suitability as a result of climate change were not necessarily the most original species and/or those displaying the most unique combination of traits. The absence of significant relationship between our functional niche-based metrics and projected response to climate change may result from the multifunction approach used, which makes difficult the formulation of *a priori* hypotheses. Further research would thus have to assess how each separate function could respond to forecasted climate change for a better understanding of the detailed mechanisms driving the projected changes. Indeed, it is well documented that the responses of most organisms to climate change (e.g. range shifts) are mainly due to their physiological constraints and tolerance limits that have been

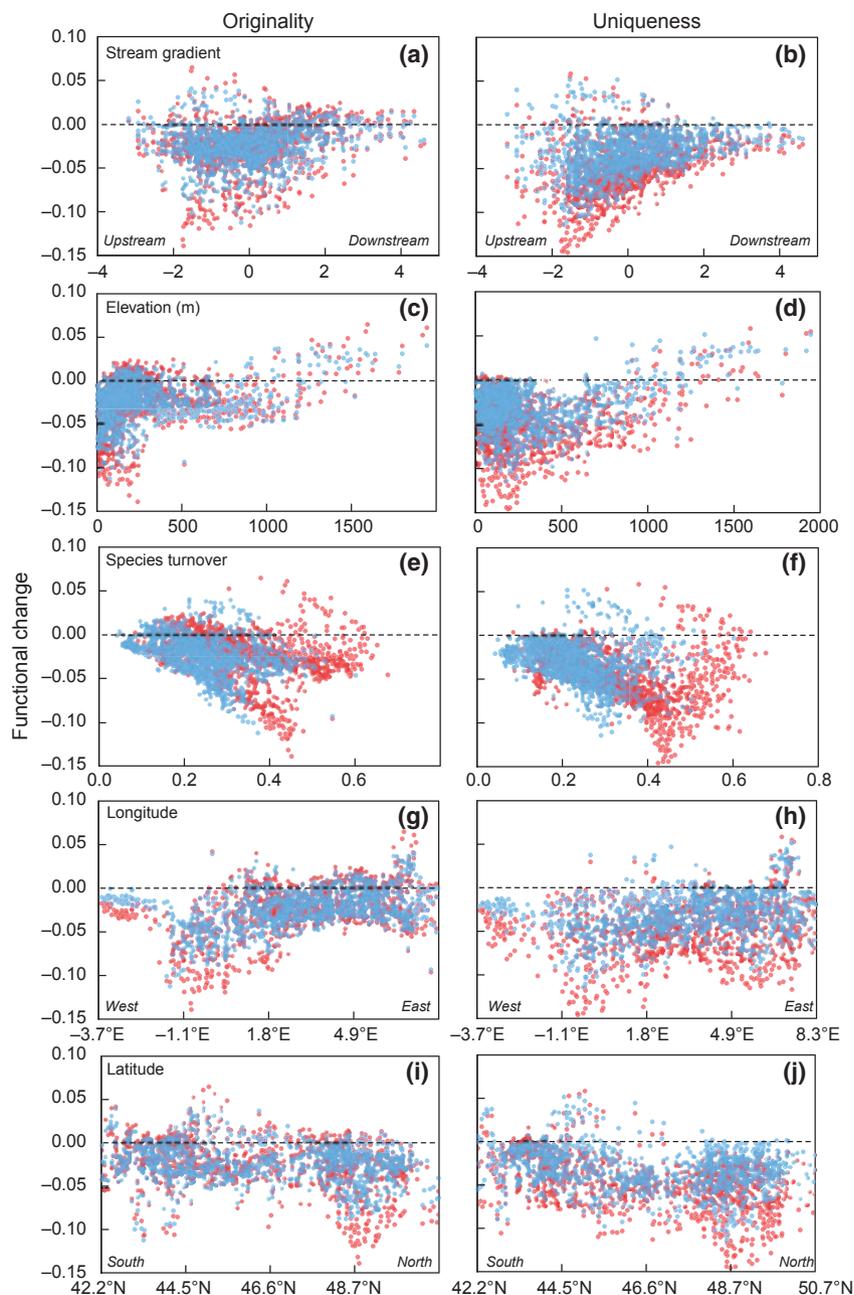


Fig. 6 Relationships between environmental descriptors and taxonomic changes, and the projected functional changes in the originality (left-handed column) and uniqueness (right-handed column) of fish assemblages according to the A1Fi (in red) and B2 (in blue) climate change scenarios. (a, b): stream gradient; (c, d): elevation (in meters); (e, f): species turnover; (g, h): longitude; (i, j): latitude.

reached or exceeded (Root *et al.*, 2003; Parmesan, 2006). These physiological limits are closely related to life-history strategies influencing for instance the fecundity, the age at maturity, or the size of eggs. Thus, it might be expected that life-history traits would be more sensitive to future climate modifications than ecomorphological traits (e.g. position in the water column), but our results did not answer this issue yet. In addition, any

wider comparison of those findings with other studies is difficult as both measures of functional originality and uniqueness are scarce. Mouillot *et al.* (2008) have highlighted the fact that marine fish species with the most original trait combinations became more abundant in a natural reserve, indicating that the most original species would benefit more from protection. Furthermore, it has been hypothesized that the most

Table 1 Outputs from two-level hierarchical models relating the changes in both functional originality and uniqueness of fish assemblages according to both A1Fi and B2 climate change scenarios using local- and regional-scale predictors. Local-scale predictors include position along the upstream–downstream gradient (G), elevation (ELE), and species turnover (T) projected under the corresponding climate change scenario. Regional-scale predictors include basin mean longitude (LON) and basin mean latitude (LAT). Hierarchical model coefficients (\pm SD) are given for predictors included in the most parsimonious model after a stepwise selection procedure. N.I. are predictors not included in the most parsimonious model

Predictor	Change in originality		Change in uniqueness	
	A1Fi	B2	A1Fi	B2
G	N.I.	N.I.	0.237 (\pm 0.043)	0.313 (\pm 0.047)
ELE	0.007 (\pm 0.002)	0.184 (\pm 0.060)	−0.140 (\pm 0.061)	N.I.
T	−0.029 (\pm 0.001)	−0.962 (\pm 0.039)	−0.547 (\pm 0.057)	−0.303 (\pm 0.058)
LON	0.016 (\pm 0.003)	0.508 (\pm 0.079)	0.223 (\pm 0.072)	0.213 (\pm 0.071)
LAT	−0.006 (\pm 0.002)	N.I.	−0.661 (\pm 0.066)	−0.419 (\pm 0.065)
G \times LON	−0.002 (\pm 0.001)	N.I.	−0.112 (\pm 0.034)	N.I.
G \times LAT	N.I.	N.I.	0.115 (\pm 0.043)	N.I.
ELE \times LON	N.I.	N.I.	0.140 (\pm 0.065)	N.I.
ELE \times LAT	N.I.	N.I.	N.I.	−0.223 (\pm 0.040)
T \times LON	0.004 (\pm 0.001)	0.153 (\pm 0.043)	N.I.	N.I.
T \times LAT	−0.006 (\pm 0.001)	N.I.	−0.207 (\pm 0.066)	−0.186 (\pm 0.062)

functionally original species are the most specialized species (Mouillot *et al.*, 2008; Devictor *et al.*, 2010) as species with a narrow ecological niche have an original combination of traits suited to that particular niche. Thus, original species might be adversely affected by habitat alterations, paralleling the well-known pattern of decline in specialist species facing environmental disturbances (Julliard *et al.*, 2004; Colles *et al.*, 2009; Filippi-Codaccioni *et al.*, 2010; Clavel *et al.*, 2011). Here, our results contrast with these patterns as we did not find any significant relationship between functional originality or functional uniqueness and responses to climate disturbances. This may be due to the use of a suite of traits representing multiple niche dimensions as a species having a single original attribute, relative to the whole pool of species, is not necessary functionally original when considering all the other traits (e.g. the grazer cyprinid, *P. toxostoma*). Nonetheless, our non-significant findings have to be mitigated somewhat as the greatest ‘winner’ species had a low functional originality, and the second most original species (*C. gobio*) was the second greatest ‘loser’. Consequently, these results should be regarded as first assessments of the impact of future climate change on stream fish using descriptors of the functional niche of species.

Individual responses of species to climate change could lead to changes at the assemblage level. In a previous study, Buisson & Grenouillet (2009) have found that future climate modifications could drive substantial changes in both the taxonomic and biological traits composition of fish assemblages. The present study goes a step further by measuring two overlooked facets

of fish species functional niche, and then, by combining these indices at the assemblage level to explore potential functional consequences of climate change on stream fish assemblages. Compared with other commonly used descriptors of functional diversity (e.g. Mouchet *et al.*, 2010), such an approach makes it possible to understand more accurately the relative contribution of each species in the projected severe decline in both functional originality and functional uniqueness of fish assemblages. The most remarkable change is the projected loss of the assemblages with the highest degree of originality and uniqueness, which will probably result both from the reduced suitability of stream reaches for some original or unique species (e.g. *C. gobio*), and simultaneously, from the greater suitability of many stream reaches for a large number of ‘winners’ (Buisson *et al.*, 2008) with low degrees of originality or uniqueness (e.g. cyprinids). This decline in functional originality and uniqueness is directly related to a loss of functional diversity. Indeed, functional richness increases with the volume of functional space occupied by species in an assemblage (Villéger *et al.*, 2008). Thus, the most original species (i.e. the most extreme species in the functional space) contribute more to maintain a high level of functional diversity than species having common traits shared by other species. Our projected decline in originality is therefore consistent with the losses of functional diversity that have been reported in response to varied environmental disturbances (Ernst *et al.*, 2006; Flynn *et al.*, 2009; Villéger *et al.*, 2010; Barragan *et al.*, 2011; Gerisch *et al.*, 2012). However, the response of functional diversity to gradients of

disturbance appears not to be unidirectional as others have documented either an increase in functional diversity (Devin *et al.*, 2005; Mendez *et al.*, 2012; Teresa & Casatti, 2012) or bell-shaped responses (intermediate disturbance hypothesis: Biswas & Mallik, 2010), often depending on the metrics used to measure functional diversity (Filippi-Codaccioni *et al.*, 2009). Further studies are therefore needed to better explore and understand the mechanisms and processes underlying such functional modifications induced by global changes.

Here, we have also found that the decrease in both functional indices measured at the assemblage level was related to a combination of biotic and abiotic factors acting locally and regionally. Given that changes in functional indices were derived from changes in the suitability of the habitat for individual species as a result of climate modifications, the relationship between projected functional changes and changes in taxonomic composition (i.e. species turnover) may appear spurious. However, the significance and direction of these relationships were not obvious as they depend on the degree of originality/uniqueness of the species the most affected by climate modifications. In addition, we have highlighted the fact that functional changes were not solely due to biotic modifications, but also varied along environmental (e.g. decrease in originality and uniqueness more pronounced at low elevations) and geographical (e.g. greater declines in originality and uniqueness in northern regions) gradients. These strong spatial patterns in the projected functional changes of fish assemblages in response to climate change may have important consequences for the design of management measures for freshwater ecosystems. Indeed, the functional facet of diversity has recently started to be included alongside taxonomic and phylogenetic diversity when designing systematic conservation priorities for freshwater fish (Strecker *et al.*, 2011). The next step would be to find out whether areas where functional indices are projected to decline the most are also those that would be of major concern in terms of taxonomic diversity and evolutionary perspectives. This would make it possible to optimize the allocation of conservation efforts and help to mitigate the effects of ongoing climate change more effectively.

We have also found that the current variability in the functional originality and functional uniqueness of fish assemblages could seriously decline in response to future climate modifications. Combined with the projected decrease in functional originality and uniqueness, this suggests an increase in functional similarity among stream fish assemblages which will tend to be dominated by species located near the center of the functional space. Other descriptors of the functional niche have also been shown to be likely to become more

similar (i.e. functional homogenization) in response to current global changes (e.g. trait diversity: Buisson & Grenouillet, 2009; community specialization index: Devictor *et al.*, 2008). Although functional homogenization has received much less attention than its taxonomic counterpart over the past decade (Olden, 2006), many recent studies have reported an increasing similarity in the functional structure of communities, which is frequently driven by the replacement of specialist species by generalist species (Lambdon *et al.*, 2008; Winter *et al.*, 2008; Clavero & Brotons, 2010). The projected simultaneous decrease and homogenization of functional indices may alter fish assemblage functioning and subsequently disrupt the ecosystem goods and services provided by freshwater systems. Indeed, having a range of functionally original and/or functionally unique species within assemblages that respond in many different ways to disturbance may actually help to stabilize ecosystem processes as a result of functional niche complementarity (Hooper *et al.*, 2005). Future stream fish assemblages with increased functional redundancy could thus become more vulnerable to large-scale environmental disturbances as a result of a loss of resistance or resilience as they would have synchronized and identical biological responses (Olden *et al.*, 2004; Olden, 2006).

Although species distribution models are now well-established techniques, it is important to keep in mind that they rely on several assumptions (Boulangéat *et al.*, 2012) which may invalidate the forecasted functional changes. Indeed, we have assumed that fish species could reach all environmentally suitable stream reaches in the future and that no barrier would obstruct fish movements. Although France has a large system of canals connecting adjacent watersheds and most studied fish species are not confined to a small number of hydrological basins, this assumption still remains questionable. In addition, by modeling separately the distribution of each species and then aggregating individual predictions, we have not accounted for biotic interactions (Guisan & Thuiller, 2005) that could be important in structuring communities. Lastly, we have assumed that the sole response of fish species to climate modifications would be to shift their ranges. However, fish could also adapt to future climate conditions by modifying their behavior (e.g. thermal refuges, earlier breeding) as it has been reported among other taxonomic groups (Parmesan & Yohe, 2003). Neglecting such adaptive responses may consequently result in overstating functional changes at the assemblage level.

To summarize, our findings illustrate how ongoing climate change could modify the functional structure of stream fish assemblages. The responses of the various

species could drive a decline in the functional diversity of fish assemblages across French streams, paralleling the well-described process of functional homogenization in response to current global changes (Clavel *et al.*, 2011). Our findings also highlight the usefulness of coupling the popular niche-based modeling approach with new functional trait-based approaches that have been identified as promising tools for addressing forthcoming challenges related to global changes (McGill *et al.*, 2006). In spite of their recognized limitations (Guisan & Thuiller, 2005), species distribution models remain the most powerful and easy-to-implement method for assessing the future effects of environmental changes on biodiversity, thus helping to design better conservation measures in anticipation of these effects. Using these models to identify the functional features of the most vulnerable species and assemblages would make it possible to go a step beyond simple taxonomic identification of the most threatened organisms. Research intended to identify particular biological attributes that explain the observed and projected trends in some species in response to climate change has already produced its first promising results (Pöyry *et al.*, 2009; Heikkinen *et al.*, 2010; Angert *et al.*, 2011; Mattila *et al.*, 2011). Lastly, shifts in species distribution may promote the emergence of novel (i.e. no-analog) assemblages which may present enormous conservation and management challenges (Williams & Jackson, 2007; Stralberg *et al.*, 2009; Urban *et al.*, 2012). Although this issue has been recently addressed from a taxonomic perspective, we argue that the functional consequences of novel species assemblages would deserve greater attention in forthcoming research. This would probably contribute to a better understanding of the future of biodiversity in a changing world.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Description of the 13 biological traits used to measure functional originality and uniqueness indices for the 35 stream fish species.

Table S2. Originality, uniqueness, mean probability of occurrence across the 1110 stream reaches for the current climatic conditions (\pm SD) and projected changes of mean probability of occurrence (\pm SD) under B2 and A1Fi climate change scenarios.