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Poleward shift in large-river fish communities detected with a novel meta-analysis framework

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Abstract

1. Ongoing global changes are causing major ecological shifts worldwide. Biological trends need to be assessed over long periods of time to better understand past and current community responses.

2. The present study developed a methodological framework for meta-analyses to be conducted that account for the temporal and spatial autocorrelation of observational data. We provided the R code for processing this framework, which enables temporal trends to be tested through the analysis of long-term, spatially structured datasets. Taking both types of autocorrelation into account resulted in more conservative but arguably more reliable statistical outcomes.

3. This meta-analysis framework was then applied to investigate long-term trends in environmental and fish-community time series in multiple stations in large French rivers over the past 4 decades.

4. General significant upward and downward trends were highlighted in water temperature and flow discharge, respectively, over the study period. Concomitantly, the density of numerous species increased, resulting in large increases in both species richness (about + 50%) and total fish abundance (approximately four-fold), but with no significant trend in species evenness. Strong changes in species composition were observed during the study period, with an overall upward trend in the relative abundance of newcomers (i.e. species not sampled during the first years of the survey), while the trend in relative abundance of non-native species was non-significant. Moreover, the strongest signal underlying community changes was replacement of northern by southern species.

5. This study showed major changes in fish density and community structure in large rivers over the past 40 years and represents, to our knowledge, one of the first large-scale actual demonstrations (i.e. based on observations rather than predictions) of an overall poleward shift of freshwater fish communities in response to ongoing global changes.

KEYWORDS
global changes, long-term surveys, meta-analysis, poleward shift, spatio-temporal autocorrelation

1 | INTRODUCTION

Terrestrial, marine, and freshwater realms are facing increasing anthropogenic threats worldwide, leading to global ecological shifts and severe decline in numerous aspects of biodiversity that are likely to be exacerbated in coming decades (Butchart et al., 2010; Scheffers et al., 2016; Tilman et al., 2017). Assessment and quantification of biological trends over long time-periods are of paramount importance to better understand past and current ecosystem responses to global changes, and to eventually enable upcoming changes to be anticipated (Bowler et al., 2017; García Molinos, Poloczanska, Olden, Lawler, & Burrows, 2018). For this purpose, analysis of long-term monitoring programmes is required (Heino, Virkkala, & Toivonen, 2009; Magurran et al., 2010; Peters, 2010).

The regulatory hydrobiological monitoring conducted in the vicinity of French nuclear power plants (NPPs) since their construction represents a remarkable survey of freshwater biodiversity in large rivers over the last 20–40 years. Undeniably, rivers are among the most threatened ecosystems, undergoing decline in biodiversity far greater than terrestrial and marine ecosystems (Dudgeon et al., 2006; Malmqvist & Rundle, 2002). Among freshwater environments, large rivers are the focus of outstanding economic and societal issues as well as complex and vast challenges regarding conservation of their biodiversity (Counihan et al., 2018; Tockner, Uehlinger, & Robinson, 2009; Vörösmarty et al., 2010), and further research is required to better identify and characterise the impact of global changes on these ecosystems.

In a previous study, Daufresne and Boët (2007) compiled a dataset from the French NPP monitoring programme involving long-term data for fish assemblages in large rivers from 1980 to 2003. Their analyses, among the first in freshwater environments, identified and characterised significant changes in the composition and structure of fish communities related to ongoing environmental change. As ectothermic organisms whose dispersal is limited within hydrographic networks, fish are highly sensitive and vulnerable to fluctuations and changes in water temperature, and are thus suitable biological models to examine the impact of climate change on aquatic biota (Ficke, Myrick, & Hansen, 2007; Olden et al., 2010).

Observed and expected responses of fish to global changes have mostly focused on the effect of changed climatic conditions, from individual to community level (e.g. Ficke et al., 2007; Heino et al., 2009; Olden et al., 2010). Based on observations or predictive models, the most commonly examined, and partially interrelated, responses of fish to climate change include: (1) shifts in species' spatial distributions, especially in relation to thermal affinity (i.e. expected differences between cold-, cool-, and warm-water species; Buisson, Thuiller, Lek, Lim, & Grenouillet, 2008; Comte, Buisson, Daufresne, & Grenouillet, 2013; Hickling, Roy, Hill, Fox, & Thomas, 2006) and biogeographical origin (i.e. expected differences between native and non-native species; Britton, Cucherousset, Davies, Godard, & Copp, 2010; Rahel &

Olden, 2008); (2) changes in community structure and composition (e.g. Daufresne & Boët, 2007; Daufresne, Roger, Capra, & Lamouroux, 2004; Poulet, Beaulaton, & Dembski, 2011); (3) taxonomic and functional community homogenisation (e.g. Buisson, Grenouillet, Villéger, Canal, & Laffaille, 2013; Villéger, Blanchet, Beauchard, Oberdorff, & Brosse, 2011); (4) plasticity or limitations of physiological adaptation (e.g. Payne et al., 2016; Sandblom et al., 2016); (5) phenological changes (e.g. earlier or later fish migration or reproduction period; Crozier, Scheuerell, & Zabel, 2011; Tao et al., 2018); and (6) changes in size structure at community level (i.e. reduced body size; Daufresne, Lengfellner, & Sommer, 2009; Gardner, Peters, Kearney, Joseph, & Heinsohn, 2011). In addition, Comte et al. (2013) showed that the number of articles reporting observed effects of climate change on freshwater fish distributions was much lower than the number of studies of forecasted effects (<15%).

The question of whether local evidence is generalisable and representative of phenomena observed at a broader scale has always been and remains central to most ecological studies (Peters, 2010; Wiens, 1989). One approach to test for general patterns in biodiversity is to perform a meta-analysis of local biological responses observed in different geographical regions (Brown et al., 2011; Cardinale, Gonzalez, Allington, & Loreau, 2018; García Molinos et al., 2018; Gurevitch, Koricheva, Nakagawa, & Stewart, 2018). Generally speaking, a meta-analysis is a systematic review of relevant studies or observations supported by statistical methods that aims to aggregate and contrast their related outcomes (effect sizes) (Gurevitch et al., 2018; Viechtbauer, 2010). Meta-analyses can also be used to aggregate estimates of the strength of the relationship between two variables measured concurrently, possibly at different locations (Koricheva, Gurevitch, & Mengersen, 2013; Viechtbauer, 2010). Meta-analyses assessing temporal trends at multiple locations typically raise the question of temporal and spatial autocorrelation: i.e. non-independence between pairs of observations at given distances in time and space, respectively (Brown et al., 2011; Gurevitch & Hedges, 1999; Koricheva et al., 2013). Indeed, it has become widely recognised that spatial and temporal autocorrelation may result in violation of the basic statistical assumption of independence between observations, leading to incorrect ecological inferences (Brown et al., 2011; Legendre, 1993; Pyper & Peterman, 1998; Roberts et al., 2017). On the one hand, corrected trend analyses taking account of temporal autocorrelation have been developed (e.g. Hamed & Rao, 1998; Pyper & Peterman, 1998), and their statistical outcomes can be subsequently used in meta-analyses (e.g. Bowler et al., 2017; Daufresne & Boët, 2007; Daufresne et al., 2009). The problem of spatial autocorrelation, on the other hand, has largely been ignored in meta-analyses, mainly because of a lack of methods able to deal with the spatial structure of observations or sampling protocols through corrective approaches (Brown et al., 2011). Nevertheless, both spatial and temporal autocorrelation has to be addressed in order to reliably characterise general, unbiased patterns of changes in biodiversity (Brown et al., 2011; Roberts et al., 2017). This is especially critical when studying dendritic ecological

systems such as river networks. Spatial constraints to organism displacements strengthen the spatial dependence of observational data, due to increased interactions between species and habitat restrictions (Campbell Grant, Lowe, & Fagan, 2007; Grenouillet et al., 2008). This results in greater spatial autocorrelation between examined ecological processes.

In this context, and >10 years after the study by Daufresne and Boët (2007), we decided to re-analyse the French NPP fish dataset, in order to update previously identified trends and highlight any subsequent changes. The dataset was updated by 12 additional years and spatially extended to 35 versus 24 sampling stations. The study aimed to: (1) develop a methodological framework allowing a meta-analysis of long-term time series while accounting for temporal and

spatial autocorrelation inherent to many ecological datasets; (2) examine environmental and biological trends in large river ecosystems over the past 4 decades; and (3) characterise recent changes in fish communities in comparison with previously identified trends.

2 | MATERIALS AND METHODS

2.1 | Data

We used data from the hydrobiological monitoring programme of 11 NPPs operated by Electricité de France and located along five large French rivers (Loire, Meuse, Rhône, Seine, and Vienne rivers; Figure 1). Near the NPPs, all these rivers can be regarded as large European rivers
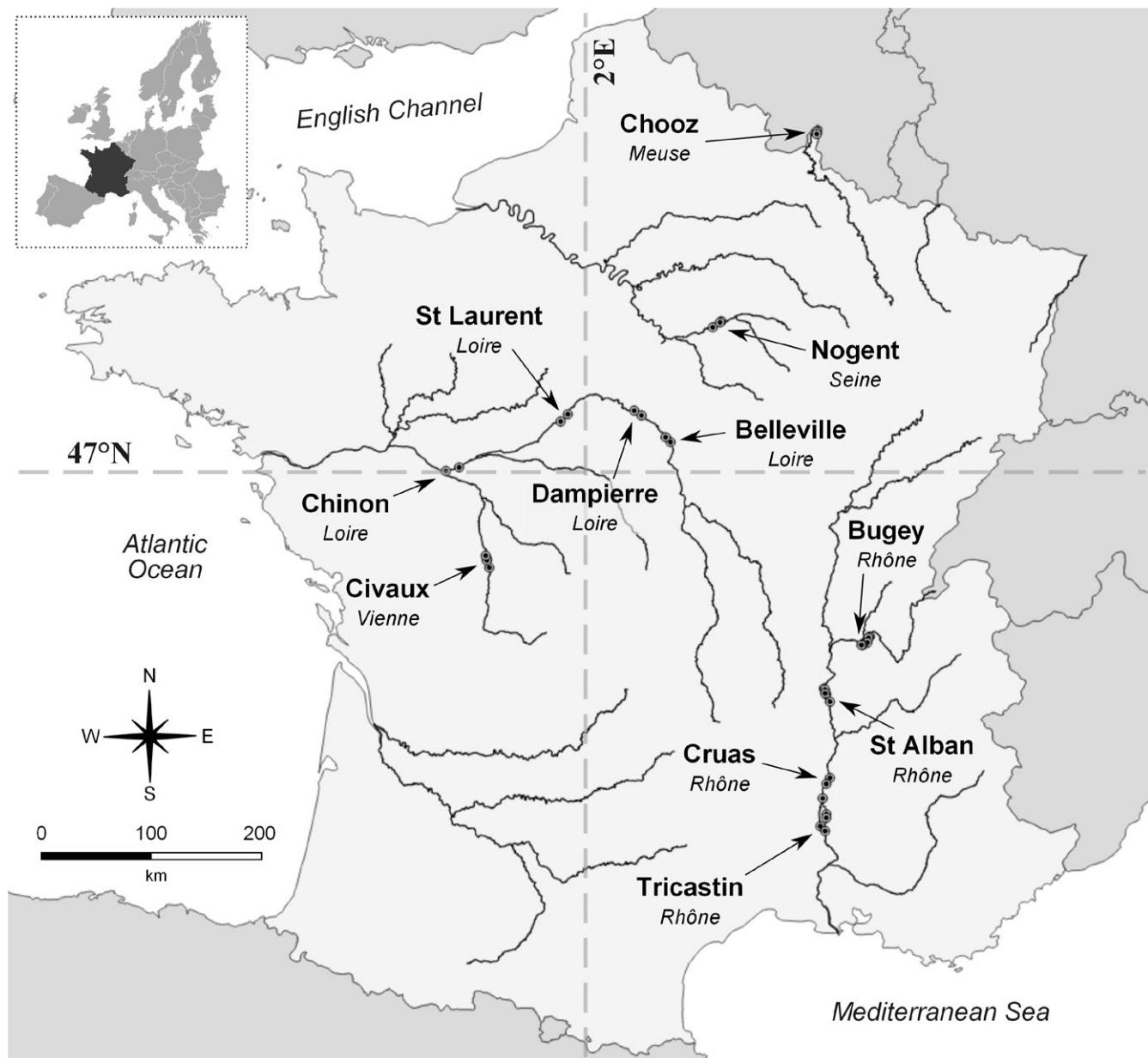
FIGURE 1 Location of the 11 study sites (i.e. nuclear power plants) and 35 stations. All sites are located within France

TABLE 1 Description of the study sites and time-series

Study site	River	Sampling period	Latitude (°N)	Upstream drainage area (km²)	Number of sampling stations	Number of samples per year
Belleville	Loire	1989–2015	47.5	34,800	2	1
Bugey	Rhône	1979–2015	45.8	15,800	7	4
Chinon	Loire	1988–2015	47.2	60,000	2	1
Chooz	Meuse	1989–2015	50.1	10,400	2	1
Civaux	Vienne	1996–2015	46.4	5,600	4	1
Cruas	Rhône	1983–2015	44.6	70,700	2	4
Dampierre	Loire	1997–2015	47.7	36,000	2	1
Nogent	Seine	1986–2015	48.5	8,900	3	2
St Alban	Rhône	1985–2015	45.3	51,500	4	4
St Laurent	Loire	1995–2015	47.7	38,300	2	1
Tricastin	Rhône	1982–2015	44.3	72,000	5	4

(Tockner et al., 2009), with average annual discharge ranging from 80 to >1,500 m³/s and average wetted width ranging from 60 to 600 m (for the Seine River at Nogent and the Rhône River at Cruas, respectively).

We compiled hourly water temperature and discharge data recorded by Electricité de France just upstream of each of the 11 NPPs over the study period. To investigate long-term changes in these two major environmental parameters, the average temperature during the reproduction period of most cyprinid species (from 1 April to 30 June, according to Daufresne & Boët, 2007) and average discharge were calculated annually for each NPP site. These absolute annual values were then standardised by the mean value over the entire study period to obtain annual anomaly values for comparison between sites.

Long-term fish assemblage data from 35 sampling stations were analysed, consisting of at least one station located upstream of each NPP (control sampling station) and one downstream (sampling station potentially disturbed by thermal discharge; Figure 1; Table 1). These 35 stations were sampled 1–4 times a year using standardised electrofishing protocols, by boat, mostly along riverbanks where sampling efficiency is commonly the highest. The corresponding time series covered periods of 19–37 years, all until 2015 (Table 1). Fish data were obtained either by point abundance sampling (Persat & Copp, 1990) or by continuous sampling (Daufresne & Boët, 2007). Following Grenouillet, Hugueny, Carrel, Olivier, and Pont (2001) and Daufresne and Boët (2007), species abundance was expressed as catch per unit effort (CPUE: i.e. the number of individuals of a given species sampled per 20 min of fishing) and the equivalence previously found between point abundance and continuous sampling (i.e. 20 sampling points correspond to 20 min of fishing) was used to calculate species CPUEs for point abundance sampling exercises. For each species at each station, CPUEs were averaged (for stations with several sampling exercises per year) over the biological year, defined as 1 July to 30 June of the next calendar year, in the light of hatching dates for most cyprinid species in large rivers (Daufresne & Boët, 2007; Daufresne et al., 2004). Six anadromous

migratory species (*Alosa alosa, Alosa fallax fallax, Alosa fallax rhodanensis, Lampetra fluviatilis, Liza ramada,* and *Petromyzon marinus*) out of the 46 different species present in the dataset were excluded from the following analyses because the sampling techniques used and the location of the sampling stations were not relevant to the assessment of interannual variability of such species. Consequently, the final dataset was made up of the CPUEs of 40 different species sampled during a total of 987 station × biological year combinations (hereinafter, *station-years*).

Next, a set of biological variables computed from this dataset was used to test for changes in the structure, composition and diversity of fish communities over the study period.

First, species CPUEs were used to study trends in the abundance of each species separately and to explore underlying patterns of change in fish communities, as recommended by Brown et al. (2011). To ensure reliable and representative results, only species occurring in sufficient number at a sufficient number of stations (i.e. average species CPUE >1 per biological year at >4 different stations; *n* = 21 species) were considered.

Second, community metrics defined below were computed on the basis of the CPUEs of the 40 species present in the dataset (including rare species). For each station-year, we calculated total abundance (i.e. the sum of CPUEs of all species present), species richness (i.e. number of species present) and Pielou's evenness index (Pielou, 1966). Next, the CPUE proportions of non-native and non-local species were calculated for each station-year as the ratio between the sum of the CPUEs of all non-native or all non-local species, respectively, and the total CPUE. As recommended by Cardinale et al. (2018), this allows us to go further in characterising changes in species composition within communities. According to Keith, Persat, Feunteun, and Allardi (2011) and Maire, Laffaille, Maire, and Buisson (2017), 10 of the 40 species were identified as non-native at the scale of the French hydrographic network (Supporting Information Table S1). To calculate the proportion of non-local species CPUEs, stations were pooled by site (i.e. NPP) and species not sampled in

the first 5 biological years of monitoring were classified as non-local for the stations of the site in question. Unlike non-native species, the list of non-local species was thus site-specific. Finally, we also calculated the CPUE proportions of northern, intermediate and southern species for each station-year. To classify the species between these three categories, we first calculated the relative position x of the study station in the European geographical range of each species (Equation 1; Daufresne & Boët, 2007; Daufresne et al., 2004).

$$x = (L_{sta} - L_{inf}) / (L_{sup} - L_{sta}) \qquad (1)$$

where L_{sta}, L_{inf} and L_{sup} are respectively the latitude (°N) of the station, and the northern and southern limits of the species' geographical range as documented in Bruslé and Quignard (2013) and Keith et al. (2011). Then, for each station, the one-third and two-thirds percentiles of the values of x for all the species observed at least once in the given time series were calculated. Species belonging to the first, second, and third tier of x values were classified as, respectively, northern, intermediate, and southern species for the station

in question. The lists of northern, intermediate, and southern species were thus station-specific.

2.2 | Data analyses

To test for temporal trends in the environmental and biological variables common to the different time series, we performed a meta-analysis of Mann–Kendall trend statistics (S) computed at each station between each variable and biological year (Daufresne & Boët, 2007; Koricheva et al., 2013). This non-parametric method is used to assess statistically whether there is a general monotonic upward or downward trend in the variable of interest over time, without this necessarily being linear. Following Hamed and Rao (1998) and Pyper and Peterman (1998), variances of S, here denoted as $Var(S)$, were corrected for temporal autocorrelation prior to meta-analysis. To account for the spatial autocorrelation between sampling stations inherent to our dataset, we used a random-effects model for the meta-analysis, where random effects are allowed to be spatially correlated according to a Gaussian correlation structure (Cressie,
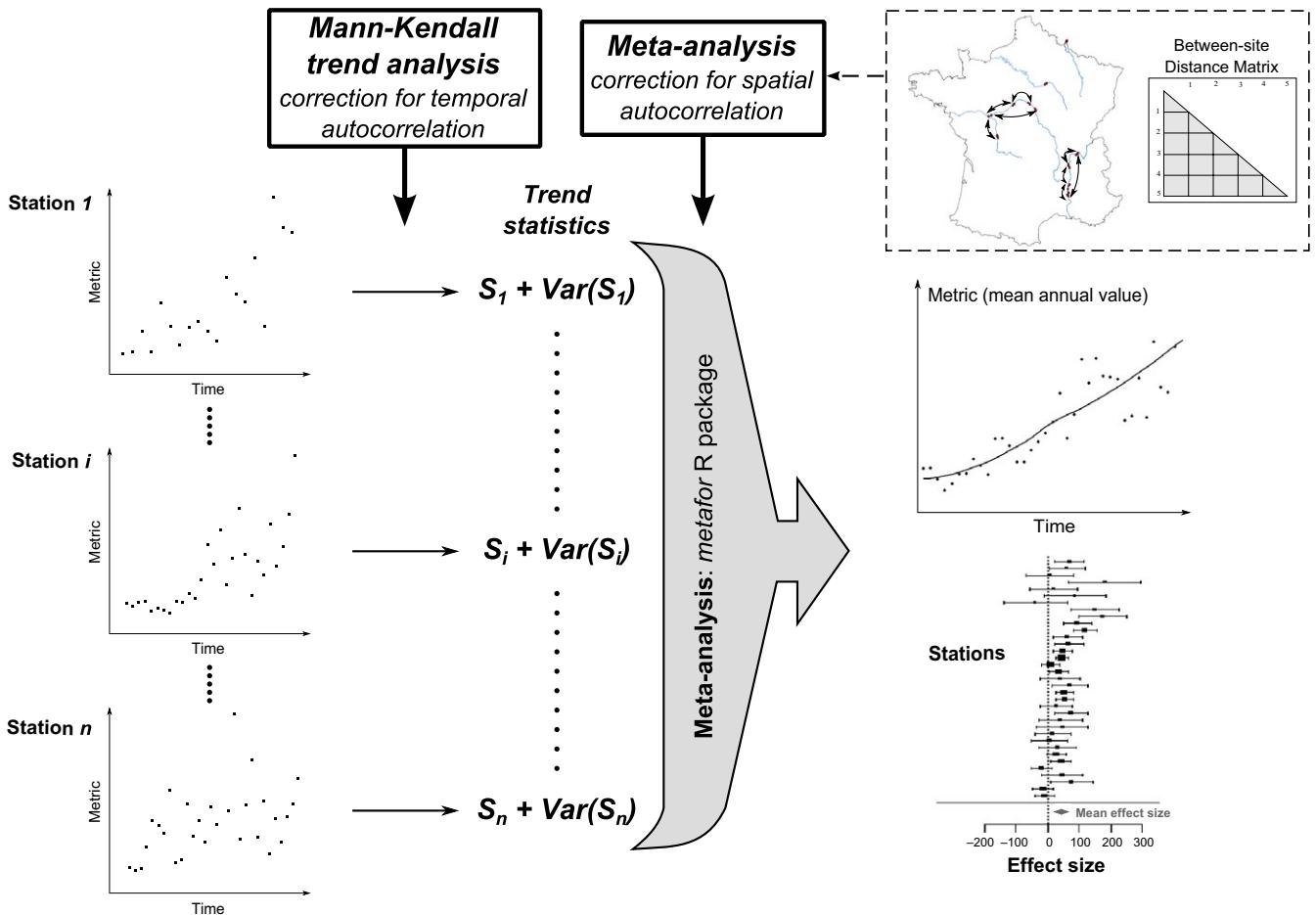
FIGURE 2 Schematic diagram of the trend meta-analysis framework. From left to right: change in the metric studied over time at each station, from which are extracted the Mann–Kendall trend statistics S_i and their associated variance $Var(S_i)$; the meta-analysis is then performed on the trend statistics S_i, taking into account both the associated variance and the spatial structure of the data through the between-site distance matrix (top-right panel); finally, the outputs of this methodological framework consist of an effect size for each station and a mean effect size (plus associated confidence intervals). For illustrative purposes, an optional representation of the change in metric mean value over time and a LOESS fitting curve is also provided

1993). For this, we first calculated the distances along the river network between each pair of stations before assembling them into a 35 × 35 distance matrix M_{dist} (min = 1 river-km; max = 423 river-km). For stations not connected through the river network (i.e. located in different catchments), a high distance value of 10,000 river-km was arbitrarily chosen. A sensitivity analysis indicated a negligible effect of this value within one order of magnitude (i.e. 1,000–10,000 river-km) on the results of the meta-analyses. The random-effects model is then given by $S_i = \mu + u_i + \varepsilon_i$, where S_i is the observed value of the Mann–Kendall trend statistic for the station i, μ is the average true outcome, u_i is a random effect to allow for heterogeneity and spatial correlation in the underlying true outcomes, and ε_i is the sampling error of S_i with known variance given by $Var(S_i)$. The random effects $u_1,...,u_n$ (with n = the number of study stations) were assumed to follow a multivariate normal distribution with a mean of zero and a variance-covariance matrix M_{vc} computed using Equation 2 (Cressie, 1993).

$$M_{vc} = \tau^2 \times \exp\left[-\left(\frac{M_{dist}}{\theta}\right)^2\right]$$ (2)

where τ^2 denotes the amount of heterogeneity in the underlying true outcomes and θ is the spatial correlation parameter for the Gaussian correlation structure. We varied the parameter θ between 1 and 1,000 to determine the value of θ that maximised the log-likelihood of the meta-analysis. The variance–covariance matrix obtained with this selected θ value was used as an input variance–covariance matrix of the random effects in the *rma.mv* function of the R software (R Development Core Team, 2017) *metafor* package (Viechtbauer, 2010). Estimates of μ and τ^2 were obtained using REML estimation with the *rma.mv* function. A synthesis of the trend meta-analysis framework developed in this study is provided in Figure 2, and the R code for processing the framework is provided in Supporting Information Appendix S1.

We applied this meta-analysis framework to identify trends in time series of flow discharge, water temperature, species CPUE, and community metrics previously described. In addition, we tested whether the trends in community metrics differed depending on the position of the station relative to the NPP (i.e. downstream or upstream), by adding this parameter as a factor in the meta-analyses.

3 | RESULTS

A total of 923,418 individual fish (equivalent to 265,683 CPUEs) of 40 different species were sampled during the whole monitoring period. This represented an average of 26,383 ± 12,738 (mean ± standard deviation) individuals and 30 ± 2 species per station.

Trend mean effect size (TMES) of annual mean discharge anomalies (i.e. mean annual discharge divided by mean discharge over the period 1980–2015) highlighted significantly decreasing values of water discharge over the study period (TMES ± SE = −113.0 ± 28.8; p < 0.0001; Figure 3). This trend represented a decrease of −21.9 m^3/s per decade (median among the 11 sites) corresponding to about −6% of the local interannual discharge per decade. Mean water temperature anomalies during the reproduction period (i.e. mean temperature from April to June each year minus the mean temperature from April to June over the period 1977–2015) significantly increased over the same period (TMES ± SE = 279.0 ± 65.6; p < 0.0001) (Figure 3). This trend corresponded to an increase of + 0.79°C per decade (median among the 11 sites).

Trend mean effect size of species CPUEs were computed separately for the 21 species satisfying our selection criteria (Figure 4). Over the study period, abundance significantly decreased for two species and significantly increased for 11. Trends in CPUE were not significant for the other eight species.

The meta-analyses of trend effect sizes of community metrics revealed significant upward trends in total fish abundance (TMES ± SE = 99.5 ± 21.7; p < 0.0001) and species richness (TMES ± SE = 54.0 ± 26.7; p = 0.043) but no significant overall trend in species evenness (TMES ± SE = −11.8 ± 35.0; p = 0.74) (Figure 5; Figure S1a). The mean number of species increased by about 50% over the study period (from an average *ca.* 12 species sampled in the 1980s
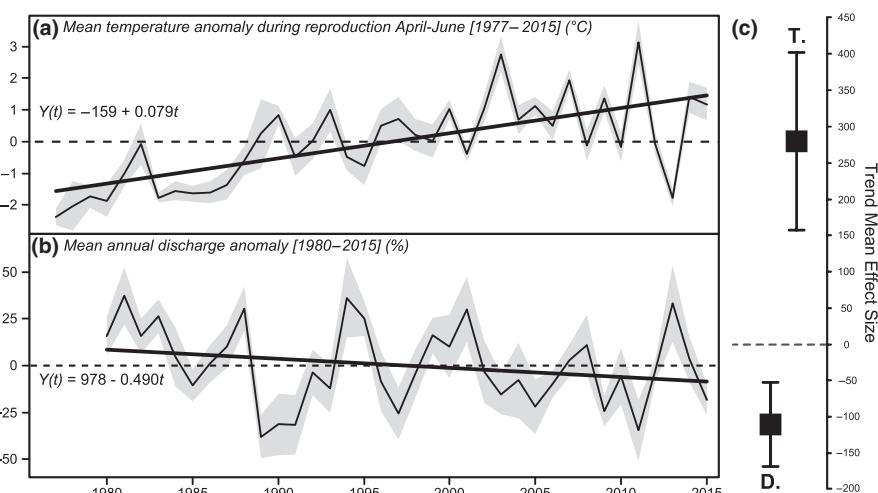
FIGURE 3 Mean annual anomalies of (a) water temperature during the reproduction period and (b) discharge calculated between the 11 sites (± standard deviation; grey intervals). Linear trend equations are also shown. (c) Associated trend mean effect size and 95% confidence intervals for discharge (D.) and water temperature (T.)
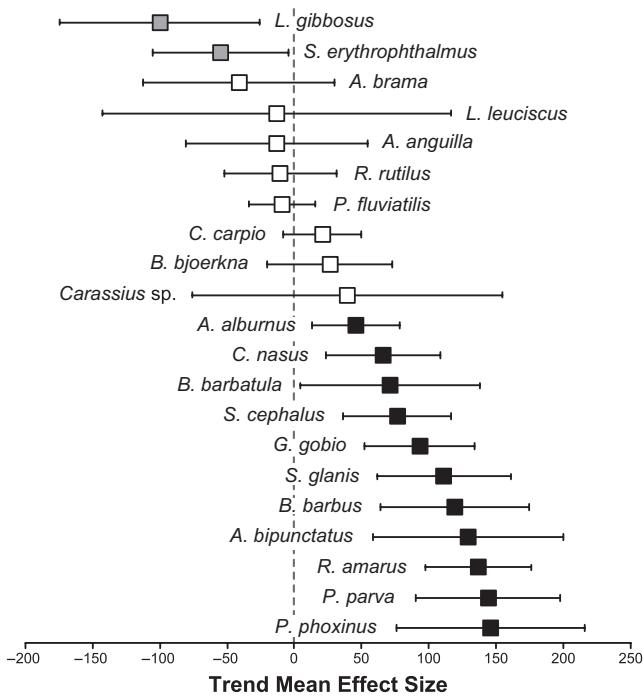
FIGURE 4 Trend mean effect sizes of species catch per unit effort (number of individuals per 20 min fishing) and their 95% confidence intervals for the 21 selected species. If the confidence interval did not intersect the 0 value (vertical dashed line), the trend was significant (upward trend: black squares; downward trend: grey squares) and otherwise non-significant (white squares). See Table S1 for the link between the scientific and common names of species
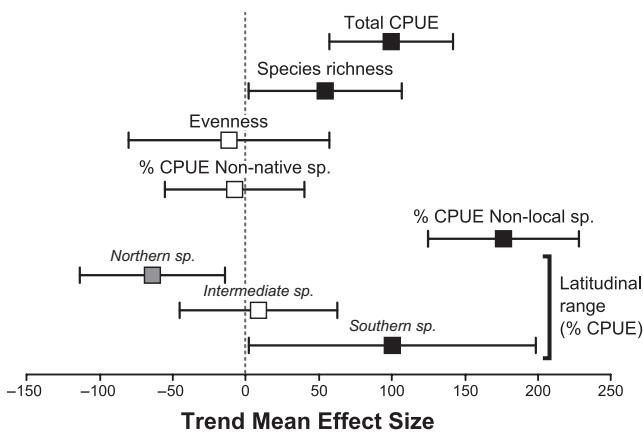
FIGURE 5 Trend mean effect size of community metrics and their 95% confidence intervals. If the confidence interval did not intersect the 0 value (vertical dashed line), the trend was significant (upward trend: black squares; downward trend: grey squares) and otherwise non-significant (white squares). sp.: species; CPUE: catch per unit effort (number of individuals per 20 min fishing)

to *ca.* 18 in the 2010s; Figure 6a); over the same period, average cumulative abundance increased approximately four-fold (from an average 100 individuals per 20 min fishing in the 1980s to >400 in the 2010s; Figure 6b). While the overall trend in the relative abundance of non-native species was not significant (TMES ± SE = −7.5 ± 24.4;

$p = 0.76$; Figure 5; Supporting Information Figure S1b), there was a strong significant upward overall trend in relative abundance of non-local species (TMES ± SE = 176.6 ± 26.4; $p < 0.0001$; Figures 5 and 6c). Regarding general trends related to species latitudinal range, changes in CPUE proportions of intermediate species were not significant (TMES ± SE = 8.7 ± 27.6; $p = 0.75$), while the CPUE proportions of northern and southern species decreased (TMES ± SE = −63.8 ± 25.5; $p = 0.012$) and increased significantly (TMES ± SE = 99.9 ± 50.1; $p = 0.046$), respectively (Figures 5 and 6d,e,f). Adding the position of the station relative to the NPP (i.e. upstream or downstream) as a factor in the meta-analyses revealed no significant different trends in community metrics between upstream and downstream stations (all $p > 0.05$).
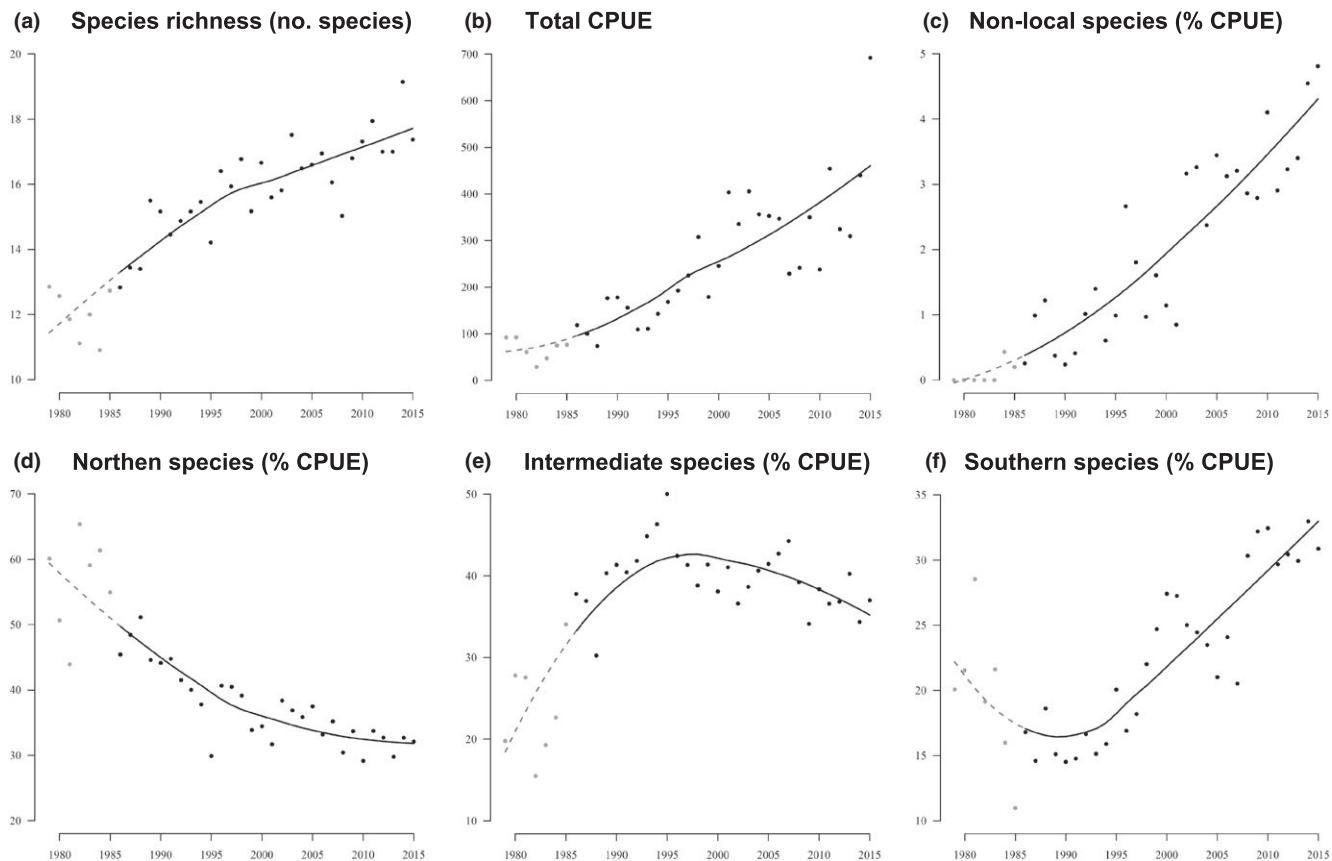
To better understand the changes in communities observed at each site, we compared the species sampled at least once during the first 5 versus the last 5 biological years of the time series grouped by site (i.e. NPP) (Figure 7; Supporting Information Table S2). For all sites except for Civaux on the Vienne River, the number of newcomer species exceeded the number of species no longer present.

4 | DISCUSSION

4.1 | General long-term changes and comparison with previously identified trends

Large rivers have been undergoing multiple and profound environmental changes with direct and indirect, and possibly interacting effects on their biodiversity (Vörösmarty et al., 2010; Zajicek, Radinger, & Wolter, 2018). Long-term data provide valuable opportunities to better understand the effects of cumulative stressors (Counihan et al., 2018) or large-scale restoration measures (Daufresne et al., 2015; Lamouroux & Olivier, 2015) on aquatic biodiversity at spatial and temporal scales relevant to the effective management of these complex river ecosystems.

The present study identified concomitant large-scale trends in environmental features (i.e. upward and downward trends in water temperature and discharge, respectively) and in the structure and composition of fish communities over the past 4 decades. Compared to the previous study by Daufresne and Boët (2007), general increases in fish total abundance, species richness and relative abundance of southern species were similarly observed. Additionally, analyses identified a significant general upward trend in the relative abundance of non-local species (i.e. species not present during the first 5 years of monitoring) but not in the relative abundance of nationally non-native species. While the analyses by Daufresne and Boët (2007) focused on southern species, we were also able to demonstrate a significant general downward trend in the relative abundance of northern species, whereas the general trend in intermediate species was nonsignificant. Given the quite low community changes associated with non-local and non-native species (<5 and 7% of total abundance on average across the study stations, respectively), it seems that the role of *new* species in the observed trends was almost

(a)   Species richness (no. species)   **(b)   Total CPUE**   **(c)   Non-local species (% CPUE)**

(d)   Northen species (% CPUE)   **(e)   Intermediate species (% CPUE)**   **(f)   Southern species (% CPUE)**

FIGURE 6 Temporal changes in community metrics. The points represent the metric's annual mean calculated for all stations available each biological year (e.g. *n* = 7 in 1979, *n* = 35 from 1997 to 2015). Curves were fitted using a LOESS smoothing procedure. The first 7 years (1979–1985) are represented in grey because of the poorer representativeness of the average value for this period, since only stations on the Rhône River were available before 1986 (Table 1). CPUE: catch per unit effort (number of individuals per 20 min fishing). See Figure 5 for the associated trend mean statistics
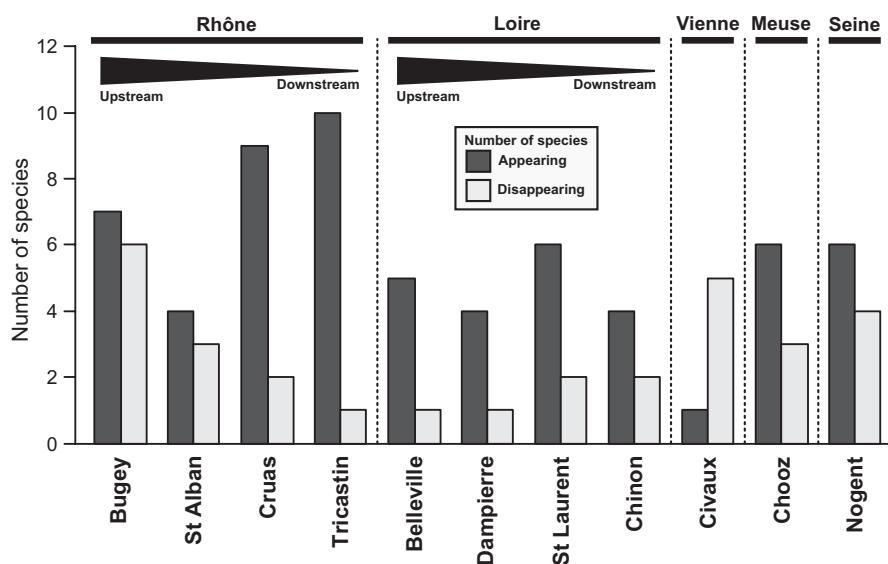
FIGURE 7 Number of species appearing (newcomer) and disappearing (no longer present) between the first 5 and last 5 biological years of each time series grouped by site (i.e. nuclear power plant). See Table S2 for the detailed list of the species concerned for each site

negligible. Therefore, it can be concluded that changes over the past 4 decades mainly involved native species that were always present locally but that showed either increase (southern species) or decrease (northern species) in relative density. No temporal trend was found for discharge on the day of sampling, indicating that the biological trends identified were not biased by changes in sampling efficiency related to changes in river stage over the study period.

Although the present study is based on similar data and methodologies, several changes and improvements were made to the study by Daufresne and Boët (2007): the studied time-series were extended by 12 years, the number of stations and study sites was increased by 11 and 4, respectively, and two additional large rivers were included (Vienne and Meuse rivers). As both spatial and temporal autocorrelations were taken into account in the meta-analyses, the data and methodology were more reliable and representative of a broader biogeographical context than in the study by Daufresne and Boët (2007). In particular, correction for spatial and temporal autocorrelation inherent in the dataset resulted in more conservative but more trustworthy tests (Brown et al., 2011; Pyper & Peterman, 1998). Therefore, applying the present meta-analysis framework brings a greater confidence in the results and trends identified compared to previously developed approaches. The price to pay for an increase in robustness (i.e. lower type-I error, or false positives) was a potential decrease in power (i.e. increase in type-II error, or false negatives). For instance, the absence of a significant trend in species evenness contrasted with decreased evenness previously reported (Daufresne & Boët, 2007). This pattern could either be a false positive finding by the study of Daufresne and Boët (2007) or a false negative finding in the present study.

Our results regarding separate CPUE trends at species level were very consistent with those of Poulet et al. (2011), who analysed trends in fish density on a larger scale (i.e. 590 stations distributed over the whole French river network, including many streams other than large rivers) but with shorter and older time series (i.e. 12 years on average, the most recent data dating from 2009). Indeed, all 11 species identified here as showing significant upward trends in CPUE also showed significantly increasing densities according to Poulet et al. (2011). Results were more contrasted between our study and that of Poulet et al. (2011) for species with downward or non-significant CPUE trends, although the species involved were those with the smallest density changes. Given these common species-level patterns in the two studies, we can be quite confident of the representativeness of our results even if extrapolated to a wider geographical scale.

We did not find any significant effect of NPPs on long-term trends in community metrics. This result was consistent with previous studies underlining marginal effects of NPPs on fish communities, probably due to the tenuous and local influence of thermal effluents on water temperature and the capacity of fish to easily flee from artificially warmed areas (Daufresne & Boët, 2007; Daufresne et al., 2004). Although some studies seemed to corroborate this finding for other taxa such as phytoplankton (Larroudé, Massei, Reyes-Marchant, Delattre, & Humbert, 2013) or macroinvertebrates (Floury, Usseglio-Polatera, Ferreol, Delattre, & Souchon, 2013), the present results apply only to interannual variations in fish at community level and do not necessarily imply absence of effects at other biological scales (population or individual) or on other, less mobile organisms.

Methodologically, and as the first aim of the study, we attempted to provide an objective method to account for the spatial and temporal structures of observational data in meta-analyses. The R code provided in Supporting Information Appendix S1 can be readily used to perform corrected temporal and spatial meta-analyses in a wide range of applications, including fields other than ecology. The present meta-analysis framework can also be adapted to other spatial correlation structures (by defining another kind of mathematical transformation for the distance matrix). Moreover, spatially structured estimates other than trend statistics can be used in this meta-analysis framework to test for effects shared between different locations or conditions. The application of such a meta-analysis framework is particularly relevant considering that large time series datasets are becoming more and more publicly available (e.g. the BioTIME dataset, Dornelas et al., 2018).

4.2 | Change in species composition and poleward shift of fish communities in large rivers

The observed overall increases in species richness and total abundance are consistent with the underlying trends at species level, which highlighted how numerous species experienced an increase in density over the study period. Similar relationships between trends at species and community levels were previously observed or predicted for freshwater fish in France (Buisson et al., 2008; Daufresne & Boët, 2007; Poulet et al., 2011) and also for other taxa in similar riverine systems (e.g. macroinvertebrates; Floury et al., 2013). The trend in species richness of around +50% over the past 4 decades was even of the same order of magnitude as the average predicted increase, ranging from +50% to +68% by 2080, based on models of the future distribution of 30 fish species in French rivers (Buisson et al., 2008). Consistent with the present results, the same study also predicted that many species would benefit from a future warmer climate resulting in substantial changes in species composition within communities. However, the observed increases in density and species richness are probably limited to the studied taxa (i.e. freshwater fish) in the studied environments (i.e. large rivers), and the impact of global changes on other animal or plant communities is likely to be detrimental (Bowler et al., 2017; Butchart et al., 2010; Scheffers et al., 2016).

For most sites, the number of newcomer species greatly exceeded the number of species no longer found in recent years. This result contrasts with that reported by Daufresne and Boët (2007), who found only a few species that had appeared or disappeared from the surveys between the first 5 and last 5 years of monitoring (i.e. a maximum of three newcomer and one disappearing species compared to the 10 newcomer and six disappearing species we found at Tricastin and Bugey, respectively). This suggests that the pictures of these ecosystems provided by the two studies, conducted about 10 years apart, differed more between the 1980s and the 2010s (present study) than between the 1980s and the 2000s (Daufresne & Boët, 2007), probably due to notable recent changes. In addition, the patterns of appearance and disappearance of species along the upstream–downstream gradient differed between the Rhône and Loire rivers in the present study. While the numbers of species appearing or disappearing was more or less comparable at the different

sites on the Loire River, the number of newcomer species and of species no longer present tended to respectively increase and decrease from upstream to downstream on the Rhône River. We see three main possible, although not mutually exclusive, explanations for these differences. Firstly, some trends in non-climatic anthropogenic factors, such as water quality, may differ between the two catchments, the Rhône River being a highly regulated river flowing through large cities whereas the Loire River has kept a more natural hydrological regime coupled, for instance, with a strong downward trend in phosphorous concentrations (Floury et al., 2013). Secondly, the fish time series for the Rhône River were longer than for the Loire River: respectively, 34 and 24 years on average. It is possible that biological changes associated with some secondary climatic trends or events, such as the global 1980s regime shift (Reid et al., 2016), were not recorded in the shortest time series, while some more recent secondary trends or events, such as the early 2000s warming slowdown (Fyfe et al., 2016), may have been more influential in these shortest time series. These secondary climatic events may also explain other features of the observed trends, such as the changes in slope seen after the first 7 biological years, for which only data on the Rhône River were available. Thirdly, these catchments have contrasted geographical orientations with: (1) superimposed altitudinal and latitudinal gradients for the Rhône River (i.e. north–south catchment orientation), which probably facilitated colonisation by downstream thermophilic species (Buisson et al., 2008; Daufresne et al., 2004); and (2) almost identical latitudes for the Loire River stations (i.e. east–west catchment orientation), which may have prevented aquatic species from tracking their climatic niche (Ficke et al., 2007).

It is now recognised that large-scale biological changes are not always observed locally (Batt, Morley, Selden, Tingley, & Pinsky, 2017; Cardinale et al., 2018); results such as the present, showing increases in species richness and abundance, may seem counterintuitive given that a worldwide decline in biodiversity is unequivocal (Butchart et al., 2010; Scheffers et al., 2016). However, apparent increases in biodiversity may actually be only transient and probably mask profound underlying changes in species identity and community structure and composition. As emphasised by Brown et al. (2011), if changes at species level are ignored, the impact of environmental change on biological communities may be mischaracterised or underestimated. Furthermore, observed species assemblages always comprise a mixture of species favoured by the current climate and species that were favoured by previous climatic conditions (Buisson et al., 2008; Daufresne & Boët, 2007); warming does not necessarily induce a sharp decline in the density of the latter species, which may persist for some time under modified climatic conditions, leading to an increase in species richness (Batt et al., 2017; Hiddink & ter Hofstede, 2008; Walther et al., 2002). However, this phenomenon can only be transient when the climate is still warming (Daufresne & Boët, 2007; Walther et al., 2002), and the striking question is: how long will this unstable equilibrium last? Daufresne and Boët (2007) hypothesised that sudden shifts in the structure of fish communities in large rivers were likely to occur within a few years after their study, as certain ecological thresholds were potentially near to being

crossed. The present results show that such a tipping point in fish community dynamics has still not been reached 12 years later. This finding strongly supports the need to continue monitoring these rivers, update the present trend analyses, and look carefully for recent changes in slope in the updated trends.

Most studies of the impact of global change, and particularly climate change, on biodiversity have attempted to identify species or groups of species that either benefited from these changes or experienced widespread decline (Buisson et al., 2013; Comte et al., 2013). One widely held idea is that rising temperatures are expected to favour non-native over native species, particularly in aquatic environments, as the former generally show broader thermal tolerance and reproduction capacity than the latter (Britton et al., 2010; Rahel & Olden, 2008). Some recent studies hypothesised, and even demonstrated, that replacement of native by non-native species has strongly contributed to biotic homogenisation from regional to global scales (Cardinale et al., 2018; Counihan et al., 2018; Kuczynski, Legendre, & Grenouillet, 2018). The present study found that several non-native species experienced strong increases in density, which may have contributed to the observed biological changes through biotic interactions such as transmission of parasites (e.g. topmouth gudgeon *Pseudorasbora parva*; Gozlan, St-Hilaire, Feist, Martin, & Kent, 2005) or increased predation (e.g. European catfish *Silurus glanis*; Boulêtreau et al., 2018), but no significant temporal trend was detected at community level for non-native species. While a quarter of the species studied are classified as non-native to the French hydrographic network, their cumulative abundance has remained quite low, accounting for only 3–6% of total fish abundance on average over the study period. Actually, nine out of the 11 species showing an overall upward trend in density were nationally native. However, there was a general upward trend in non-local species, ranging from <1 to >17% of total abundance, depending on the station, when averaged over the last 5 years of each time series, highlighting the fact that this trend was supported by native rather than non-native species. Interestingly, the species with the strongest downward trend in density, the pumpkinseed *Lepomis gibbosus*, is a non-native species at the French national scale, with low affinity for high temperatures at a certain stage of its life cycle (Daufresne & Boët, 2007; Keith et al., 2011). This finding supports the hypothesis formulated by Rahel and Olden (2008) that some non-native cold-water species may be unable to persist within their invaded range under warmer climatic conditions.

Another characteristic of species that is likely to contribute to the observed community trends is their thermal affinity and requirements (Brown et al., 2011; Daufresne & Boët, 2007). However, we did not directly investigate temporal trends in fish thermal guilds, as the existing classifications do not systematically coincide with each other (e.g. Daufresne & Boët, 2007; Souchon & Tissot, 2012; Teletchea et al., 2009). This highlights the complexity of characterising the physiological responses of fish species to water temperature, which can vary depending on their life stage (Poulet et al., 2011; Souchon & Tissot, 2012).

To further explore large-scale biodiversity patterns related to climate niche tracking (i.e. the process by which species remain in

their preferred climatic conditions over time by following limiting variables through geographical space; García Molinos et al., 2018), Brown et al. (2011) recommended examining proxies based on the spatial distribution of species rather than their thermal requirements. More specifically, they pointed out that classifying species into three groups (northern, intermediate, or southern) according to the position of the observation within their distributional range makes it possible to interpret changes in observed distributions in terms of species' biogeographical affinities. For instance, Hiddink and ter Hofstede (2008), studying marine fish communities of the North Sea, highlighted a strong upward trend in species richness over a 22-year period, which they linked to an overall increase in the spatial range of southern species while the opposite trend was observed for northern species. However, such poleward shifts have been observed mainly in the oceans, with little evidence in freshwater environments, especially at community level and at large scales (Pecl et al., 2017; but see Hickling et al., 2006). The present meta-analysis framework was able to show that the relative cumulative abundance of southern fish species increased significantly over the study period, to the detriment of northern species while the relative abundance of intermediate species remained quite stable.

The present study examined trends in water temperature and discharge as potential key drivers of changes in the composition of freshwater fish communities (Booth, Bond, & Macreadie, 2011). However, other environmental changes are likely to have occurred locally over the same period and may also have contributed to the observed biological changes (Malmqvist & Rundle, 2002; Zajicek et al., 2018). Apart from hydroclimatic trends, changes in water quality, and especially in phosphorous concentrations, following improvements in wastewater treatment probably had considerable influence on aquatic populations (Durance & Ormerod, 2009; Floury, Usseglio-Polatera, Delattre, & Souchon, 2017). Several studies demonstrated that improved water quality has ecological consequences for various organisms all along the trophic network, such as phytoplankton (Larroudé et al., 2013) and macroinvertebrates (Floury et al., 2013) in the Loire River or fish in various large rivers in the U.S.A. (Counihan et al., 2018) and probably also in France (Poulet et al., 2011). Nonetheless, if ecological responses across many regions, assessed for example by meta-analysis, are shown to be similar and generally tending in the same direction (e.g. poleward shift in species distributions), then it can be confidently presumed that global drivers such as climate change are involved (García Molinos et al., 2018). Taken together, these findings highlight the central role of climate change in the observed trends and its profound implications for freshwater ecosystems. Our greatest concern is certainly that such changes in natural systems, expected over the long-term, can in fact already be ascertained from the analysis of relatively recent observational data.

4.3 | Underlying ecological mechanisms and future research directions

Many studies have pointed out that future work on the impact of climate change should include the ecological attributes of species in order to investigate the mechanisms underlying ecological responses (e.g. Buisson et al., 2013; Comte et al., 2013; Floury et al., 2017). According to Angert et al. (2011) and Ficke et al. (2007), the magnitude of changes in spatial distribution may be expected to be related to three characteristics of species: (1) dispersal capacity; (2) intrinsic rate of increase, measured through reproductive life-history traits such as generation time and offspring number; and (3) specialisation in given environmental conditions, assessed by metrics such as range of diet or of thermal tolerance. In addition, these characteristics are also likely to evolve depending on the species' adaptive potential (Comte & Olden, 2017). In this context, at least two hypotheses deserve to be explored using the present dataset.

The first is that opposing responses to warmer climate can be expected for species with r and K reproductive strategies: the former are characterised by high energy investment in reproduction and are often categorised as opportunists, whereas the latter are long-lived species investing more heavily in fewer offspring and are generally specialists (Nichols, Conley, Batt, & Tipton, 1976). Under changing climate, r strategists (e.g. common bleak *Alburnus alburnus*, schneider *Alburnoides bipunctatus*, gudgeon *Gobio gobio*; Keith et al., 2011; Teletchea et al., 2009) may more easily track their climatic niche, having higher reproduction capacity than K strategists such as the pumpkinseed, which may be less able to face rapid environmental change.

The second hypothesis is related to fish body size. Several studies have now provided evidence that reduced body size is the third universal ecological response to global warming in aquatic systems, besides species range shifts towards higher altitudes and latitudes and phenological changes (Daufresne et al., 2009; Gardner et al., 2011). For instance, in addition to the opposing trends in southern and northern fish species, Hiddink and ter Hofstede (2008) linked the increase in species richness of marine fish in the North Sea with the expansion of the range of many small-sized species. According to Daufresne et al. (2009), small species such as the topmouth gudgeon or the bitterling are more likely to benefit from warming than large species such as the European eel *Anguilla anguilla* or the common bream *Abramis brama*. Actually, the trends in separate species densities identified in this study seem to corroborate the previously stated hypotheses regarding fish body size and reproduction strategy but this needs to be tested in a more comprehensive manner. One way to further test these hypotheses would be to combine the present meta-analysis framework with functional approaches based on a comprehensive description of species' ecological traits, with emphasis on reproduction and dispersal capacity as well as body size. Continuing the monitoring of large river ecosystems is, moreover, of primary importance to be able to test these hypotheses and the possibly transient nature of the observed phenomena.

Overall, species range shifts are likely to induce increasing competition between species in relation to increased species richness and density and decreased food availability, as well as the deterioration of ecosystem dynamics and functioning, and spread of harmful invasive species and diseases, which could together lead to local and global extinctions of species (García Molinos et al., 2018; Scheffers

et al., 2016). Given the economic, social, and conservation implications of species range shifts around the world (Pecl et al., 2017), a comprehensive understanding of the underlying mechanisms of such ecological responses to a changing climate and of species characteristics underlying their vulnerability or adaptability to climate change is therefore urgently needed.

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SUPPORTING INFORMATION

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