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Human pressures modulate climate-warming-induced changes in size spectra of stream fish communities

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Ignasi Arranz [1] ✉, **Gaël Grenouillet** [1,2] & **Julien Cucherousset** [1]

Climate warming can negatively affect the body size of ectothermic organisms and, based on known temperature–size rules, tends to benefit small-bodied organisms. Our understanding of the interactive effects of climate warming and other environmental factors on the temporal changes of body size structure is limited. We quantified the annual trends in size spectra of 583 stream fish communities sampled for more than 20 years across France. The results show that climate warming steepened the slope of the community size spectrum in streams with limited impacts from other human pressures. These changes were caused by increasing abundance of small-bodied individuals and decreasing abundance of large-bodied individuals. However, opposite effects of climate warming on the size spectrum slopes were observed in streams facing high levels of other human pressures. This demonstrates that the effects of temperature on body size structure can depend on other human pressures, disrupting the natural patterns of size spectra in wild communities with potentially strong implications for the fluxes of energy and nutrients in ecosystems.

Body size is a key biological trait of organisms due to its influence on physiological, ecological and evolutionary processes acting at multiple levels of biological organization from population dynamics and community stability to ecosystem functioning[1]. Climate warming can lead to reduced individual body size caused by direct effects of increased temperature on metabolic rates[2–4] that can ultimately decrease population mean body size and alter body size distributions in communities. The climate-induced decrease in body size is commonly accepted[5], has been observed in most ectothermic species in experimental conditions[6,7] and is theoretically predicted[8,9]. However, recent empirical studies found little evidence that warming-induced reduction in body size was a general rule[10,11], suggesting that additional empirical research is needed to understand how climate warming shapes wild communities.

Size-dependent temperature effects can lead to different predictions on how climate warming affects wild communities[8,12–14]. This can be in part due to the typical hump shape of thermal performance curves in ectotherms, with the highest individual performance at intermediate optimal temperatures[13]. Climate warming can therefore induce contrasting effects on populations depending on their position in the thermal gradient and on processes occurring at lower levels of biological organization such as interactions among individuals[15] or physiological responses[8]. Several mechanisms can explain the predominantly size-dependent effects of temperature. Climate warming can decrease the oxygen consumption of organisms, which can then reduce physiological performance[16] (particularly for larger-bodied individuals, which may cease growing[8]). The metabolic-level boundary hypothesis suggests that metabolic intensity modulates the influence of the surface-area- and volume-related resource demand by constraining metabolism[12]. Cold temperatures can increase viscosity and reduce oxygen supply due to thicker boundary layers around the animal's body, resulting in higher respiratory costs in small individuals than in large individuals that are less influenced by viscosity[14]. This suggests that climate warming can shift community size structure towards a dominance of small-bodied individuals, and accounting for individual

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[1]Laboratoire Evolution et Diversité Biologique UMR 5174, Université Toulouse III—Paul Sabatier, CNRS, IRD, Toulouse, France. [2]Institut Universitaire de France, Paris, France. ✉e-mail: ignasiarranz@gmail.com

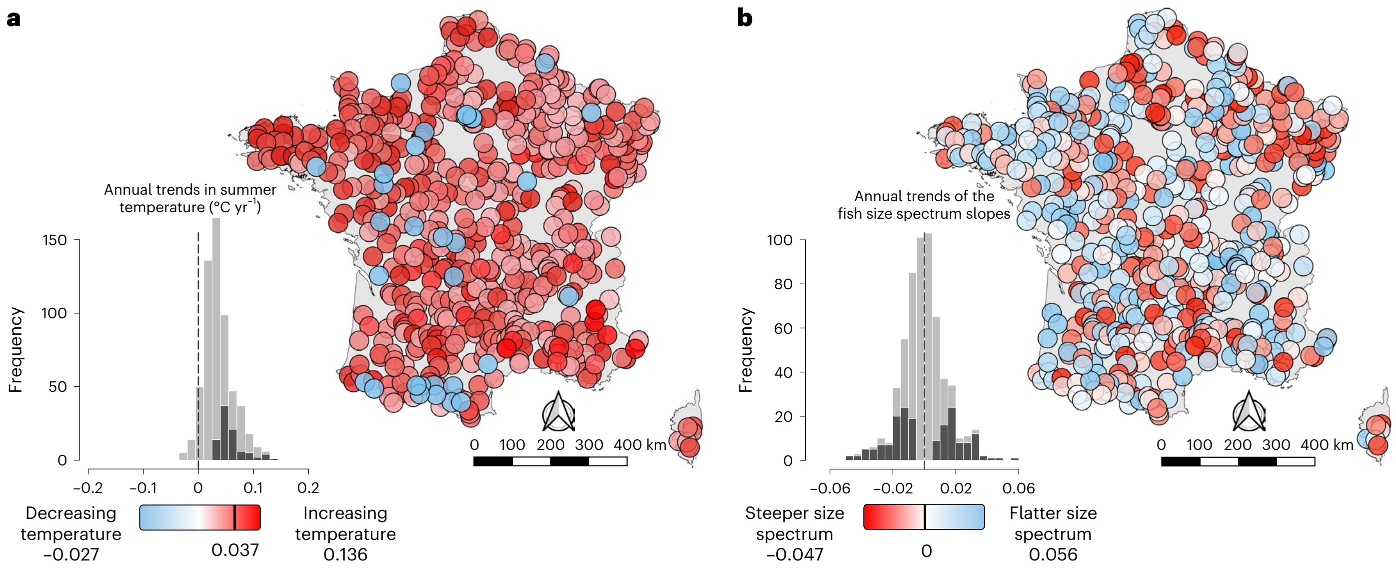

Fig. 1 | Annual trends in summer water temperature and size spectrum slopes across stream locations in France from 1994 to 2018. a, Summer water temperature (°C yr^{-1}). The colour bar shows annual temperature change (°C yr^{-1}). **b**, Size spectrum slopes. The colour bar shows the annual size spectrum slope change. The histograms show the frequency distribution of each variable with dark grey bars for significant ($P < 0.05$) and light grey bars for non-significant ($P > 0.05$) trends. The dashed line set at zero indicates no temporal changes. The black line in the colour bars represents the average value.

body size variation is therefore crucial to fully appreciate the effects of climate warming on wild communities.

Global change research has recently revealed that the effects of climate warming can be modulated by other human pressures[17–20]. For instance, Morris et al.[17] observed that the effects of climate warming could be exacerbated, mitigated or even reversed by increasing levels of contamination, biological invasions or habitat alteration in freshwater ecosystems, suggesting that climate warming cannot be considered in isolation from other human pressures. Despite recent efforts in highlighting the importance of such interaction effects[21,22], the evidence of potential interactions between climate warming and other human pressures acting on body size distributions remains largely unexplored in wild communities.

The community size spectrum—that is, the relationship of abundance or biomass with body size classes[1,23]—represents an insightful approach to identifying the mechanisms of community responses to climate warming. Indeed, the community size spectrum is, by nature, independent of species identity and relies on the metabolic theory, with predators being larger than their prey due to the energy loss through successive trophic levels[9]. The size spectrum slope quantifies the decrease in numerical abundance of individuals as body size increases[1,23] and remains invariant under steady-state conditions in space and time[24], even when species composition changes[25]. The size spectrum slope has been reported to vary in communities facing different human pressures[26] such as land use[27], biological invasions[25] and exploitation[28], but our knowledge on the interactive effects of climate warming and other environmental (for example, natural or anthropogenic) factors on the temporal trends in community size spectra is still limited.

The general objective of this study was to determine whether climate warming interacted with other human pressures to shape the annual trends in size spectra in wild communities. We used stream fish as model organisms and one of the most extensive biomonitoring datasets documenting nearly five million individual fish body sizes collected in 583 stream locations with 9,748 fish surveys over more than 20 years across France. We hypothesized a general steepening of the size spectrum slope (that is, a more negative exponent) in response to climate warming in streams unimpacted by other human pressures because small-bodied individuals have physiological advantages from increased water temperature compared with large-bodied individuals[8,15]. We also hypothesized that these effects were modulated in streams impacted by other human pressures because these pressures can induce opposite shifts in the community structure[17,29]. Finally, we hypothesized stronger changes in size spectrum slopes in the downstream parts of river networks than in the upstream parts because the distribution ranges of fish species are shifting towards cooler areas located upstream[30].

Results

No spatial patterns in the annual trends in size spectra

Across all studied stream locations, water temperature increased by 0.037 °C yr^{-1} on average between 1994 and 2018, and increased water temperature over the past 20 years was observed in 95% of the stream locations (Fig. 1a). There was no clear pattern in the annual trends in size spectra (Fig. 1b): 52% of stream locations displayed negative trends (that is, steeper slopes over time), whereas 48% displayed positive trends (that is, flatter slopes over time) (Fig. 1b).

Changes in the annual trends in size spectra are context dependent

The interaction term between climate warming and human pressures significantly affected the annual trends in size spectrum slopes (average estimate, 0.001; average 95% confidence interval (CI), (0.001, 0.003); $P = 0.007$; Extended Data Table 1 and Supplementary Table 1). Specifically, in streams not impacted by other human pressures, climate warming was negatively related to the annual trends in size spectrum slopes—that is, size spectrum slopes became steeper with increasing climate warming (Fig. 2a). These steeper slopes resulted from an increased abundance of small individuals (<15.5 g) accompanied by a decreased abundance of large individuals (31.5–255.5 g) (Fig. 3, Supplementary Fig. 1 and Supplementary Table 2). In contrast, in streams impacted by human pressures, climate warming positively affected the annual trends in size spectra towards more positive (flatter) size spectrum slopes over time (Fig. 2a). Moreover, the annual trends in size spectra were significantly affected by the position along the upstream–downstream gradient (estimate, −0.002; 95% CI, (−0.003, −0.001);

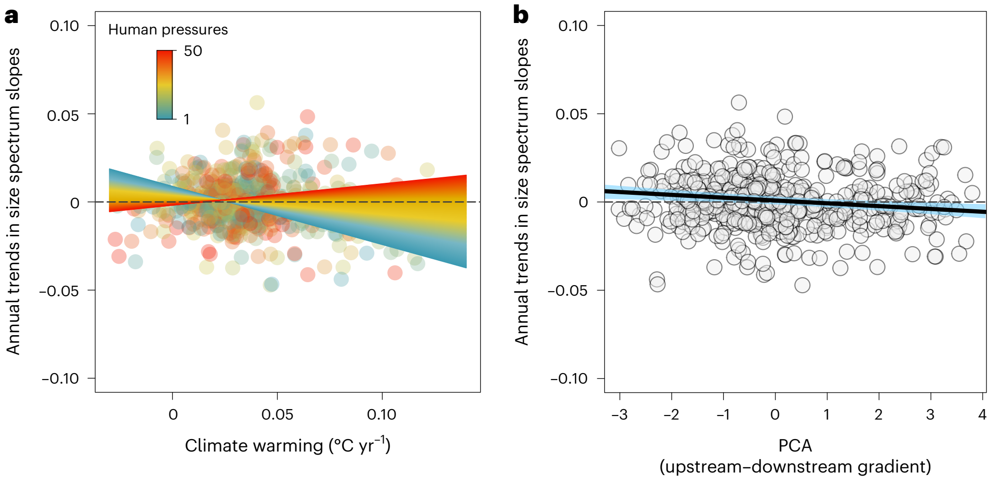

Fig. 2 | Factors influencing the annual trends in size spectrum slopes in streams across France. a, Effects of the interaction between climate warming and human pressures on the annual trends in size spectrum slopes. The coloured lines, corresponding to different levels of human pressures, are drawn using the coefficient estimates from the best model (Extended Data Table 1 and Supplementary Table 1) to compute the slope for climate warming while holding the value of human pressures constant at values ranging from 1 to 50. **b**, Effects of the upstream–downstream gradient on the annual trends in size spectrum slopes. The solid black line represents the linear regression, and the blue shading represents the 95% CI. Note that the positive and negative values in the annual trends of size spectrum slopes (*y* axes) refer to flatter and steeper size spectrum slopes over time, respectively.

$P = 0.022$; Fig. 2b, Extended Data Table 1 and Supplementary Table 1), with the downstream parts of river networks displaying steeper size spectrum slopes over time than the upstream parts.

Discussion

Our study empirically demonstrates a reconfiguration of the size structure of fish communities occurring over a long temporal scale and caused by global environmental changes. Our results show that climate warming and human pressures interactively modulate the temporal changes in size spectrum slopes. Climate warming steepened the slopes of the size spectra in streams with limited human pressures by increasing the proportion of small-bodied individuals in wild communities. These results are predicted by metabolic constraints[4] and temperature–size rules[2,3] and are consistent with previous studies that have focused on specific taxa[10,15,31] or were based on mesocosm experiments[7,32]. However, the effect of climate warming changed from negative to positive in streams with high levels of human pressures, suggesting that the temperature–size rules are not always supported when other human-induced perturbations are in play.

In stream ecosystems with low levels of human pressures, climate warming can push the size spectra towards communities composed of smaller individuals because of direct temperature effects on individual physiology[4]. Small-bodied individuals have more physiological advantages to face the effects of climate warming than large-bodied individuals since large-bodied individuals usually have lower temperature optima and narrower thermal limits of performance than small-bodied individuals[16]. The physiological exposure to increasing temperature may limit the growth rates of large-bodied individuals[8], a finding observed for other ectothermic organisms such as insects[33] and reptiles[34]. The declining number of large-bodied individuals may also be caused by energetic constraints, as climate warming may indirectly reduce food availability[35] and induce shorter lifespans[36]. While small-bodied individuals are likely to dominate in more impacted ecosystems[37,38], large-bodied individuals may reduce energy intake due to limited food availability or display decreasing fitness due to accelerating metabolic costs at higher temperatures[35]. These shifts in community size structure can alter consumer–resource dynamics and thus induce cascading effects on lower trophic levels, thereby reshuffling food web structures[39]. Our results could therefore have strong implications for ecosystem functioning because large-bodied individuals usually contribute substantially to important ecological functions[7,40] that remain to be quantified in the wild.

In streams facing higher levels of human pressures, we found that fish communities displayed higher relative abundance of large-bodied individuals over time, a finding challenging the hypothesis that human pressures generally threaten larger individuals[17,29]. In the present study, human pressures were quantified using an index integrating several types of human activities[41], making it particularly difficult to decipher the individual driver of the observed changes. Using multiple lines of evidence, we hypothesize that two mutually non-exclusive mechanisms may induce the observed results. The first is fish stocking by angling clubs. Although it is not possible to identify hatchery-reared fish during field sampling, we observed that individuals legally stocked across France[42] were larger, for each species, than individuals used to calculate size spectra in the present study (Extended Data Fig. 1). The second is biological invasions by non-native species. As observed at the global scale[43], we found that non-native individuals were significantly larger in body size than native populations in streams across France and that streams with high levels of human pressure also exhibited large proportions of non-native individuals in their communities (Extended Data Fig. 1). While these mechanisms could not be formally tested, our results underline the importance of considering other human pressures as potential confounding drivers when studying the effects of climate warming, as observed for habitat alteration, land use changes and eutrophication[17,44].

Fish communities located in downstream parts of streams also exhibited a stronger steepening (that is, more negative slopes) of the size spectra. In contrast to previous studies that focused on spatial variations of fish species[45] or trait diversity[46] along the downstream–upstream gradient, our study reveals that the temporal changes in fish body size structure differ along the downstream–upstream gradient. Our results may be explained by two mechanisms. The first is an increased reproductive success of small-bodied species in downstream parts. Fish communities in downstream parts tend to be dominated by small-bodied cyprinids, which are generally more adapted to warm conditions and likely to be favoured by higher temperatures in more downstream parts[45,47]. The second is the natural pattern proposed by Knouft[48] whereby fish communities with higher proportion of small-bodied species are more common in downstream parts.

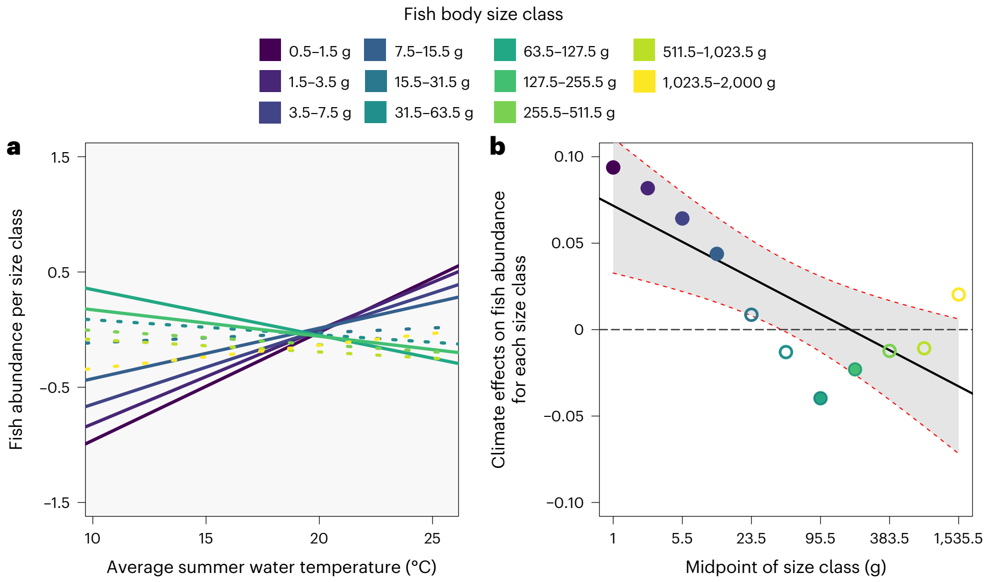

Fig. 3 | Temperature effects on fish abundance per size class. a, Relationship between summer water temperature and fish abundance per size class. The coloured lines represent the results from equation (5) (the details for the model estimates are provided in Supplementary Table 2). The dashed lines indicate no significant trend in the abundance per size class as a function of the summer water temperature. **b**, The climate effects on fish abundance per size class. The coloured points represent the values from **a** across body size classes ($n = 11$ size classes). The grey shading represents the 95% CI. The continuous lines in **a** and filled circles in **b** indicate a significant ($P < 0.05$) relationship between summer water temperature and the abundance per size class.

In conclusion, the current and predicted future increases in water temperature and their interaction with other human pressures may drive important shifts in community size structure with consequences for ecosystem functioning, given that several ecosystem functions (including trophic transfer of energy and productivity) are linked with size spectrum theory[1,23]. Using a size spectrum approach may represent a promising avenue for future research to assess the complex interaction effects of climate warming and other human pressures on the dynamics of energy and nutrient fluxes in ecosystems.

Methods

Fish data selection

Fish sampling was performed by the Office Français de la Biodiversité using a standardized monitoring programme from 1994 to 2018[49] following the recommendations of the European Committee for Standardization[50,51]. Fish communities were sampled with three standard electrofishing methods depending on stream width and area: multi-pass removal (mostly two passes) in wadable streams, single-pass by boat in non-wadable streams and the two methods in conjunction[51]. The stream locations covered all regions of the dendritic network (from order 1 to 8) where fish were present. Fish caught were individually identified to species, counted and measured (standard length in mm and total mass in g) before releasing. When fish mass was not recorded, we transformed fish length to fish mass using species length–mass relationships from the present data (Supplementary Table 3).

We adopted strict data screening to select comparable samples with robust data that can fully represent the local size structure of freshwater fish communities among streams. We considered strictly freshwater and diadromous fish species but removed lampreys (jawless) and fish species with a life cycle mainly occurring in marine and brackish environments (see the details in Supplementary Table 4). We selected sampling occasions from May to October to limit the transient effects of seasonal events such as the sudden increases in fish density from spring reproduction. Multiple samplings within a given year could occur, but only for a very limited proportion of the dataset (Extended Data Fig. 2a). In these cases, we used the average abundance of each fish species across multiple samplings. Given that we aimed to retain sufficient statistical power to detect long-term changes, we selected stream locations that were systematically monitored for at least 10 years since 1994 (median, 17 years; s.d., 4.75). To achieve robust calculations of size spectra, we selected stream locations with at least 100 individuals (median, 333; s.d., 515.70) captured per year. Importantly, our dataset mainly contained communities with a body size range of at least three orders of magnitude (that is, from 0.1 g to >100 g; Extended Data Fig. 2b), following previous recommendations for calculating size spectra[52]. In total, 9,748 sampling occasions were included in the analyses, representing a total selection of 583 stream locations (Supplementary Fig. 2). The dataset contained 4,692,552 individual fish belonging to 65 species.

Climate-related variables

We reconstructed the daily temperature per stream location to have an accurate long temporal coverage of climate warming. The daily air temperatures were provided by Météo France and extracted from the high-resolution (8-km-by-8-km grid) SAFRAN atmospheric analysis over France[53]. To account for the sigmoidal relationship between air and water temperature, we estimated summer water temperature (from June to August) using the temperature air data following ref. 54. For each location, two climate-related variables were calculated (Extended Data Table 2): (1) climatic conditions (°C) as the average temperature of the three years before the first sampling (Extended Data Fig. 3) and (2) long-term trends in summer water temperature (°C yr^{-1}, referred to as climate warming; Fig. 1a). The three years before the first survey were included to account for previous climatic effects on fish recruitment. Climate warming was estimated in each stream location using the coefficients of the ordinary least squares regressions between the mean annual summer water temperature and the years of the survey period (including the three years before the first sampling).

Stream spatial structure

Two variables were considered to represent the upstream–downstream gradient (Extended Data Table 2): the drainage area upstream of the sampling location (km^2) and the distance to the source (km). We used a principal component analysis (PCA) to cope with the strong correlation between these two spatial variables, previously $\log_{10}$-transformed. The first axis of the PCA, accounting for 98.22% of the total variation, was used as a synthetic variable describing the upstream–downstream gradient in the stream network, with negative values corresponding to the most upstream locations and positive ones to the most downstream locations.

The level of human pressures was estimated using the Global Human Footprint Index (referred to as human pressures[41]). This is a cumulative index reflecting several human pressures based on population density, human activities, degree of navigable waterways and land use (crop and pasture lands)[41]. Human pressures ranged from 0 (unimpacted environmental conditions) to 50 (impacted with high levels of pressures). We used the 2009 map with a spatial resolution of 1 km^2 and a buffer zone of a 10 km radius around each stream location[41]. We calculated human pressures in each stream location by taking the average value of human pressures within each buffer zone (Extended Data Table 2). The calculation was performed by using the package sf[55] in the software R v.4.1.0 (ref. 56).

Size spectrum in local fish community

We only used fish individuals with a body mass in the range between 0.5 g and 2,000 g to account for potential body size biases in electrofishing efficiency that affect the capture of the smallest (<20 mm; that is, approximately 0.5 g) and the largest individuals (Extended Data Fig. 4)[57,58]. Removed individuals represented 5.48% of the entire dataset. We calculated the size spectrum in each fish community using maximum likelihood estimates (MLEs) following the recommendations of refs. 59,60. The MLE for each community was computed using a negative log-likelihood function following the equations:

$$f(x_i) = -n \times \ln\left(\frac{b+1}{x_{\max}^{b+1} - x_{\min}^{b+1}}\right) - b\sum_{i=1}^{n}\ln(x_i), b \neq -1$$

$$f(x_i) = n \times \ln(\ln(x_{\max}) - \ln(x_{\min})) + \sum_{i=1}^{n}\ln(x_i), b = -1$$

where $f(x_i)$ is the probability density function of a stream location i, x_i is the raw size data, $x_{\max}$ and $x_{\min}$ are the maximum and minimum values of that stream location's observed size data, n is the number of individual sizes and b is the estimated slope of the size spectrum. The equation was taken from the sizeSpectra package to calculate the negative log-likelihood for the bounded power-law distribution (named negLL.PLB[61]; see the details for the individual size spectrum slopes in Extended Data Fig. 5).

To assess the robustness of our results, we also calculated the size spectrum slope using a binning method because it has a long-standing importance in size spectrum theory[23]. We classified body sizes using a geometric series of 2 g (Supplementary Table 5). The binning size spectrum slope was calculated in each stream location using an ordinary least squares regression of the $\log_2$ of the fish numerical abundance normalized by the bin width (dependent variable) against the $\log_2$ of the midpoint size class (independent variable). The community size spectrum slopes and 95% CIs (lower limit and upper limit) obtained using the MLE and binning methods were calculated using the modified package sizeSpectra[61]. We validated our approaches (that is, MLE and binning) by comparing our results to those obtained using another body mass range (that is, 1 g to 2,500 g), and they were similar (Extended Data Fig. 6 and Supplementary Table 6). The results were also similar irrespective of the method used to calculate the size spectrum and of the size threshold to select individuals (Supplementary Tables 7–9), validating the robustness of our study.

Statistical analyses

Temporal trends in the size spectrum slopes. We used a simple model to calculate the temporal trends in size spectrum slopes per stream location by computing ordinary least squares linear regressions:

$$\text{Size spectrum slopes}_i = \beta_0 + \beta_1\text{year}_i + \varepsilon_i \tag{1}$$

where β_0 and β_1 are the linear parameters of the stream location i and ε_i is the error term. We used the estimate β_1 of equation (1) to represent the strength and direction of the temporal trends in the size spectrum slope across years for each stream location (Fig. 1b and Extended Data Fig. 7). Positive values indicate flatter slopes over time (that is, body size structure shifting towards a larger proportion of large-bodied individuals relative to small-bodied individuals), whereas negative values indicate steeper slopes over time (that is, a shift towards a larger proportion of small-bodied individuals relative to large-bodied individuals).

Determinants of temporal trends in the size spectrum slopes. We used a generalized linear mixed model to identify the processes shaping the temporal trends in the size spectrum slopes. Because climate warming can act differently along the geographical and environmental characteristics of the stream network (such as elevation and topography), we also tested the possibility of interactions among parameters representing climatic conditions (that is, the average summer water temperature of the three years before the first fish sampling), upstream–downstream gradient and human pressures. The full mixed-effect model was

$$\begin{aligned}
&\text{Annual trends in size spectrum slopes}_i = \beta_0 + \beta_1\text{climate warming}_i \\
&+\beta_2(\text{upstream-downstream gradient})_i + \beta_3\text{climatic conditions}_i \\
&+\beta_4\text{human pressures}_i + \beta_5\text{climate warming}_i \\
&\times(\text{upstream-downstream gradient})_i \\
&+\beta_6\text{climate warming}_i \times \text{climatic conditions}_i \\
&+\beta_7\text{climate warming}_i \times \text{human pressures}_i + u_i + \varepsilon_i
\end{aligned} \tag{2}$$

where β_0 to β_7 are the linear parameters for the stream location i, u_i is the random part and ε_i is the error term. To account for potential temporal autocorrelation among survey years (for example, similar environmental conditions in locations sampled in the same year) and the effect of unequal numbers of sampling surveys among locations (for example, the precision of the temporal trends may increase with the number of surveys), we used a nested random design with the number of sampling surveys nested within the year of the first sampling. However, the random term did not significantly affect the response ($P = 0.12$). The final (best) fixed model was determined using stepwise backward selection to obtain the final model with the lowest AIC value (Supplementary Table 1). We controlled the random part of the mixed models and determined the fixed part. Multicollinearity and correlation among the explicative variables were checked using variation inflation factors, but these were low among the predictors (variation inflation factor < 2), suggesting that the effects of the upstream–downstream gradient and climate conditions could be evaluated independently (Extended Data Fig. 8). All explicative variables were standardized to compare predictors. Semi-partial R^2 for each predictor was calculated following Stoffel et al.[62]. Linear mixed-effects models were fit using the lmer function in the R package lme4[63], the variation inflation factors were calculated using the package car[64] and the stepwise selection was done in the package MASS[65] in the software R v.4.1.0 (ref. 56).

Climate effects on the size spectrum. We quantified the climate effects on size classes using the accumulative abundance of fish of each size class and summer water temperature per fish survey. To do this, we performed the following linear mixed model:

$$\text{fish abundance}_{ij} = \beta_0 + \beta_1\text{summer temperature}_{ij} + u_{ij} + \varepsilon_{ij} \tag{3}$$

where β_0 and β_1 are the linear parameters of the location i and year j, the random part u_{ij} is the sampling location and ε_{ij} is the error term.

We then tested whether equation (3) showed positive (that is, breakdown of the temperature–size rule), null or negative (that is, the expected temperature–size rule) effects on each size class.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The temporal trends in the fish size spectra and the main predictors are available at https://doi.org/10.5281/zenodo.7792635. Source data are provided with this paper.

Code availability

The code is available at https://doi.org/10.5281/zenodo.7792635.

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Author contributions

I.A., G.G. and J.C. conceived the study. I.A. performed the analyses and wrote the first draft of the paper. I.A., G.G. and J.C. reviewed and edited the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to Ignasi Arranz.

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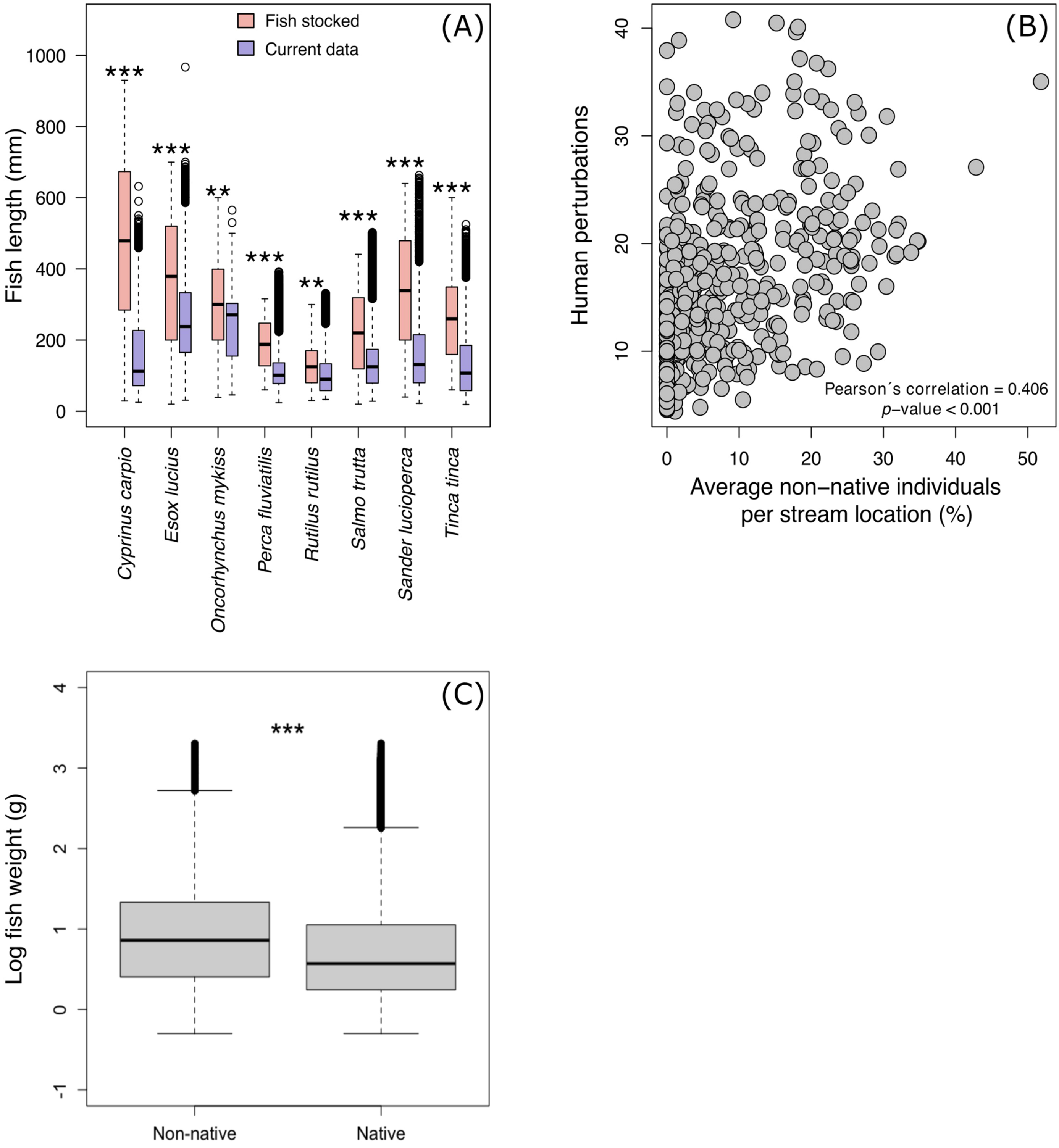
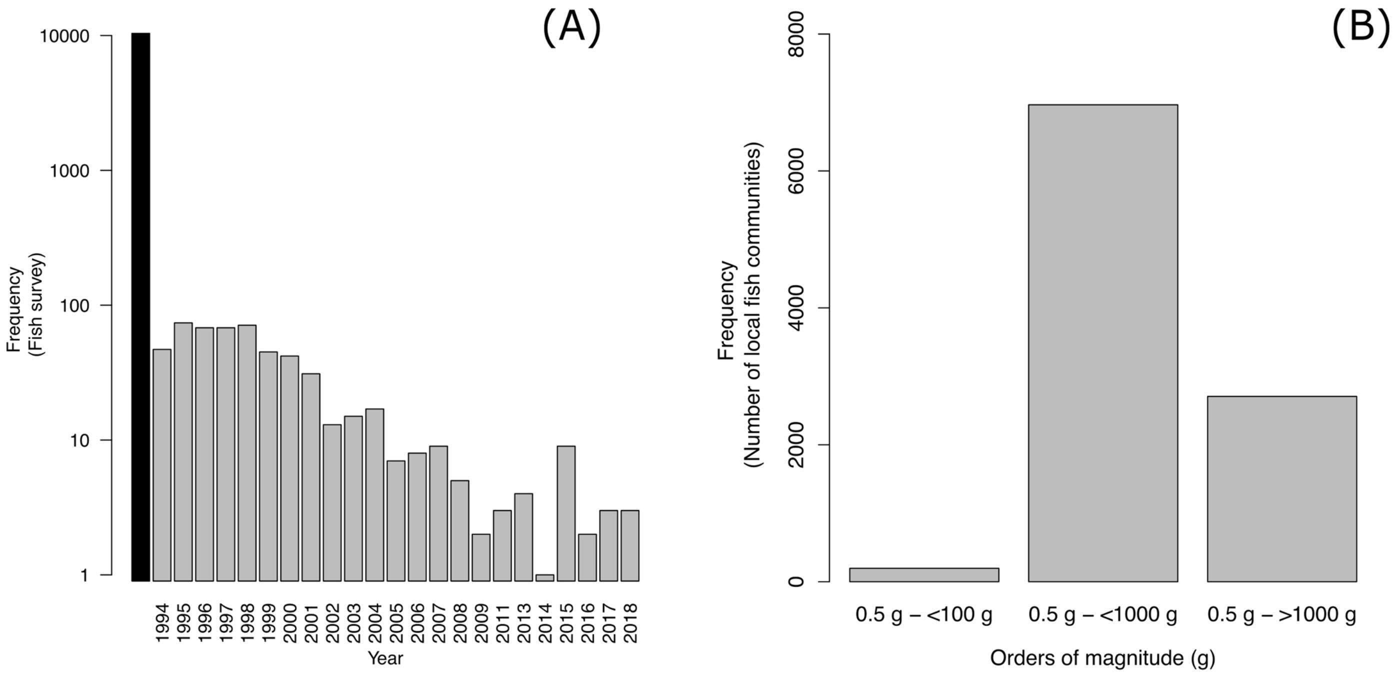
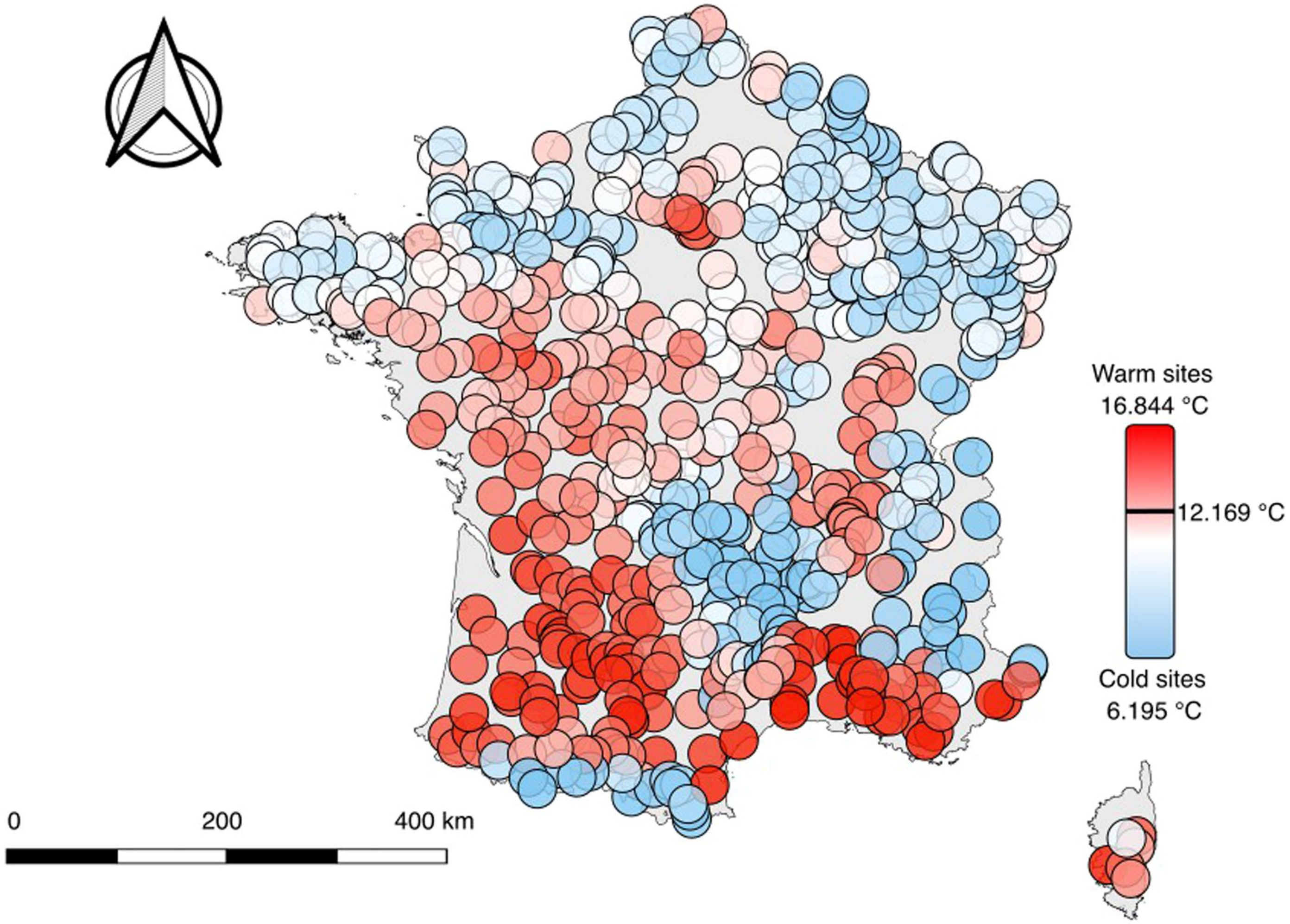


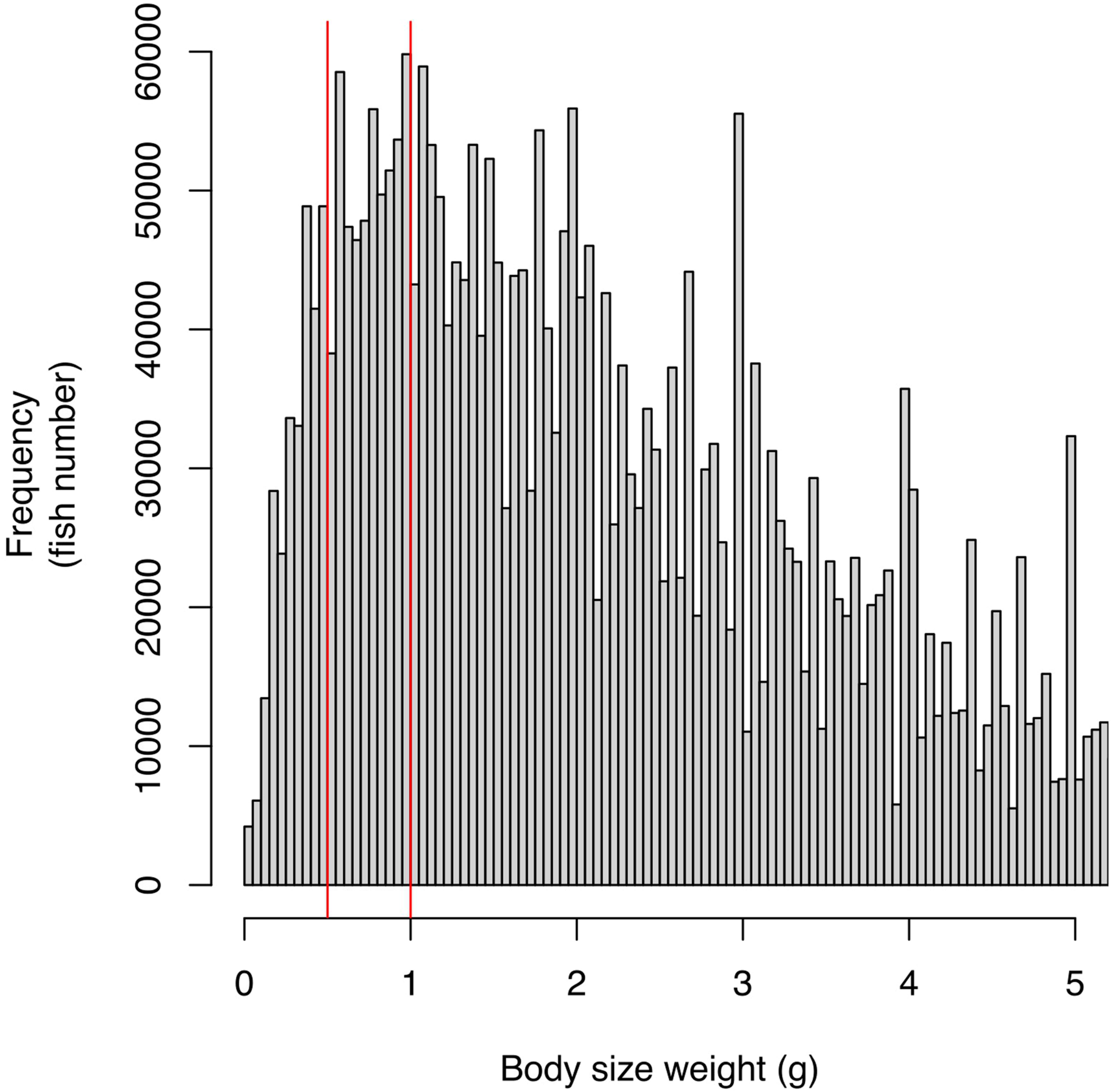
Extended Data Fig. 1 | Potential causes of human pressures on the annual trends in the size spectrum slopes. Multiple lines of evidence testing the potential drivers affecting fish size spectra in streams with high levels of human pressures. (**a**) Body length of fish stocked by managers in France (red boxplots) and body length of our fish analyses in the present study (blue boxplots). (**b**) Correlation between the level of fish biological invasions and the index of human perturbations. (**c**) Boxplot showing the comparison of fish mass (g) between non-native and native individuals in the dataset used in the present study (ANOVA, F = 11,871, $P < 0.001$). Body length of stocked fish were obtained from Cucherousset et al.[42]. *** ($P < 0.001$); ** ($P < 0.01$); * ($P < 0.05$). The boxplots in (A) and (C) display the distribution of the data with the lower and upper box boundaries 25th and 75th percentiles, respectively. The line inside the box represents the median value and the lower and upper error lines 10th and 90th percentiles, respectively. The statistical tests followed the F-distribution with a two-tailed test and no adjustments for multiple comparisons were made.



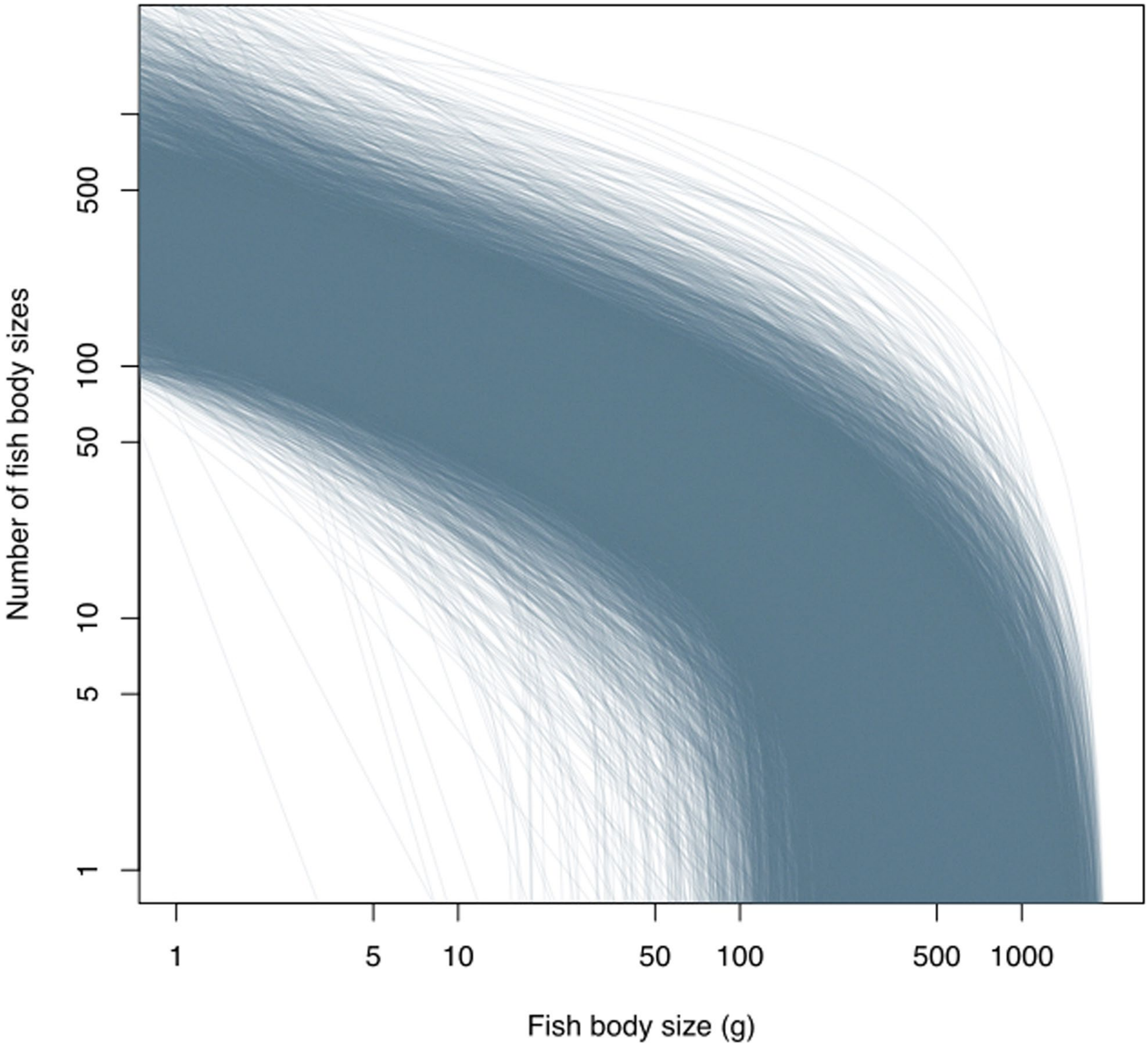
Extended Data Fig. 2 | Characteristics of the local fish surveys. (**a**) Number of fish surveys (log-transformed) with multiple samplings within a given year during the studied period (1994 – 2018). The black bar represents the number of fish surveys with only one sampling and the grey bars the number of fish surveys with multiple samplings. (**b**) Distribution of the number of local fish communities according to the number of orders of magnitude (g) in base 10.



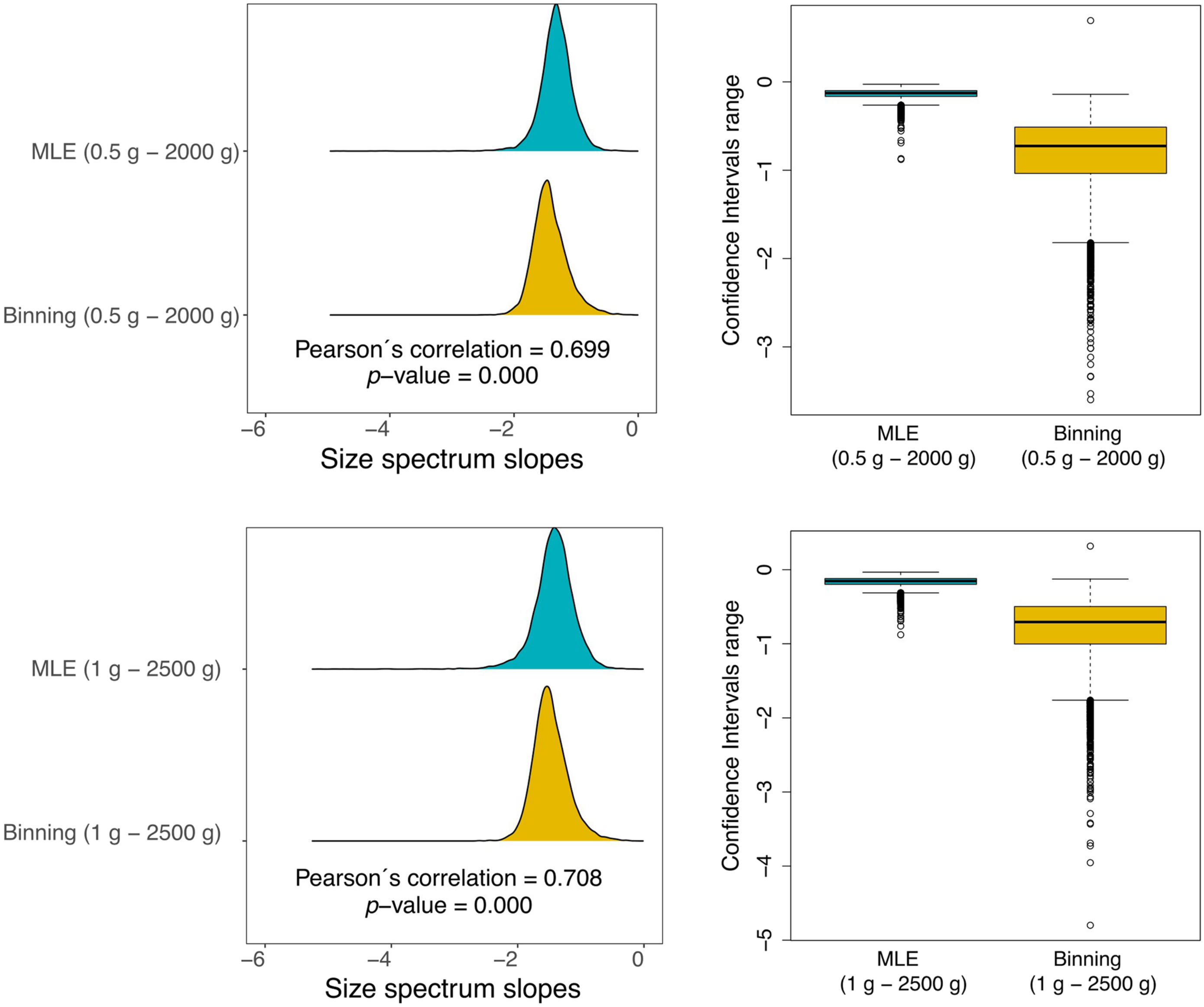
Extended Data Fig. 3 | Geographical variation of the climatic conditions across streams locations. Climatic conditions (that is, average summer water temperature of the three years before the first fish sampling) of the stream locations reflect a wide range of conditions across France. The value of 12.169 °C in the color bar indicates the mean of climatic conditions across all stream locations.



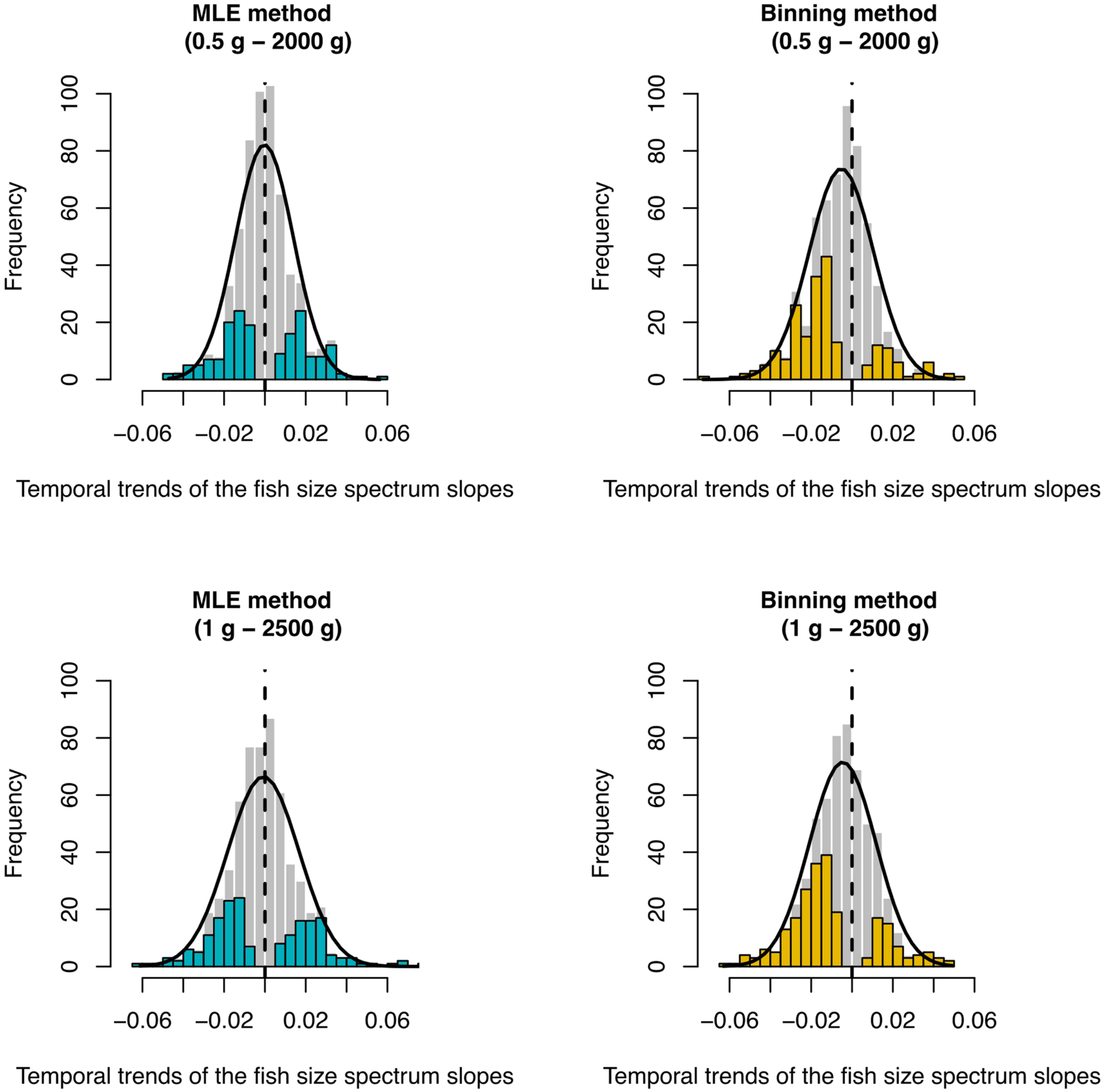
Extended Data Fig. 4 | Body size thresholds of the smallest fish. Body size distribution of the smallest fish (0 to 5 g) from the entire dataset. Fish < 0.5 g were underrepresented in the samples. The red vertical lines represent the thresholds (0.5 g and 1 g) used for size spectrum calculations.



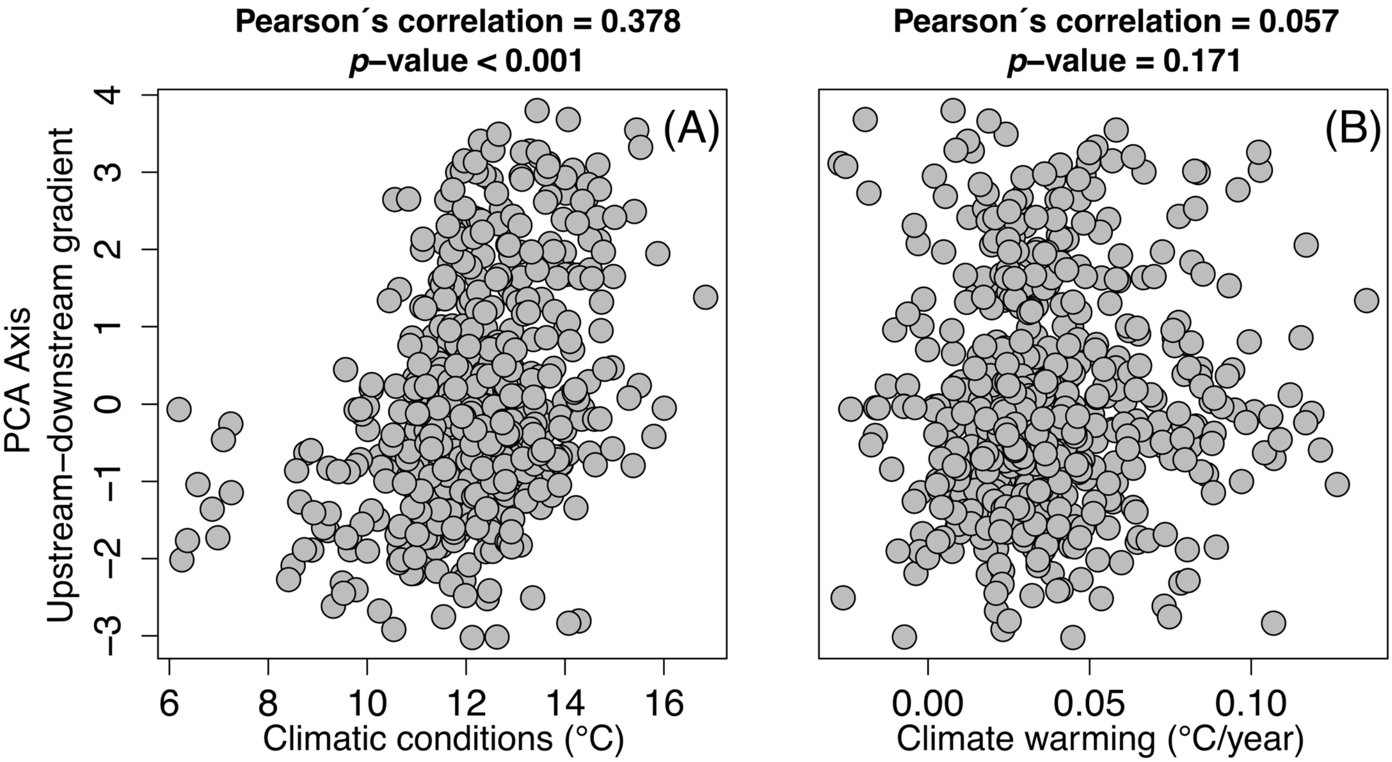
Extended Data Fig. 5 | Individual size spectrum slopes across all fish surveys. All size spectrum slopes (log-log scale) calculated using the MLE method (body size range 0.5 g – 2000 g). The size spectrum slopes were estimated as the negative log-likelihood function between the decreasing number of fish body size (Y-axis) as fish body size (X-axis) increases. The grey lines refer to the abundance size spectrum fitted using the MLE method across all fish surveys.



Extended Data Fig. 6 | Different methods to estimate fish size spectrum slopes. Comparison of size spectrum methods using the MLE (blue) and binning (yellow) and two different body size ranges (0.5 g – 2000 g and 1 g – 2500 g). Methods were strongly correlated but Confidence Intervals ranges (CI upper limit – CI lower limit; 95 %) were narrower using the MLE method than the binning method. The statistical test followed the Pearson's *r* with a two-tailed test and no adjustments for multiple comparisons were made.



Extended Data Fig. 7 | Comparison of the annual trends in size spectrum slopes based on different methodologies. Frequency distribution of the annual trends in size spectrum slopes for two size spectrum calculation methods (MLE and binning) and using different size ranges (0.5 g – 2000 g; 1 g – 2500 g). Color bars indicate the significant trends ($P < 0.05$) whereas the grey bars indicate non-significant trends ($P > 0.05$). A dashed line set at zero indicates no temporal changes in size spectrum slopes.



Extended Data Fig. 8 | Correlations among climate variables and upstream-downstream gradient. Pearson's correlations between (**a**) climatic conditions and the upstream-downstream gradient and between (**b**) climate warming and the upstream-downstream gradient.

Extended Data Table 1 | Processes shaping the annual trends in the size spectrum slopes

Predictor	***Estimate***	**MR^2**	**CR^2**	**SE**	**t**	***p*-value**
Upstream-downstream gradient	-0.002 (-0.003—-0.001)	0.011	0.059	0.001	-2.301	**0.022**
Human pressures	0.001 (-0.001—0.002)	0.002	0.051	0.001	1.100	0.272
Climate warming	-0.002 (-0.001—0.001)	0.001	0.050	0.001	-1.064	0.288
Climate warming*Human pressures	0.001 (0.001—0.003)	0.012	0.061	0.001	-2.713	**0.007**

Best generalized linear mixed model (GLMM) relating the temporal trends in size spectrum slopes to the main drivers in Equation 2. Annual trends in size spectrum slopes were calculated with the MLE method and a body size range from 0.5 g to 2,000 g. Random effects included the first year of fish sampling and the number of times sampled in each stream location. MR^2: marginal R^2; CR^2: conditional R^2. Significant *p*-values are displayed in bold. The statistical tests followed the Student's *t*-distribution with a two-tailed test and no adjustments for multiple comparisons were made.

Extended Data Table 2 | Overview of the environmental conditions across stream locations

Group	Variable	Units	Mean	Median	SD	Min	Max
Climatic	Climate warming	°C·year^{-1}	0.036	0.032	0.026	-0.027	0.136
	Climatic conditions	°C	12.169	12.153	1.471	6.195	16.844
Topographic	Distance to the source	km	84.720	29.480	135.061	0.900	893.000
	Surface of the upstream watershed	km^2	3,671	224	11,873	2	110,248
Anthropogenic	Human pressures	-	16.272	15.021	7.461	4.431	40.784

Summary statistics of environmental conditions in the sampled locations: climatic, topographic, and anthropogenic variables.

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Corresponding author(s): Ignasi Arranz
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Study description	We used an extensive biomonitoring datasets containing nearly five million of individual fish body sizes collected in 583 stream locations over > 20 years across France.
Research sample	In total, 9,748 sampling occasions were included in the analyses and the dataset contained 4,692,552 individual fish belonging to 65 species.
Sampling strategy	We restricted locations that were systematically monitored for at least 10 years since 1994. We also removed brackish and jawless species.
Data collection	Data collection was done by Office Français de la Biodiversité (OFB) using a standardized monitoring program.
Timing and spatial scale	Sampling occasions were limited from May to October to to limit the transient effects of seasonal events such as the sudden increases in fish density from spring reproduction.
Data exclusions	To retain sufficient statistical power to detect long-term changes, we restricted locations that were systematically monitored for at least 10 years since 1994. To ensure enough data and achieve robust calculations of size spectra, we selected locations where at least 100 individuals were captured per year at a location.
Reproducibility	We did not conduct an experimental work. All data provide from intensive field campaigns.
Randomization	We considered a nested random design with the number of sampling surveys nested with the year of the first sampling.
Blinding	Our study involves wild communities sampled across all parts of the river network so blinding was not relevant to our study.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	All sampling for each stream location was done in daylight hours.
Location	All stream locations were located in French basins and covered a surface of the upstream watershed from 2km2 to 110km2.
Access & import/export	All data is available at http://www.naiades.eaufrance.fr/ and the recent publication Irz et al. (2022). Irz, P., Vigneron, T., Poulet, N., Cosson, E., Point, T., Baglinière, E., & Porcher, J.-P. (2022). A long-term monitoring database on fish and crayfish species in French rivers. Knowledge & Management of Aquatic Ecosystems, 25, 1–10.
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