

Concomitant impacts of climate change, fragmentation and non-native species have led to reorganization of fish communities since the 1980s

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Funding information

Investissement d'Avenir, Grant/Award Number: ANR-10-LABX-0025 and ANR-10-LABX-41

Editor: Jonathan Belmaker

Abstract

Aim: In response to climate change, species distribution shifts resulting from local extinctions, colonizations and variations in population abundances potentially lead to community-level reorganizations. Here, we assess changes over time in stream fish communities, quantify the extent to which these changes are attributable to population declines or increases and identify their main drivers.

Location: France.

Time period: 1980–2012.

Major taxa studied: Stream fish species.

Methods: We used abundance-monitoring data to quantify changes in composition and uniqueness for 332 stream fish communities between a cold historical period (1980–1993) and a warm contemporary period (2004–2012). Then, we used a model-averaging procedure to test the impacts of factors related to climate, land use and non-native species density and their interacting effects in shaping community reorganization.

Results: We observed biotic homogenization over time in stream fish communities, although some communities experienced differentiation. Changes in composition mainly resulted from population declines and were favoured by an increase in temperature seasonality and in non-native species density. Population declines decreased with fragmentation and changes in non-native species density, whereas population increases were negatively driven by changes in precipitation and positively by fragmentation. Our results provide evidence that environmental changes can interact with other factors (e.g., upstream–downstream, fragmentation intensity) to determine community reorganization.

Main conclusions: In the context of global change, fish assemblage reorganizations mainly result from population declines of species. These reorganizations are spatially structured and driven by both climatic and human-related stressors. Here, we emphasize the need to take into account several components of global change, because the interplay between stressors might play a key role in the ongoing biodiversity changes.

KEYWORDS

alpha diversity, assemblage reorganization, beta diversity, community uniqueness, freshwater fish, global change, temporal changes

1 | INTRODUCTION

Climate change is a key driver of a large number of idiosyncratic species responses (Intergovernmental Panel on Climate Change, 2014). For instance, a change in distribution, generally polewards in latitude and/or upwards in elevation, is a well-known response to ongoing changes (e.g., Perry, Low, Ellis, & Reynolds, 2005). Climate change also leads to population responses, such as demographic variations, which depend on climatic exposure and species sensitivities to those changes (Laidre et al., 2008) and on the abilities of species to adapt locally (e.g., Møller, Rubolini, & Lehikoinen, 2008). These changes in species occurrences (i.e., local extinctions and colonizations) and in species abundances (i.e., population trends) may have significant impacts on the composition of higher organization levels (i.e., communities, food webs and ecosystems), potentially leading to novel assemblages and potentially affecting community dynamics, biodiversity maintenance and ecosystem functioning (Barbet-Massin & Jetz, 2015).

A large number of studies have previously investigated changes in assemblage composition, using various indices describing species richness and taxonomic diversity (Magurran, 2004) or, more recently, integrating trait information across species, such as the species' thermal optima averaged within a local community (e.g., community temperature index; Devictor, Julliard, Couvet, & Jiguet, 2008). It is now well known that changes in community composition are strongly determined by changes in environmental conditions, such as climate warming, change in precipitation or increased atmospheric CO₂ (e.g., Devictor et al., 2008; Walther et al., 2002). However, recent studies have suggested that community shifts were not only attributable to climate change but also depended on non-climatic components of global change, such as land use intensification (e.g., Laliberté et al., 2010) or introductions of non-native species (Chapin et al., 2000). Although the individual impact of each driver is fairly well understood, ecological responses to multiple changes may differ. For example, Mora, Metzger, Rollo, and Myers (2007) found that rotifer population declines were up to 50 times faster when environmental warming, overexploitation and habitat fragmentation were acting together. Finally, the relative contributions of environmental determinants of assemblage dynamics are spatially variable. For instance, Hof, Araújo, Jetz, and Rahbek (2011) showed that main threat to frog diversity was climate change in Africa, whereas it was increased parasitism in Europe.

As a consequence of spatially structured changes in environmental conditions, changes in diversity are unlikely to be homogeneous across space, thus leading to changes in dissimilarity between communities (i.e., beta diversity) over time. Hence, communities may experience either differentiation (increased dissimilarity) or homogenization (decreased dissimilarity). Few studies have found taxonomic differentiation (e.g., Leprieur, Beauchard, Hugué, Grenouillet, & Brosse, 2008), and biotic homogenization seems to be the most common phenomenon (McKinney & Lockwood, 1999). This pattern seems to be strongly linked to the ongoing climate change. For instance, Davey, Chamberlain, Newson, Noble, and Johnston (2012) showed that the homogenization experienced by bird communities was mainly driven

by increased temperatures. However, climate change is not the only driver of community homogenization, and anthropogenic factors also play a key role in shaping assemblage reorganization. For instance, McKinney (2006) highlighted that the biotic homogenization of flora as well as fauna throughout the world was strongly linked with increased urbanization. The introduction of non-native species, largely accepted as a component of human-induced global change (Vitousek, D'Antonio, Loope, Rejmanek, & Westbrooks, 1997), also leads to homogenized ecological communities. For instance, Winter et al. (2009) suggested that the introductions of non-native plants occurring since AD 1500 have induced homogenization of European flora assemblages.

There are a large number of measures associated with the dissimilarity concept (e.g., Faith, Minchin, & Belbin, 1987; Koleff, Gaston, & Lennon, 2003). A recently proposed and appealing approach is the decomposition of the global beta diversity into local contributions to beta diversity (LCBD) of each community (Legendre, 2013; Legendre & De Cáceres, 2013) in order to obtain a comparative indicator of assemblage uniqueness. The LCBD values for individual communities are computed with reference to all communities in a study, with a large LCBD value indicating a community with strongly different composition compared with the average community. Moreover, LCBD values computed for two different systems allow the comparison between these two systems (Legendre & De Cáceres, 2013). By looking at how uniqueness has changed over time, one can assess the effectiveness of conservation policies. Moreover, temporal changes in LCBD can be used to deepen our understanding of the consequences of environmental changes at the community level. However, changes in LCBD do not indicate an absolute change in community structure, rather a relative change, and thus do not allow the underlying mechanisms leading to these observed changes to be identified. In contrast, the temporal beta index (TBI) has been proposed to describe the temporal changes in different communities between two time periods in terms of community composition (Legendre 2015; Legendre & Salvat, 2015). The maximal value is obtained when all species present have been replaced between the two surveys. Moreover, this index can be decomposed into gains and losses of species or individuals depending of the type of data (i.e., occurrences or abundances) and thus highlights the underlying mechanisms of changes. Thus, the simultaneous use of both indices (i.e., change in LCBD and TBI) is complementary, because they both provide information about temporal changes in the community, but whereas one is relative and indicates changes in uniqueness, the other is absolute and provides information about changes in composition.

Here, we used a dataset derived from a long-term programme that monitors stream fish communities across France to investigate changes in diversity over time. Freshwater systems are highly vulnerable to multiple stressors (Jackson, Loewen, Vinebrooke, & Chimimba, 2015), and fish have been suggested to be a good indicator group for multistressor situations (Nôges et al., 2015). In the present study, we aimed at (a) quantifying the changes over time in composition and uniqueness of freshwater fish communities and (b) determining the drivers of these changes and their interplay with spatial structure and habitat fragmentation. Specifically, we used the LCBD and TBI indices,

computed over > 300 resurveyed communities between a historical (1980–1993) and a contemporary (2004–2012) period. Then, we quantified the effects of climatic and non-climatic factors on temporal changes in LCBD and TBI, while accounting for potential interactions among these drivers.

2 | MATERIAL AND METHODS

2.1 | Community data

Fish community data were taken from the database of the French Office national de l'eau et des milieux aquatiques (Onema) database (available online: www.image.eaufrance.fr), where stream reaches were surveyed at location point following a standard electrofishing protocol during low-flow months (Poulet, Beaulaton, & Dembski, 2011). For small streams, fish were captured by wading, mostly by two-pass removal, whereas for larger rivers, samplings were done by boat and by fractional sampling strategies of the different types of mesohabitat (Poulet et al., 2011). Fish were identified to species level, counted and released. Among all surveyed sites, we selected 332 sites that had been visited during two time periods: a historical, cold period (from 1980 to 1993) and a contemporary, warm period (from 2004 to 2012). When one site was surveyed more than once during one period, we selected the sampling occasion that maximized the time interval between the two periods (mean time interval = 20.45 ± 4.85 years). Abundances data were converted into densities (number of individuals per 100 m²) to avoid bias, because the area of stream sampled differed among sites (mean sampled area = 945 ± 465 m²).

Initially, to describe beta diversity at the national scale, we used pairwise distances computed from the density data between sites for each time period separately. Then, we decomposed the global beta diversity into LCBD indices (Legendre, 2013). In order to quantify changes in spatial beta diversity through time and especially in uniqueness, we computed the differences between contemporary and historical LCBD values. These changes can be computed because LCBD values are basically distances from an average community and are standardized such that the sum is equal to one. This standardization allows the comparison of LCBD values across systems at different spatial locations but also at different temporal periods (Legendre & De Cáceres, 2013). Finally, we estimated temporal changes in community composition using TBI (Legendre, 2015). These computation steps are summarized in Figure 1.

All distance-based measures (beta diversity, LCBD and TBI) were computed from the percentage difference index (Legendre & De Cáceres, 2013), also called the Bray–Curtis dissimilarity in some softwares. This index varies from zero (communities are exactly the same) to one (communities have no shared species). The use of this dissimilarity allowed us to decompose local TBI values into gains and losses. Considering data vectors y_1 and y_2 corresponding to the multispecies observations at times T1 and T2 for a site, a_j is the part of the abundance of species j that is common to the two survey vectors: $a_j = \min(y_{1j}, y_{2j})$ and A is the sum of the a_j values for all species representing the unscaled similarity between two surveys. In addition, b_j is the part of

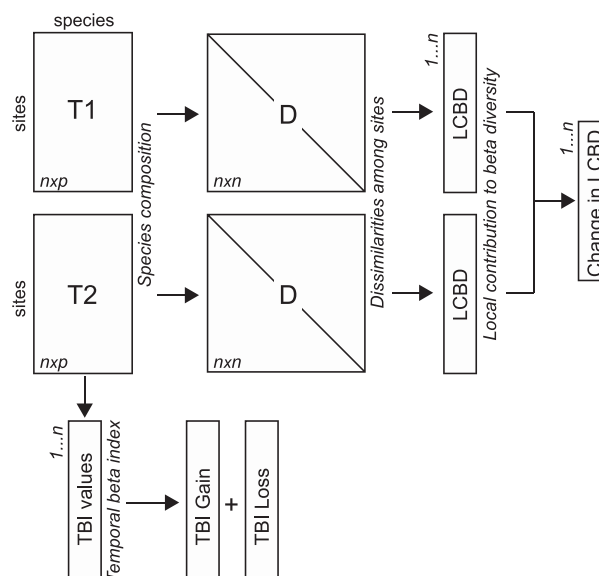


FIGURE 1 Methodological approach comparing community data (n sites \times p species) for two time periods, T1 and T2. From these data, we computed a dissimilarity matrix ($n \times n$ sites) for each time period using the percentage of difference index (also called Bray–Curtis dissimilarity). Based on these two dissimilarity matrices, we calculated the local contribution to beta diversity (LCBD) for each time period, and finally, estimated the change in LCBD as $LCBD_{T2} - LCBD_{T1}$. In addition, from community data and using the percentage of difference index, we computed the temporal beta diversity index (TBI), which we decomposed into gain and loss components. The gain and loss are the sum of gained and lost individuals, respectively, over all species present in the community

the abundance of species j that is higher in survey 1 than in survey 2: $b_j = y_{1j} - y_{2j}$, and B is the sum of the b_j values for all species, being the unscaled sum of species losses between T1 and T2, added over all species. Finally, c_j is the part of the abundance of species j that is higher in survey 2 than in survey 1: $c_j = y_{2j} - y_{1j}$, and C is the sum of the c_j values for all species, that is the unscaled sum of species gains between T1 and T2, added over all species. Thus, the unscaled dissimilarity is represented by $(B + C)$. The values A , B and C are the building elements of the TBI, $TBI = (B + C)/(2A + B + C)$ (for computational details, see Supporting Information Appendix S1). If occurrence data are used, A , B and C correspond to the number of species, whereas if abundance data are used, as in the present study, they correspond to the number of individuals. Moreover, gains (C) and losses (B) can be used raw (as in the present study) but can also be standardized by the observed change, in order to determine the extent to which this change is driven by gains or losses.

2.2 | Determinants of community changes

Daily climatic data (temperatures and precipitation) were provided by Météo France and extracted since 1965 from the high-resolution (8 km \times 8 km grid) SAFRAN (Systèmes d'Analyse Fournissant des Renseignements Adaptés à la Nivologie) atmospheric analysis over France (Le Moigne, 2002). For each site, we calculated the annual

mean temperature, annual temperature seasonality ($100 \times \text{SD}$ of temperatures) and annual precipitation. We thus obtained time series for each sampled site, beginning the year of the first sampling of the community and ending the year of the second sampling of the community (mean duration of climatic time series = 20 ± 5 years). Then we estimated temporal trends in these three climatic variables using generalized least-squares models to account for temporal autocorrelation, with an autocorrelation structure of order one, and expressed as the slope of the linear regression over the period covering the two sampling events (hereafter TEMP, TSEAS and PREC for temporal trends in annual mean temperature, annual temperature seasonality and annual precipitation, respectively).

The French Land Cover database (European Union – SOeS, CORINE Land Cover, 2006) was used to quantify within each hydrographic zone (i.e., SSHYD from BDCARTAGE) the changes in the percentage of five land-use categories between 1990 and 2006 (i.e., urbanized land, cropland, forest and grassland, wetland and water surfaces). We then performed a principal components analysis (PCA) on these five variables and kept the first two axes as synthetic variables accounting for 45 and 22% of the total variance, respectively. The first axis (LC1) was positively correlated with temporal trends of forest and grasslands and with temporal trends of water surfaces and negatively correlated with change in cropland. The second axis (LC2) represented temporal changes in urban areas and wetlands.

Stream width and distance from the source were extracted from the theoretical hydrographic network (RHT) of streams in France (Pella, Lejot, Lamouroux, & Snelder, 2012) for each site. Then we performed a PCA of these two variables and kept the first axis, which explained 96.6% of the variance, and represented the upstream–downstream gradient (G; negative values corresponded to the most upstream sites and positive values to the most downstream sites).

Fragmentation (FRAG) was quantified from the referential of flow obstacles (ROE; www.sandre.eaufrance.fr/atlascatalogue), which provides flow barriers at the national scale, as the number of dams 10 m high in each hydrographic zone. This metric allowed us to assess the cumulative effect of dams at a large scale on diversity changes. Indeed, Cooper, Infante, Wehrly, Wang, and Brenden (2016) highlighted the need to consider the cumulative effect of dams along the stream network, because few studies have investigated the impact of several dams simultaneously (but see Cumming, 2004; Slawski, Veraldi, Pescitelli, & Pauers, 2008).

Finally, we quantified the changes in the densities of non-native fish species as the difference in non-native densities (NNDs) between the two study periods for each site.

2.3 | Statistical analyses

To test whether there has been a biotic homogenization of fish communities in France since the 1990s, we compared beta diversity values (i.e., distance matrix for each time period) using a paired Wilcoxon test. We also compared \log_{10} -transformed LCBD indices during the cold and warm periods using a linear model.

We used a model-averaging procedure to assess the effects of multiple drivers on temporal changes in LCBD, TBI and their decomposition into gains and losses. We considered all possible multi-predictor models ($n = 1,335$) that included five terms or fewer to avoid overfitting (Knappe & de Valpine, 2011), including first-order interactions only with the two temporally static variables (i.e., G and FRAG). We used a Box–Cox transformation for each response variable, previously standardized ($\lambda_{\text{DELTA LCBD}} = 1$; $\lambda_{\text{TBI}} = 1.5$; $\lambda_{\text{GAIN}} = 2$; $\lambda_{\text{LOSS}} = -1.5$); the predictors were transformed to z-scores to standardize their slope coefficients (β), and pseudo- R^2 values were calculated for each model following Nagelkerke (1991). We then evaluated the candidate models using the Akaike information criterion weights of each model that we summed from the largest to the smallest until the sum was equal to .95. From the selected models, we calculated model-averaged slope coefficients using the Akaike weights of each model (Burnham & Anderson, 2002) and associated 95% confidence intervals (Johnson & Omland, 2004). For all models, we checked visually that residuals were normally distributed.

We did all the analyses by considering first all species co-occurring in the community and then by considering only native species in order to assess the impact of non-native species on patterns of community changes and drivers of these patterns.

Data from BDCARTAGE, CORINE Landcover database, RHT and ROE were extracted with QGIS 2.6.1, and all statistical analyses were performed with R 3.1.3 (R Core Team 2017). The LCBD have been computed with the R software *beta.div*, available in the online appendix of Legendre and De Cáceres (2013), and TBI have been computed with the R software *TBI* (Legendre, 2015). The Box–Cox transformation was applied with the *MASS* R package, and the model-averaging procedure has been conducted with *MuMIn* and *AICcmodavg* R packages.

3 | RESULTS

3.1 | Changes in beta diversity

Beta diversity significantly decreased during the warm period ($p < .001$). By comparing historical and contemporary LCBD values, we found that some communities experienced differentiation (i.e., historical value higher than contemporary), whereas homogenization occurred in others (i.e., historical value lower than contemporary; Supporting Information Appendix S2). No spatial pattern was apparent in temporal changes in LCBD (Figure 2a). The TBIs were high (mean = $.62 \pm .23$), and these changes were homogeneously distributed across France (Figure 2b). The observed temporal changes in community composition were mainly attributable to losses of individuals (mean relative importance of loss = .65), for which we did not observed any spatial structure (Figure 2c).

3.2 | Drivers of community changes

The model-averaging procedure selected 595 models to explain changes in LCBD, for which pseudo- R^2 ranged between .006 and .06. For TBI, gains and losses, 287, 59 and 487 models were selected,

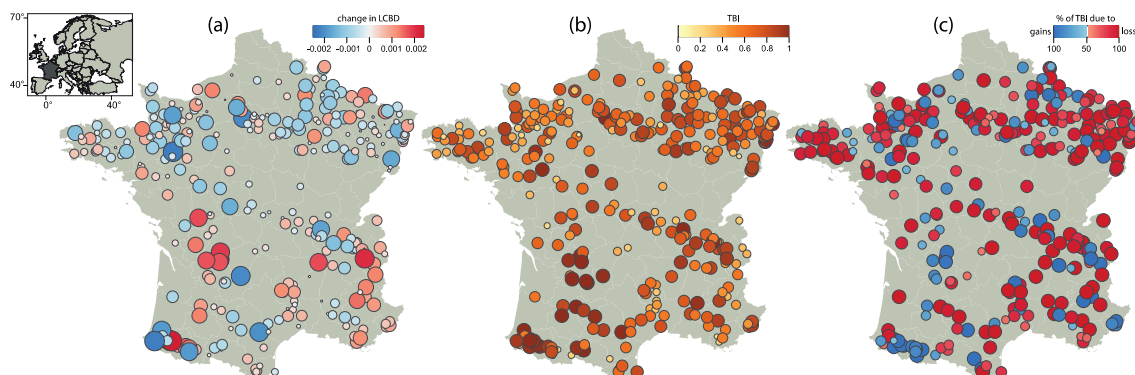


FIGURE 2 Map of (a) the temporal changes in local contributions to beta diversity (LCBD), (b) the temporal beta index values (TBI) and (c) the main process leading to change in composition [either losses (red) or gains (blue)]

respectively. Pseudo- R^2 varied between .11 and .15 for TBI, between .001 and .06 for gains and between .03 and .08 for losses.

Temporal changes in LCBD were mainly driven by both NND and TSEAS (Figure 3a).

Temporal beta index values were positively correlated with temporal changes in temperature seasonality (TSEAS) and with the position along the upstream–downstream gradient (G; Figure 3c). Moreover, the effect of change in non-native species density depended on the position along the upstream–downstream gradient ($NND \times G$; i.e., stronger impact of non-native species density change was observed downstream; Figure 3c). After decomposing TBI into gains and losses, gains were negatively correlated with temporal changes in precipitation (PREC), and the interaction between precipitation change and number of dams was significantly positive ($FRAG \times PREC$; Figure 3e), revealing that the increase in gains was associated with increased precipitation for sites located in highly fragmented sub-basins (Figure 4a). Species losses were positively correlated with the position along the upstream–downstream gradient (G) and negatively with the number of dams (FRAG). Moreover, the interaction between the position along the gradient (G) and changes in non-native species density (NND) was significantly positive (Figure 3g), revealing that declines in population and change in non-native densities were negatively correlated in headwaters, whereas the relationship reversed (i.e., positive relationship) downstream (Figure 4b).

3.3 | Impact of non-native species

We found strong correlations between indices based on all species and on native species only (R^2 ranged between .80 and .87). Although spatial patterns were consistent, we found differences in the drivers explaining the indices computed on complete or native communities. Overall, non-native species blurred the relationships observed when only native species were considered. For instance, we found that the interaction between changes in non-native species (NND) and fragmentation influencing TBI values was significant only when considering native species (Figure 3d). Similar results were observed for the influence of temperature seasonality changes (TSEAS) on gains. We also found a change in the direction of effect of PREC on gains (Figure 3f) depending on whether non-native species were considered

in the analysis. Finally, changes in non-native species densities (NND) had a significant negative influence on losses when considering native assemblages. The interaction between NND and the upstream–downstream gradient ($NND \times G$) was significantly positive (Figure 3h). This result revealed that the relationship between losses and NND was positive downstream but negative in headwaters (Figure 4c).

4 | DISCUSSION

Our results revealed an influence of the upstream–downstream gradient structuring community changes. We also found that climate change played a key role in affecting fish communities. In particular, temperature seasonality and precipitation had an influence on temporal changes in uniqueness of assemblages (LCBD) and in their composition (TBI). Human-related changes, such as fragmentation and changes in non-native species densities, were also correlated with changes in community composition. We found that these anthropogenic threats were not homogeneous across space and acted in concert with other climatic variables, leading to an important reorganization of freshwater fish communities over time. Finally, although we found relationships between some components of global changes and community changes over time, the goodness-of-fit of our models did not allow the use of these models in order to predict community responses to future changes in environmental conditions. This low goodness-of-fit could have been improved by the integration of changes over time in more environmental factors, such as pollutants and discharges. This finding highlights the importance of taking into account the multifactorial aspect of global changes in order to assess community responses.

4.1 | Spatial structure of the changes in assemblage composition

Population declines since 1980 were stronger in downstream sections of rivers, where greater changes in community composition occurred. Two non-exclusive hypotheses could explain this pattern. First, the most important changes observed downstream could result from the fact that downstream sections are the most impacted by human activities (Meybeck, 1998), and this anthropogenic effect promotes rearrangement of assemblages (McKinney, 2006). Second, upstream

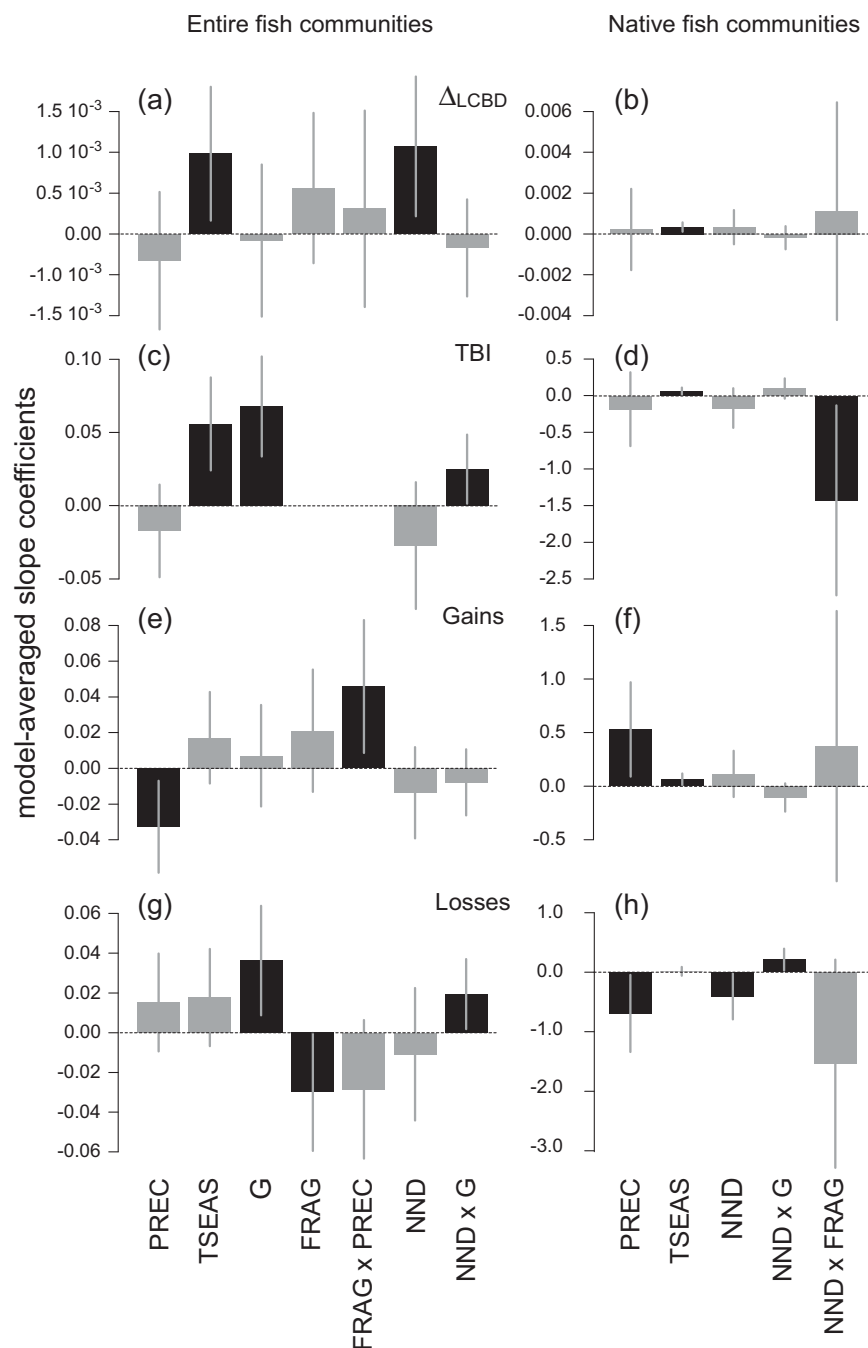


FIGURE 3 Results of model averaging for (a and b) changes in local contributions to beta diversity, (c and d) TBI, and components of TBI corresponding to (e and f) gains and (g and h) losses of individuals between the cold and the warm period. Error bars represent 95% confidence intervals of the standardized mean slope coefficients, computed from the selected model. Results are presented for indices based on all species (a, c, e, g) and on native species only (b, d, f, h). Only significant coefficients (in black) for at least one response variable are shown (FRAG = number of dams; G = upstream–downstream gradient; NND = change in non-native species densities; PREC = change in annual precipitation; TBI = temporal beta index; TSEAS = change in temperature seasonality)

sections are less reachable than downstream portions because of the higher number of obstacles acting as geographical barriers between stream sections (Rahel, 2007). Given that the spatial structure of fish communities changes according to the upstream–downstream gradient, it thus appears that downstream sections of rivers are the most susceptible to being affected by global change. Thus, it appears that the downstream parts of streams need to receive priority attention in terms of

conservation, in order to reconcile human interests in river exploitation with freshwater diversity sustainability (Dudgeon et al., 2006).

4.2 | Impact of climate change on community changes

During the most recent decades, rivers in France mainly experienced an increase in mean temperature and seasonality as well as changes in

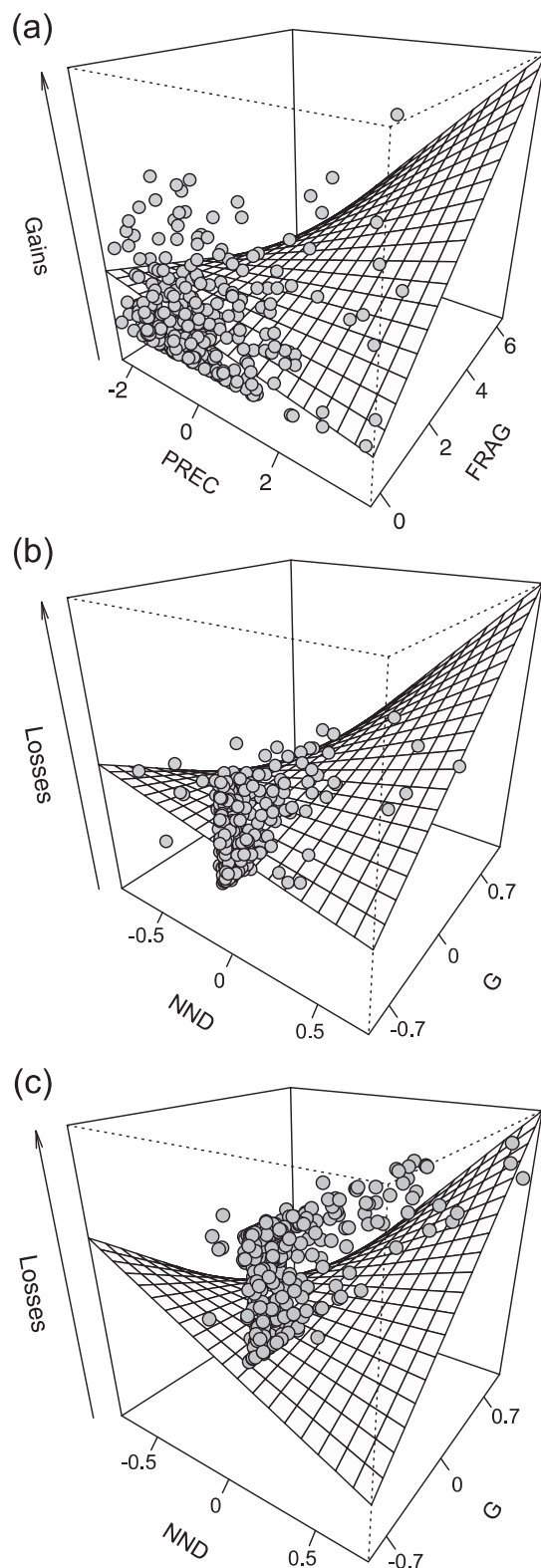


FIGURE 4 Role of the strongest interactions between predictors (codes as in Figure 3) in predicting the relative importance of (a) total gains, (b) total losses and (c) native species losses. The three-dimensional surfaces were drawn from model-averaged slope coefficients, and each point represents a community (FRAG = number of dams; G = upstream–downstream gradient; NND = change in non-native species densities; PREC = change in annual precipitation)

precipitation (Supporting Information Appendix S3). Although most previous studies addressing observed assemblage changes have primarily focused on mean temperature changes (e.g., Chen, Hill, Ohlemüller, Roy, & Thomas, 2011), in our study the temporal trends in mean temperature did not explain any of the changes observed in fish community structure. In particular, trends in temperature seasonality were a better predictor than trends in mean temperature regarding changes in community composition. Changes in precipitation were also a key climatic factor impacting gains. Overall, these results underpin the importance of taking into account several aspects of the current climate change, because species niche is not defined only according to mean temperature but is multidimensional and thus can include the tolerance to high climate wetness or dryness and the capacity to inhabit habitats experiencing a broad range of temperatures.

4.3 | Impact of human-related change on community changes

Besides climate change, human activities represent a threat to stream communities, which is increasingly important in numerous ways, including habitat degradation and destruction (Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998) and the introduction of non-native species (Rahel, 2007). Our results provided evidence that losses in population abundances were strongly linked with fragmentation. Reservoirs, by softening environmental variability (Leroy-Poff, Olden, Merritt, & Pepin, 2007), may limit population declines. Moreover, Martínez-Abraín and Jiménez (2016) proposed the idea that reservoirs, and more generally natural systems modified by human activities, can act as substitutive habitat to declining populations, permitting them to inhabit in suboptimal habitat conditions and thus limit their decline.

Non-native species are currently considered to be one of the major threats to biodiversity induced by human activities (Vitousek et al., 1997). We found that changes in community composition were mostly related to local declines in population, linked to temporal changes in non-native species density. Headwater assemblages were characterized by an increase in non-native species densities leading to low losses, suggesting that arrivals of new species compensated to some extent for the loss of native species. On the contrary, downstream reaches presented the opposite patterns, with an increase in the abundance of non-native species linked to population declines. Previous studies in other taxa have demonstrated that an increase in non-native species abundances could reduce the abundance of native species (e.g., Gurevitch & Padilla, 2004), suggesting that native species could be experiencing higher competition and/or predation pressure in invaded systems. A hypothesis to explain the decline of native species in lower reaches is that downstream communities might be under higher competition pressure than headwaters (Carvalho & Tejerina-Garro, 2014). This competition might be exacerbated by the introductions of new species, which are likely to out-compete native species and could ultimately lead to a decrease in native species densities. To assess whether non-native species actually out-compete native freshwater fish species, and thus understand the mechanisms underlying population declines, further studies need to address the functional similarity between non-

native and native species. High functional similarity between native and non-native species leads to high competition pressure among species, making assemblages more vulnerable to future colonization events (Olden, Poff, Douglas, Douglas, & Fausch, 2004).

We found that increased density of non-native species in fish communities increased the uniqueness (LCBD) of colonized communities (i.e., differentiation). Although this result seems to contradict previous studies about the influence of non-native species on homogenization, this relationship between non-native species density changes and uniqueness could be attributable to the fact that non-native species, at the beginning of their invasion, would be rare and thus would temporarily increase beta diversity. This hypothesis is in agreement with Toussaint, Beauchard, Oberdorff, Brosse, and Vill  ger (2014), who suggested that differentiation (i.e., larger LCBD) could precede homogenization (i.e., smaller LCBD) as introduced species spread and gradually invade all communities. In the present study, LCBD indices helped us to measure the effect of invasive species on beta diversity. The impoverishment of diversity because of decreased uniqueness in community composition, leading to a decrease in functional redundancy, can ultimately result in decreased resistance and resilience of communities (Folke et al., 2004).

Finally, although we found strong positive correlations between indices based on all species and on native species only, we found that non-native species blurred the environmental influences on community structure. For instance, in the present study, we highlighted that the effect of changes in precipitation on community was reversed depending on whether non-native species were taken into account. Although native communities were strongly and positively influenced by changes in precipitation, non-native species blurred this relationship, which became negative and weak when all species were considered. This result suggests that the increase in native population abundances was stronger when communities experienced more important rainfall. On the contrary, the increase in non-native abundances was more important in systems that became dryer over time. Previous studies have suggested that non-native species could reverse the influence of abiotic factors on community structure (e.g., Carboni, Thuillier, Izzi, & Acosta, 2010) or blur the influence of these determinants, because they are usually not distributed according to some environmental gradients but rather according to the intensity of human activity (Blanchet et al., 2009; Leprieur et al., 2008). Overall, this finding suggests that non-native and native species did not respond in the same way to environmental changes. Understanding the response of the entire community, including non-native species, is still essential, because these species are part of the system and thus influence its functioning. But our findings suggest that the environmental factors favouring non-native species are not necessarily the same as the ones favouring native species, and this needs to be considered when conservation policies are elaborated.

4.4 | Interplay between stressors and environmental structure

Stressors and their effects on community are unlikely to be uniform across space. Here, we found that the impact of changes in non-native

species density on fish population abundance changes is structured along the upstream–downstream gradient, highlighting that sections of rivers that are most susceptible to change in structure are located downstream. The stronger influence of non-native species observed downstream is probably attributable to the fact that these species are generally warm-water species adapted to large river conditions and favoured by downstream conditions (e.g., *Silurus glanis*, *Micropterus salmoides*, *Cyprinus carpio*). Dalkvist, Sibly, and Topping (2013) found a similar influence of landscape structure (e.g., unmanaged areas, distance from the source of the disturbance) on the impact of disturbance on rodent population dynamics.

Although current knowledge about stressors on assemblage dynamics offers a comprehensive view of their individual impacts on diversity, the need to focus our research on understanding the joint impacts of these stressors now seems obvious (C  t  , Darling, & Brown, 2016; Ormerod, Dobson, Hildrew, & Townsend, 2010). The increasing number of studies highlighting the effects of multiple stressors that act synergistically underlines the need to take into account multiple current threats and their interaction on diversity. Interactions between these threats have been found previously for different systems. For instance, for Canadian freshwater systems Schindler (2001) reported interactions between a variety of stressors, among which were temperatures and human-related pressures, such as pollutants, non-native species introductions, overexploitation and habitat alteration. Here, our results suggest an interaction between changes in precipitation over time and habitat fragmentation on community changes. Fragmentation, when precipitation increases, is linked to increases in local population abundances. Reservoirs, providing new habitats, may allow downstream species to colonize upstream sections of streams (e.g., Rahel & Olden, 2008). Indeed, these new habitats may be characterized by a large amount of unexploited resources by the present species, facilitating colonization by new species and/or allowing occurring species to increase in abundances. Moreover, fragmentation can segregate communities and thus limits dispersion and, ultimately, leads to short-term and transient higher densities known as the crowding effect (Saunders, Hobbs, & Margues, 1991).

5 | CONCLUSION

In the present study, we demonstrated that the temporal evolution of community composition and uniqueness, quantified by means of two recently proposed indices (Legendre & De C  ceres, 2013; Legendre & Salvat, 2015), is driven by several components of the ongoing global change. Moreover, we found that the impacts of environmental changes may vary across space and are not independent from each other, highlighting the need to take into account several stressors and their interplay. Further studies should focus on understanding the impact of these taxonomic changes with a functional approach and aim to characterize communities by their functional composition and uniqueness. Thus, understanding of the effect of global change might be improved by the integration of the functional facet of biodiversity.

ACKNOWLEDGMENTS

Évolution et Diversité Biologique lab was supported by 'Investissement d'Avenir' grants (Centre d'Étude de la Biodiversité Amazonienne, ref. ANR-10-LABX-0025; TULIP, ref. ANR-10-LABX-41). We are indebted to the *Office national de l'eau et des milieux aquatiques* (Onema) for providing fish data, and we thank the many fieldworkers who contributed to the fish records. We would like to thank the two anonymous reviewers for comments that greatly improve the manuscript.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Kuczynski L, Legendre P, Grenouillet G. Concomitant impacts of climate change, fragmentation and non-native species have led to reorganization of fish communities since the 1980s. *Global Ecol Biogeogr*. 2017;00:1–10. <https://doi.org/10.1111/geb.12690>