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Climate Impacts on Lake Food-Webs Are Mediated by Biological Invasions

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ABSTRACT

Climate change and biological invasions are among the most important drivers of biodiversity and ecosystem change. Despite major advances in understanding their ecological impacts, these drivers are often considered individually, overlooking their possible complex interrelationship. By applying structural equation modeling to an extensive nationwide dataset of 430 fish communities across 257 French lakes, we investigated how taxonomic, size, and trophic diversities are impacted by climate warming and exotic species occurrence. Our goal was to compare their relative signature or lasting impacts after these factors had taken effect and to determine whether climate warming and biological invasions mediate the current state of community diversities. Drawing on a set of interconnected hypotheses, we suggest that biological invasions could be an important indirect effect of climate warming. This aspect must be considered to fully grasp the overall effects of climate change, beyond just its direct thermal impacts. Our results support our hypothesis that climate warming negatively impacts size and trophic diversities. However, these effects are mostly mediated by the warming-induced increase in exotic species richness, which, in turn, promotes total species richness. These results suggest that exotic species have a substantial role in determining the impact of climate change, obscuring the diversity patterns predicted by temperature alone. We conclude that the impacts of climate change cannot be understood without considering its mediated effects via biological invasions, underscoring the need to grasp their intertwined roles in predicting and managing ecological consequences.

1 | Introduction

Climate change and biological invasions are major drivers of biodiversity and ecosystem change (Jaureguiberry et al. 2022). Both can profoundly impact ecological communities in terms of composition and interaction networks, thereby fragilizing ecosystems functioning (Jaureguiberry et al. 2022; Sentis et al. 2021). Although often considered independently, climate change and biological invasions can

exhibit a complex interrelationship (Sentis et al. 2021; Walther et al. 2009). Climate change can directly shape the trophic and size structures of communities through habitat change, as well as metabolic, demographic, and evolutionary mechanisms (Woodward et al. 2010), but also indirectly through the facilitation of biological invasions (Roy et al. 2024). This facilitation is supported by different mechanisms such as habitat expansion and enhanced survival and reproduction rates of exotic species (Walther et al. 2009). Yet, climate change

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can also impede biological invasions by creating unsuitable conditions for some exotic species and increasing competition from native species (Walther et al. 2009). The outcome of climate change, in particular warming, on biological invasions' success can consequently vary depending on its influence on species and consequent trophic interactions, as well as on the persistence of native predators or competitors (Sentis et al. 2021; Tylianakis et al. 2008). Specifically, climate warming can increase top-down control on invaders, preventing biological invasions or facilitating them by releasing such control following predator extirpation (Bradley et al. 2010; Lu et al. 2013). The diverse impacts of climate warming on biological invasions hence complicate our understanding of its effects on species and communities (Bruehl et al. 2021). It is therefore crucial to investigate how climate warming and biological invasions together affect community structure and species interactions, as the indirect effects of warming often surpass their direct impacts on physiology and demography (Ockendon et al. 2014). However, while some research addressed the interplay of climate warming and biological invasions on biodiversity, particularly focusing on taxonomic diversity (Azzurro et al. 2019; Ilarri et al. 2022), there is still a gap in understanding their intricate effects on size and trophic diversities within ecological communities.

Both climate warming and biological invasions are expected to affect community size structure (i.e., the distribution of body sizes of organisms within a community, hereafter CSS), a key predictor of ecological functions at multiple organizational levels (White et al. 2007). High temperatures tend to favor smaller body sizes at the individual, population, and species levels (Atkinson 1994; James 1970; Salewski and Watt 2017). Thus, warmer conditions can alter CSS by reducing the relative proportion of large-bodied organisms, characterized by steeper CSS slopes (Dossena et al. 2012; Yvon-Durocher et al. 2011), and by reducing the total community biomass, thereby lowering the CSS's elevation (Allen et al. 2002; Bazin et al. 2024). Beyond these direct thermal effects, climate warming can also impact CSS through biological invasions, as exotic species in freshwater ecosystems tend to be larger than native species (Arranz et al. 2021, 2023; Blanchet et al. 2010). In this context, the effect of climate warming, mediated by biological invasions, on CSS is likely to counterbalance its direct thermal effects.

CSS's alteration is also expected to cascade up to the whole food-web structure as body size determines species trophic niche, trophic position and interactions strength (Woodward et al. 2005). With warming, food-webs are expected to exhibit shorter food-chains and a simpler structure, resulting from the loss of large, high trophic-level species (Barbosa and Siqueira 2023; Bonnaffé et al. 2021, 2024; O'Gorman et al. 2019). Effects of biological invasions can also propagate through food webs and strongly modify their structures through changes in the relative abundance of trophic levels or in the interactions between resident species (David et al. 2017; Sentis et al. 2021). The magnitude of these changes yet depends strongly on the position of the exotic species in the food web (Gallardo et al. 2016; Vagnon et al. 2022). In particular, exotic predators at the top of the food web exert more detrimental direct and indirect effects on native species than trophically analogous native predators (Jackson et al. 2017).

Their presence can lead to the replacement of multiple species at the same trophic level or reduce diversity at lower trophic levels (Vagnon et al. 2023), ultimately simplifying the food web structure and potentially exacerbating the direct effects of climate warming.

Altogether, the current state-of-the-art suggests that the impacts of climate change and biological invasions are intertwined and depend on how they influence the links between species composition (hereafter taxonomic diversity), trait distribution such as body size (hereafter size diversity) and species interactions within food webs (hereafter trophic diversity). Yet, we lack empirical evidence of these links, leaving a substantial gap in our understanding of the ecological consequences of climate change and its direct and indirect effects through biological invasions. To fill this gap, we analyzed 430 fish communities across 257 lakes nationwide in France by assessing the links between taxonomic (i.e., exotic species richness and total species richness), size (i.e., CSS slope and elevation), and trophic (i.e., connectance and maximum trophic level in food-webs) diversities. We used simulated lake epilimnion temperatures (Sharaf et al. 2023a) to investigate how temperature condition (annual mean epilimnion temperature averaged over the past 5 years prior to each sampling event) and climate warming (long-term trends in annual mean epilimnion temperature over the last 40 years prior to each sampling event) are shaping ecological diversities. We considered both temperature condition and climate warming to disentangle how warm temperatures are from how fast they have changed. Previous studies often emphasize the static aspects of climate warming, overlooking its dynamic component—the rate of temperature change—which has been shown to affect community stability (Chang et al. 2020). This distinction is crucial for comprehensively understanding climatic effects, including the thermal legacy and the conditions that favor biological invasions. To achieve this, we tested 27 interconnected hypotheses, supported by ecological theories, to elucidate how climate-related variables influence taxonomic, size, and trophic diversities (Table S1). Specifically, we anticipate that climate warming would directly reduce taxonomic and size diversity, subsequently decreasing trophic diversity. Additionally, we expect climate warming to facilitate the presence of exotic species, which would mediate its effects, further reducing taxonomic richness and exacerbating impacts on size and trophic diversities (Table S1). As a result, we offer one of the first empirical assessments embedding biological invasions as a mediating factor of climate change to evaluate both its direct and indirect effects on the current state of community diversities.

2 | Materials and Methods

2.1 | Lake Temperature Data

We analyzed 257 lakes throughout Metropolitan France (Figure S1). Among these lakes, 49 are natural and 208 are artificial (i.e., 189 reservoirs, 11 gravel pits and 8 other artificial lakes including 5 ponds and 3 quarry lakes). For these lakes, daily epilimnion (i.e., surface) water temperature simulations were conducted using the two-layer semi-empirical Ottosson-Kettle-Prats Lake Model (OKPLM; Prats and Danis 2019) and obtained from Sharaf et al. (2023b). This model simulates both

epilimnion and hypolimnion temperatures based on the lake's geomorphological characteristics (including maximum depth, volume, surface area, latitude, and altitude) as input data, along with air temperature and solar radiation as meteorological forcing (see details in Sharaf et al. 2023a). Available OKPLM simulations for the 257 lakes considered in this study were either run with calibrated ($n = 134$) or default ($n = 123$) model parameters. Using these simulation data, we calculated two climate-related variables for each lake and sampling event: (1) temperature condition ($^{\circ}\text{C}$) as the annual mean epilimnion temperature of the 5 years before each sampling event to account for previous climatic effects on fish recruitment, and (2) climate warming as the long-term trends in annual mean epilimnion temperature ($^{\circ}\text{C dec}^{-1}$) over the past 40 years preceding each sampling event. Climate warming was estimated by calculating the Sen's slope through the modified Mann-Kendall test (Yue and Wang 2004), using the 'modifiedmk' R package (Patakamuri and O'Brien 2021). For each lake, the rate of temperature change over time was quantified using the slope coefficient, and its significance was assessed based on the associated p -value. The uncertainty analysis of simulated epilimnion temperatures indicated that the median of the 90% confidence interval for simulations across our set of lakes ($n = 257$) was 3.1°C (see Sharaf et al. 2023a for more details).

2.2 | Fish Communities

Fish communities were sampled between 2005 and 2019 in the 257 lakes (Figure S1) using the standardized Norden gill-net protocol (CEN 2005, 2015). Sampling was conducted in late summer and early autumn, where the predefined number of nets per lake depended on the area and depth of the lake (Appelberg et al. 1995). Specifically, in benthic habitat, multimesh gillnets (12 panels of 5–55 mm knot-to-knot; 30 m long and 1.5 m high) were set, and in deep lakes (> 10 m), sampling was completed using pelagic multimesh gillnets (11 panels of 6.5 to 55 mm knot-to-knot; 27.5 m long and 6 m high), which were lowered by 6-m increments each day, starting at the surface and until they were above the sediment. A total of 430 sampling events (i.e., fishing operations) were conducted in the 257 lakes during the study period (with an average of 1.7 sampling events per lake; Figure S1). During sampling events, captured fish were identified to the species level and measured individually unless they were too numerous. In the latter case, they were divided into groups based on their taxonomy and body size, in which the body size of a subset of individuals was measured. The body size of unmeasured individuals was estimated based on the assumption that body size within a group follows a normal distribution (for more details, see Danet et al. 2021). Following Daupagne et al. (2021), the range of fish body size was restricted to 2.5–96.5 cm, to avoid selectivity bias due to poor retention in the gear and to infrequent catches (i.e., juveniles or small fish can swim through the mesh and the largest individuals can bypass the nets more easily). In addition, each species was classified as native or exotic following the National Inventory of Natural Heritage (MNHN & OFB [Ed.], 2003), a reference platform on the state and conservation of biodiversity and geodiversity in France (Figure S2). The term “exotic” is used broadly to include all fish species, whether they have been translocated from other

drainage systems within a geographic region or introduced from outside the region, such as from another continent.

2.3 | Community Size Spectrum

Fish size spectra from each sampling event were calculated using a bin-normalized method, as in other size spectra studies in lotic ecosystems (Arranz et al. 2019; Emmrich et al. 2014; Marin et al. 2023). First, we classified the individual fish body size into 6 classes that follow a geometric series of two in which size intervals are narrow at small body sizes but become progressively wider as body size increases (Table S2; Sprules and Barth 2016). We then estimated the size spectrum for each sampling event using an ordinary-least square (OLS) regression model between the \log_2 value of the midpoint of each size class and the \log_2 value of the total abundance of individuals per size class, normalized by bin width (Sprules and Barth 2016). The width of the size classes increases progressively with body size, potentially influencing the size spectrum calculations, but normalization avoids these effects and allows comparisons between studies (Sprules and Barth 2016). The slope of the linear model represents the rate at which abundance changes with increasing body size. It provides information on the relative proportion of small- and large-bodied individuals and on the efficiency of biomass transfer through body size distributions (Blanchard et al. 2009). The elevation of the size spectrum is expressed as the height of the midpoint on the y -axis after scaling as the centered intercept to avoid high correlations with the slope (Sprules and Barth 2016). It relates to community richness and is a proxy for food-web capacity or the abundance/biomass supported within the system (Murry and Farrell 2014). The bin-normalized size spectrum approach allows obtaining complementary descriptors of the size spectrum parameters (elevation and slope), although the slope value is best estimated with the maximum likelihood estimation (MLE) (Edwards et al. 2017). This approach provides similar slope estimates to the MLE method.

2.4 | Food-Web Inference and Structure

To obtain the local food-web structure of fish communities, we first built a metaweb that is a compilation of potential trophic links among all trophic species and resources present in our dataset. We applied the method developed by Bonnaffé et al. (2021) and Danet et al. (2021) for fish communities in French streams, recently expanded to include French lake communities prior to 2018 (Bonnaffé et al. 2024). This approach accounts for ontogenetic diet shifts and determines trophic links based on species identity and body size. Specifically, each fish species was divided into nine body size classes (i.e., trophic species) distributed evenly over the range of their measured body size. The nine evenly spaced size classes were chosen as the optimal number for robust comparisons of food web structures (Bonnaffé et al. 2021; Danet et al. 2021). This approach standardizes size categories across species, ensuring that the focus remains on the food web structure and trophic interactions, rather than on the detailed size distribution within the community, as is the case in size spectrum analysis. Seven potential “resources” were also included in the metaweb to account for the presence of primary

producers (i.e., detritus, biofilm, phytoplankton; trophic level 1), primary and secondary consumers, such as zooplankton and zoobenthos. The resulting metaweb contained 52 fish species divided into nine size classes and 7 resource nodes, resulting in 475 nodes (i.e., $52 \times 9 + 7$) enabling it to span the full range of trophic levels.

Fish–resource trophic interactions within the metaweb were established using published information on fish diet across ontogeny. Fish–resource interactions were assumed to be present if this interaction was reported in the literature for a given fish ontogenetic stage (with each fish species having two or three size-dependent ontogenetic stages) (Bonnaffé et al. 2021; Danet et al. 2021). Fish–fish interactions (i.e., piscivory) were defined based on predator–prey body size ratios. The predation window of a piscivorous trophic species was defined as 3%–45% of the midpoint of its body size class (Claessen et al. 2002; Mittelbach and Persson 1998). An interaction was set between a piscivorous trophic species and all fish prey whose body size class midpoint fell within the piscivore's predation window. Resource–resource interactions (e.g., zooplankton–phytoplankton), established based on published information, were also incorporated into the food web reconstructions to ensure the food webs are rooted and to enable the computation of trophic metrics (see below).

Finally, for each sampling event, we inferred the local food-web structure by extracting from the metaweb, trophic species and resources as well as their trophic links. To characterise the structure of each local food-web, we computed connectance and maximum trophic level (Thompson et al. 2012). Connectance is the proportion of realised interactions (L) out of the maximum number of possible interactions ($N \times (N - 1)$; excluding self-consumption of trophic species and resources) informing on the food-web complexity. N represents the number of nodes, which here corresponds to the total number of resource categories combined with the number of trophic species (i.e., the number of size classes for each species) present in the food web. Therefore, low connectance indicates that few links exist between entities within the food web. The maximum trophic level is the highest trophic level occupied by a consumer in the food-web informing on the breadth of the vertical dimension of the food-web. The trophic level of a consumer-node is calculated as one plus the weighted average of the trophic levels of its prey-nodes (the trophic level of basal species being one). The two metrics were calculated using the 'NetIndices' R package (Kones et al. 2009).

2.5 | Statistical Analyses

We investigated how climate-related variables (i.e., temperature condition and climate warming) affect the size (i.e., CSS slope and elevation) and trophic (i.e., connectance and maximum trophic level in food-webs) properties of freshwater fish communities both directly and indirectly through their effects on taxonomic diversity due to biological invasions (i.e., exotic species richness and total species richness). To do so, we used a Structural Equation Model (SEM), a powerful multivariate method (Fan et al. 2016).

SEMs integrate multiple predictors and response variables into a single causal network, where paths represent hypothesized

relationships. By incorporating all variables and pathways into a single comprehensive model, SEMs account for multiple testing, thereby reducing the risk of inflated Type I errors. This method is particularly valuable when response variables also act as predictors for other response variables, allowing for the analysis of both direct and indirect effects (Grace 2022; Lefcheck 2016). Direct effects represent the immediate relationship between a predictor variable and a response variable, while indirect effects capture relationships between a predictor variable and a response that are mediated by one or more intermediate variables. By considering both types of effects, SEMs provide a holistic assessment of total effects, calculated as the sum of direct and indirect contributions for each predictor variable. However, a limitation of this method is its inability to incorporate interactions among predictor variables.

Here, our *a priori* relationships were derived from a literature review, where, for instance, temperature was hypothesized to influence food web structure directly by impacting thermally sensitive species or indirectly by facilitating invasive species. This resulted in the formulation of 27 interconnected hypotheses (see Table S1), where the key relationships within the SEM can be summarized as follows: (1) climate-related variables, taxonomic, and size diversity directly affect trophic diversity, (2) climate-related variables and taxonomic diversity affect size diversity, (3) climate-related variables affect taxonomic diversity that may result from biological invasions. This design aimed to disentangle the direct and indirect effects of climate warming and biological invasions, once these factors have occurred, on the current taxonomic, size, and trophic diversities of lake fish communities.

The SEM was constructed using the 'piecewiseSEM' R package (Lefcheck 2016) based on gaussian linear mixed-effects models fitted using the 'lme4' R package (Bates et al. 2015). We set sites as a random effect on the intercept to account for site variations, particularly those related to differences in geomorphology and trophic state, as nutrient variables have not been sampled across all lakes. We checked for the absence of multi-collinearity among variables using the variance inflation factor (VIF; Table S3). The overall piecewise structural equation model fit, indicating that the hypothesized relationships align with the data, was assessed using Fisher's C test with the requirement of statistical insignificance ($p > 0.05$) as the criterion for consistency. Direct, indirect and total effects within the SEM were estimated using the 1000-fold bootstrapping method by the 'semEff' R package (Murphy 2022), providing robust estimates and assessing the statistical significance of these effects.

The R code to reproduce the analyses, along with all raw and derived data, is archived on Zenodo (Leclerc 2025).

3 | Results

3.1 | Distribution of Forcing and Community Response Variables

Temperature conditions observed across lakes ranged from 5.75°C to 18.42°C (mean \pm σ = 13.75 ± 1.78) while climate warmings spanned from -0.18°C to $0.74^\circ\text{C dec}^{-1}$ (mean \pm σ = 0.31 ± 0.16 ; Figure 1A). A vast majority of the studied lakes (92.6%)

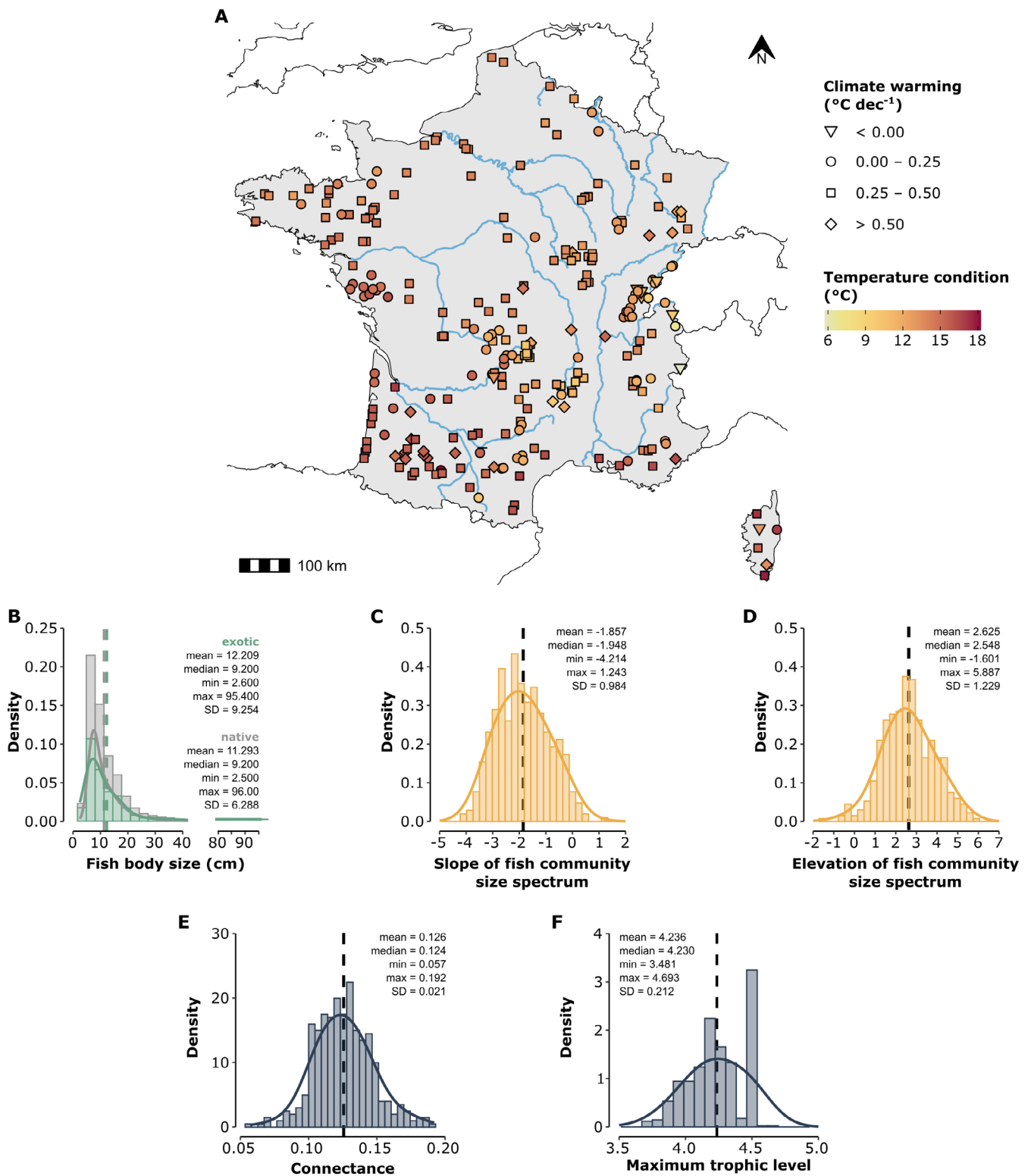


FIGURE 1 | Characteristics of lake temperature, individuals body size of native and exotic species, community size spectra, and food-web structure. (A) Map of temperature condition ($^{\circ}\text{C}$; yellow-red colour gradient) and climate warming ($^{\circ}\text{C dec}^{-1}$; shape gradient). Density estimation with histogram and kernel-smoothing of (B) body size of fish individuals (cm) of native and exotic species, (C) slope of fish community size spectrum, (D) elevation of fish community size spectrum, (E) food-web connectance, and (F) maximum trophic level of food-webs. On panel A, for lakes with multiple sampling events, the mean value of temperature condition and climate warming were considered. On panels B to F, the dashed vertical lines represent the mean values of fish community composition, community size spectra, and food-web attributes. Notice the x-axis break for panel B.

experienced significant warming (i.e., slope coefficient > 0 and $p < 0.05$).

Across lakes, 52 fish species were inventoried, and 19 of them were exotic (Figure S2). Within lakes, we found that total fish richness varied from 3 to 18 species (mean $\pm \sigma = 9 \pm 2$) and exotic fish richness ranged between 0 and 6 species (mean $\pm \sigma = 2 \pm 1$). Overall, individuals of exotic species had significantly larger body sizes than those of native species (GLM procedure with Gamma error distribution and inverse link function, $F = -37.5$, $p < 0.001$; Figure 1B). Specifically, the exotic to native fish mean body size ratio was greater than 1 in 80.6% of the sampling events, indicating that individuals of exotic fish species are, on average, larger than those of native fish species in most sampling events (Figure S3A). This percentage decreases to 62.9% if one considers the ratio of the maximum body size of exotic fish species relative to the maximum body size of native fish species (Figure S3B).

As in previous studies on freshwater fish communities (Arranz et al. 2023; Marin et al. 2023), we found mainly negative CSS slopes (mean $\pm \sigma = -1.86 \pm 0.98$; Figure 1C). This suggests a higher proportion of small-bodied individuals compared to large-bodied ones within the community. Moreover, CSS elevation, which reflects the overall abundance of organisms across different size classes within the community, also showed variability (mean $\pm \sigma = 2.62 \pm 1.22$; Figure 1D), but was within the range of average elevations found in previous studies (Marin et al. 2023).

Food-web connectance ranged from 0.05 to 0.19 (mean $\pm \sigma = 0.13 \pm 0.02$; Figure 1E). This indicates significant variability in food-web complexity, yet with values comparable to the average connectance of 0.1–0.2 reported in other aquatic ecosystems, suggesting similarly simple trophic structures (Dunne et al. 2002). Additionally, the maximum trophic level varied between 3.5 and 4.7 (mean $\pm \sigma = 4.2 \pm 0.2$; Figure 1F), aligning with previously reported ranges of food-chain lengths in lakes (Jake Vander Zanden and Fetzer 2007).

3.2 | Effects of Temperature on Fish Taxonomic, Size, and Trophic Diversity

To unravel the intricate effects of climate change and biological invasions on the size and trophic structures of fish communities, we performed a SEM analysis. This allowed us to explore 27 potential relationships among climate-related variables, taxonomic, size, and trophic diversities (Table S1). Our final model, which retained 13 out of 27 hypothesized paths (Fisher's $C = 0.417$, $p = 0.812$; Figure 2), explained a large part of the variance in temperature condition ($R^2_c = 0.97$), taxonomic diversity (R^2_c exotic species rich. = 0.55; R^2_c tot. species rich. = 0.79) and trophic diversity (R^2_c connectance = 0.51; R^2_c max. troph. level = 0.51). Regarding size diversity, the model accounted for a substantial portion of the variability in the CSS elevation ($R^2_c = 0.41$), though it was less explanatory for the CSS slope ($R^2_c = 0.13$; Figure 2). Moreover, site variations (random effects), which considered differences in site-specific factors, beyond temperature and invasion, accounted for substantial portions of the variation in temperature condition

and metrics related to taxonomic, size and trophic diversities (Figure 2).

The reliability of the SEM enables us to examine the partitioning of the direct and indirect effects of the predictive variables (Figure S4), as well as their total effects on the response variable (Figure 3). This analysis reveals that fish taxonomic, size, and trophic diversities were strongly dependent on climate-related variables (Figures 2 and 3). In line with our hypothesis, lakes with warmer temperatures had a steeper CSS slope ($r\delta = -0.10$, where $r\delta$ denotes the standardized regression coefficient) and weakly connected food webs ($r\delta = -0.17$); the latter effect being explained by both direct and indirect effects mediated by total species richness and CSS elevation (Figures 2 and 3A; Figure S4A). As expected, climate warming increased exotic species richness, but this effect was relatively small and mainly due to the indirect effects of climate warming through temperature conditions ($r\delta = 0.11$, Figures 2 and 3B; Figure S4B). Indeed, we found a strong relationship between the temperature condition and the richness of exotic species, with warmer lakes hosting more exotic species ($r\delta = 0.38$). However, lakes hosting more native species did not show a significant relationship between native and exotic species richness (Figure S5). Also, temperature condition had a positive effect on total species richness. Interestingly, this effect was mostly mediated by an increase in exotic species richness in warmer lakes (Figures 2 and 3A; Figure S4A) which increased total species richness ($r\delta = 0.58$) and expectedly reduced connectance. Moreover, exotic species directly decreased maximum trophic level and CSS elevation, but these negative effects were counterbalanced by their indirect positive effects mediated by the increase in total species richness ($r\delta = 0.18$ for CSS elevation and $r\delta = 0.28$ for maximum trophic level). As a result, exotic species richness did not show a significant total effect on metrics related to maximum trophic level and community size spectra (Figures 2 and 3C; Figure S4C). Finally, the CSS slope had no effects on trophic diversity metrics, whereas the CSS elevation showed effects on both trophic diversity metrics (Figures 2 and 3E,F; Figure S4E,F). Significantly, CSS elevation negatively affected connectance through a direct effect ($r\delta = -0.22$) and positively influenced maximum trophic level, which can be explained by both direct and indirect effects mediated by connectance. Notably, these patterns may vary across different lake types (Figure S6), highlighting the potential influence of lake-specific factors on the observed relationships. Moreover, likely due to the higher representation of reservoirs, the overall pattern closely aligns with them.

4 | Discussion

Climate change and biological invasions have emerged as the primary causes of changes in community composition and species traits, respectively (Jaureguiberry et al. 2022). Understanding the complex interplay between these two threats poses a significant challenge for biodiversity research, complicating efforts to discern whether biological invasions independently contribute to biodiversity loss or whether they are secondary to fundamental physical factors related to climate change (Williams-Subiza and Epele 2021). Here, we provide a new perspective on how climate change and biological invasions are intertwined, aiming to quantify their impacts on

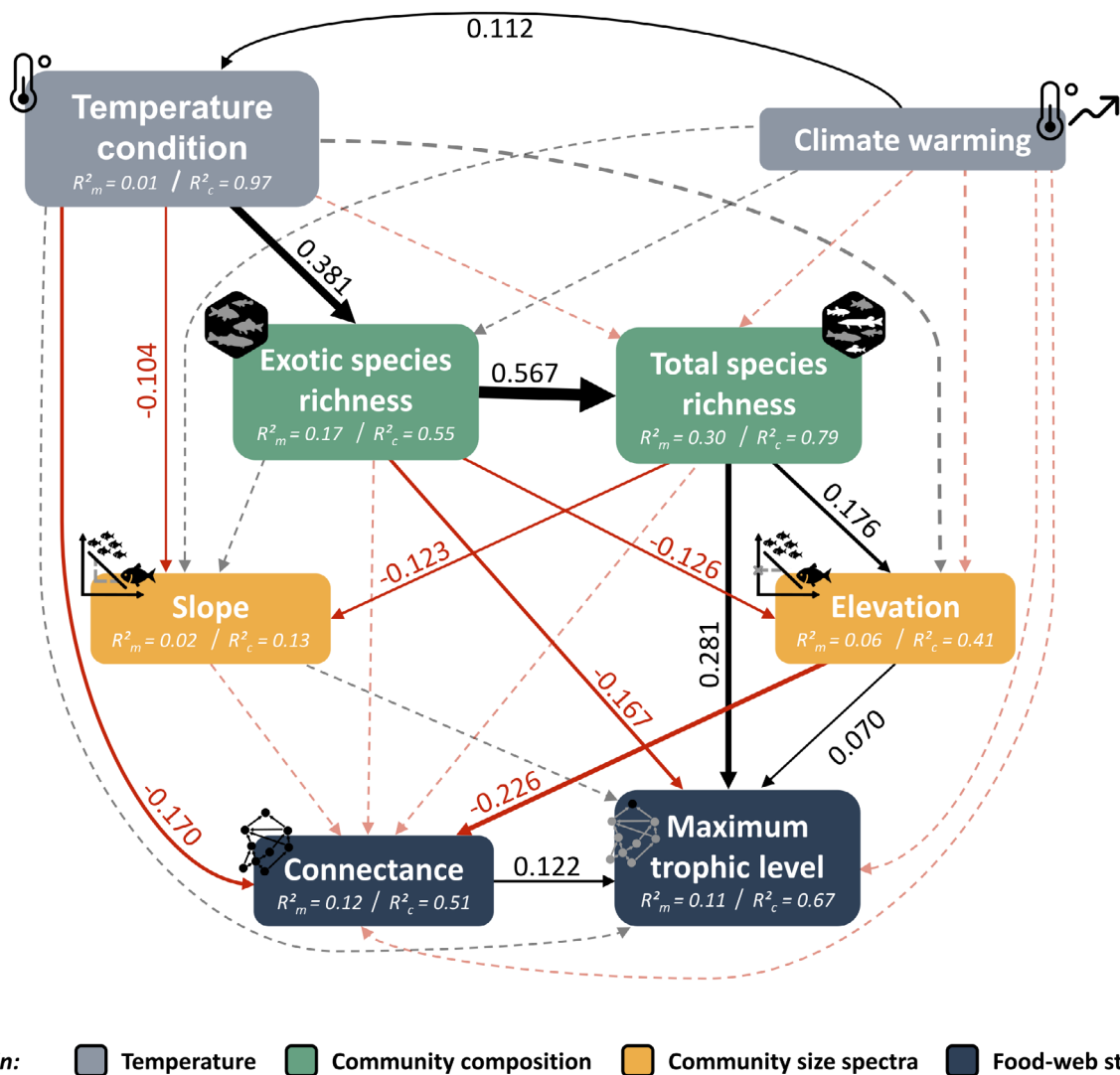


FIGURE 2 | Structural equation model depicting the direct effects of climate-related variables (i.e., temperature condition and climate warming) on fish taxonomic (i.e., exotic species richness and total species richness), size (i.e., slope and elevation of CSS), and trophic (i.e., connectance and maximum trophic level in food-webs) diversities for the 430 sampling events conducted across French lakes ($n = 257$). The regression coefficients estimated by the SEM were standardized to compare their magnitude and express the variation of x and y in standard deviation units. Arrows represent unidirectional relationships between variables and are scaled on the absolute value of the standardized regression coefficient. Positive relationships are denoted by black arrows, negative by red, significant by solid, and dashed are not significant. Additionally, the marginal R^2 (R_m^2 ; fixed factors only) and the conditional R^2 (R_c^2 ; all factors, including random effect) values for each latent and response variable are provided.

the current taxonomic, size, and trophic diversities of freshwater fish communities. We found that temperature conditions influenced by climate warming exert important effects on these different diversities, primarily through indirect pathways mediated by biological invasions.

4.1 | Temperature Condition, Influenced by Climate Warming, Plays a Significant Role in Shaping Freshwater Fish Diversity

While previous studies reported a decline in the vertical structure and an increase in connectance within freshwater food webs in response to long-term warming trends (Barbosa and Siqueira 2023), we found no direct or indirect effects of the rate of climate warming on food-web structure. It has already been shown that temperature trends are relatively poor indicators

of the thermodynamic phenomena in lakes, such as stratification—an important physical phenomenon for lake biota and water quality (Kraemer et al. 2015). Thus, it appears that even though the majority of lakes were warming, the rate at which climate is warming had little effect on fish communities. On the opposite, temperature conditions which were influenced by climate warming showed effects on the current taxonomic, size, and trophic diversities of freshwater fish communities, with a stronger impact observed in natural lakes compared to reservoirs (Figure S6). Particularly, we found a negative correlation between temperature conditions and both the CSS slope and the food-web connectance. In freshwater ecosystems, warmer conditions tend to favor smaller-bodied organisms over larger ones (Gardner et al. 2011), as larger consumers tend to process matter and energy less efficiently at higher temperatures (Sentis et al. 2024). Accordingly, we found that fish communities exhibit steeper slopes of the size spectrum under warmer

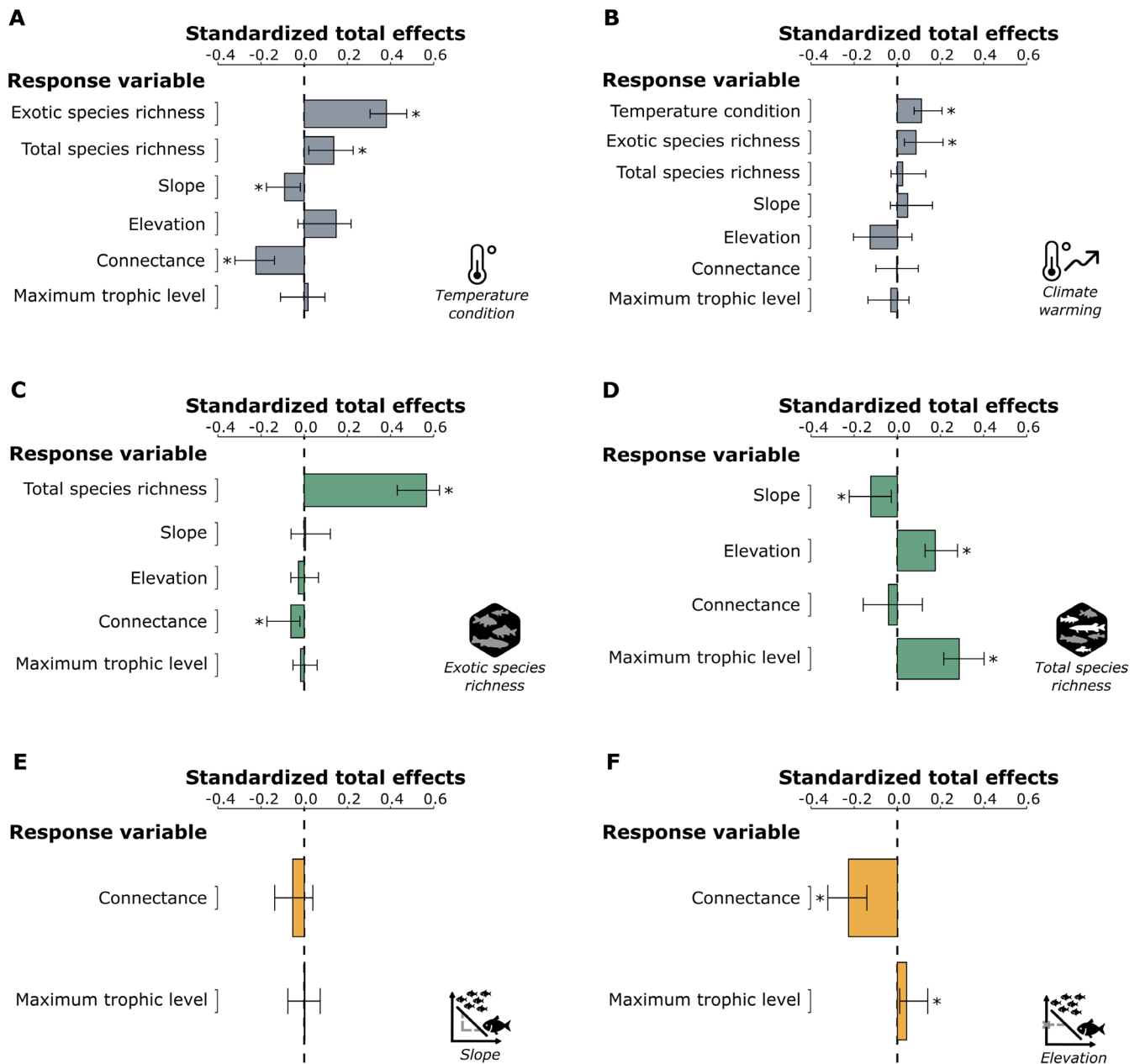


FIGURE 3 | Standard total effects (direct plus indirect effects) of climate-related variables, fish taxonomic and size diversity. Effects of (A) temperature condition, (B) climate warming, (C) exotic species richness, (D) total species richness, (E) CSS slope, and (F) CSS elevation. Bars and error bars represent mean \pm 95% confidence intervals (CI); $n = 1000$ bootstrapped estimates for each response. Significant effects are indicated by an asterisk (*). Bars are coloured according to the data domain of the predictor variable. Grey bars represent climate-related variables as predictors, green bars represent variables related to fish taxonomic diversity, and yellow bars represent variables related to fish size diversity. Standard direct and indirect effects are represented in Figure S3.

temperature conditions, implying a reduction in the proportion of large-bodied individuals as temperature increases, consistent with prior research (Dossena et al. 2012; Marin et al. 2023; Yvon-Durocher et al. 2011). We would thus expect a cascading effect on food-web structure, as species' trophic niches, trophic positions, and interactions are typically determined by body size (Cohen et al. 2003; Riede et al. 2011). Our results suggest a decrease in connectance in warmer lakes, aligning with observations in other freshwater ecosystems (Merz et al. 2023; O'Gorman et al. 2019). This could be explained by the tendency of top predators to have a broader niche breadth (Ho et al. 2022; Woodward et al. 2005) and their loss potentially simplifies

interaction networks. While this could also result in shorter food chains (Bonnafe et al. 2021; O'Gorman et al. 2019), our study did not reveal such outcomes. Overall, these findings have significant ecological implications, particularly for the resilience and stability of freshwater ecosystems in the face of climate change. Since large fish often serve as apex predators or ecosystem engineers, their decline, along with the simplification of food-web structures, could disrupt energy flow and trigger cascading effects on biodiversity, nutrient cycling, and ecosystem functioning and services (Estes et al. 2011). Notably, while temperature conditions influenced size and trophic diversities, these effects were mediated by the presence of exotic species,

highlighting the complex interplay between climate change and biological invasions.

4.2 | Biological Invasions Mediate the Impact of Temperature Condition on Fish Communities

We found that temperature conditions, influenced by climate warming, are positively related to the richness of exotic species. This is consistent with the tolerant invaders hypothesis, where the heat tolerance of exotic species provides them an advantage over related native species in warmer lakes (Bates et al. 2013; Jessop et al. 2023). Consequently, as more lakes are warming, it indirectly favors exotic fishes due to more suitable temperatures (Woolway et al. 2022). Contrary to expectations, we found a positive correlation between exotic species richness and total species richness. However, some existing literature indicates that exotic species do not always immediately reduce species diversity in invaded habitats (Gallardo et al. 2016). This suggests a time lag in the effects of biological invasions (Gallardo et al. 2016) or that habitat and resource availability may facilitate species co-existence (Bruehl et al. 2021). In addition, we found a negative total effect of exotic species on connectance, particularly in reservoirs (Figure S6), which was unexpected. Exotic species are often assumed to be trophic generalists (i.e., species with a large number of trophic links; Bernery et al. 2023) which should increase connectance. However, invasive freshwater fish species are not necessarily characterized by higher trophic levels compared to native species, nor are they top predators with a broader niche breadth (Jessop et al. 2023). This negative relationship between exotic species richness and connectance could be attributed to stronger biotic resistance to biological invasions in highly connected food webs compared to less connected ones (Smith-Ramesh et al. 2017). In addition, we did not find a significant total effect of exotic species richness on CSS slope and elevation, as well as on maximum trophic level. However, compensatory effects were evident between significant direct and indirect effects of exotic species richness on maximum trophic level and CSS elevation, particularly through total species richness. Although biological invasions may affect fish size, which contributes to size and trophic diversities, plastic responses or environmental factors like nutrient availability could also be influential. Further research is needed to clarify whether exotic species richness is the primary driver of changes in size structure or if these patterns are shaped by factors such as fish age. We also found that total species richness showed a significant positive effect on the maximum trophic level and CSS elevation, as well as a negative effect on the CSS slope, as already shown in the literature (Table S1). Our findings thus suggest that the effects of climate change on communities cannot be fully understood without considering biological invasions (Williams-Subiza and Epele 2021). Climate-driven increases in exotic species may alter community structure and trophic interactions over time, potentially simplifying food webs and disrupting ecosystem functioning. While exotic species initially boost total species richness, their long-term effects remain uncertain, as delayed negative impacts could emerge through competition, predation, or habitat changes (Sentis et al. 2021). However, our analysis does not differentiate between exotic species originating from outside their natural geographical range and those translocated within regional drainage basins, nor does it distinguish

accidental introductions (e.g., via fishing activities) from deliberate ones, such as stocking practices or within-country translocations. Incorporating both the origin and mechanisms of species establishment into the analysis would provide a more nuanced understanding of the effects of biological invasions. In addition to temperature and invasion, other site-specific factors—such as physical and chemical conditions or lake types (see Figure S6)—likely contribute to the observed patterns (Leclerc et al. 2023). For example, reservoirs may act as stepping stones for exotic species, enabling their spread across connected ecosystems (Johnson et al. 2008). These factors, alongside fishing activities and stocking practices, may actively alter community composition, masking natural patterns of invasion susceptibility. Furthermore, previous invasions and climate change may have already extirpated or reduced vulnerable native species, particularly those with specific functional traits (e.g., coldwater species; (Comte et al. 2013; Daufresne and Boët 2007)), complicating their detection and disrupting expected relationships. This may partly explain why we found no relationship between native and exotic species richness (Figure S5), contrary to the rich-get-richer hypothesis, which posits that species-rich native communities are more susceptible to invasions due to greater niche availability (Stohlgren et al. 2006). To better understand these patterns and their underlying drivers, longer time-series data are needed to clarify these interactions and assess their long-term effects on native and total species diversity.

4.3 | Size and Trophic Diversities Carry Different Information

We found that the elevation of fish community size spectrum is related to both metrics of the food-web structure. Conversely, the slope of the size spectrum showed no significant correlation with either maximum trophic level or connectance. This finding is somewhat unexpected, as the literature often suggests a close association between the community size spectrum and the food-web structure, although such assertions have seldom been tested (Blanchard et al. 2017; Brose et al. 2017). Typically, the slope of the community size spectrum is considered a proxy for trophic or ecological efficiency within food-webs (Murry and Farrell 2014) and therefore should be related to the maximum trophic level and connectance. However, we did not observe such relationships, despite using an allometric approach to infer piscivory interactions (Bonnaiffé et al. 2021; Danet et al. 2021). One possible explanation for this discrepancy is that the community size spectrum method operates at an individual scale, whereas the food-web analysis is conducted at a (trophic) species scale. Consequently, the slope of the community size spectrum may remain identical when considering one or multiple species, while the food-web structure depends on species richness and the range of species body size. This could partly explain the discrepancy between the slope of the community size spectrum and the structural metrics of the food-web, emphasizing the importance of considering both community facets. Nonetheless, we did find that the elevation of the fish community size spectrum is positively related to the maximum trophic level, while being negatively related to connectance. Elevation is commonly regarded as an index of food-web capacity or productivity potential (Murry and Farrell 2014) and is expected to vary positively with the maximum trophic level and negatively with

connectance. Studies have shown that communities with lower richness tend to exhibit lower maximum trophic levels (Maceda-veiga et al. 2018) but higher connectance (Riede et al. 2010; Schmid-Araya et al. 2002). Overall, our findings suggest that the trophic and size structures of freshwater fish communities are not strongly interlinked, but rather provide complementary perspectives on the ecological impacts of temperature. This distinction highlights the need to consider both trophic and size diversities when assessing the impacts of climate change and biological invasions. Integrating both size and trophic diversities can offer a more comprehensive understanding of ecosystem responses to environmental changes and inform more effective conservation and management strategies.

4.4 | Conclusions and Perspectives

Our research reveals empirical and significant impacts of temperature conditions, influenced by climate warming, on different key facets of fish communities, including taxonomic, size, and trophic diversities. We emphasize that these impacts are mediated by biological invasions, which act both as a consequence and a driver of the ecological effects of climate change. However, while our assessment of direct and indirect effects provides an important step toward understanding the relationship between climate change and invasions, further work is required to comprehensively unravel their interactions and feedbacks. Additionally, our results indicate that community size spectra and food-web structure are not closely intertwined, suggesting that they provide complementary insights on community structure responses to the impacts of climate change and biological invasions (Petchey and Belgrano 2010). These findings should stimulate future investigations into the intricate interplay of climate change and biological invasions, potentially elucidating key facets of community and ecosystem vulnerability to global change. Moreover, we stress the importance of advancing our understanding of the connections between trophic and size structures within communities. This is particularly crucial as both community facets can influence stability, persistence, and productivity (Blanchard et al. 2017; Danet et al. 2021) and can provide valuable insights into how communities respond to environmental changes (Woodward et al. 2005). This research is especially urgent in natural ecosystems already severely impacted by biological invasions, as these effects are expected to worsen with the accelerating pace of climate change (Roy et al. 2024).

Author Contributions

Camille Leclerc: conceptualization, data curation, formal analysis, methodology, software, validation, visualization, writing – original draft. **Victor Frossard:** conceptualization, methodology, writing – review and editing. **Najwa Sharaf:** formal analysis, methodology, software, writing – review and editing. **Simon Bazin:** formal analysis, methodology, software, writing – review and editing. **Rosalie Bruel:** methodology, visualization, writing – review and editing. **Arnaud Sentis:** conceptualization, funding acquisition, methodology, project administration, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and R code that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.13142281> and Github at <https://github.com/CamilleLeclerc/ClimateChangeFacetsFishCommunity>. Temperature data were obtained from <https://doi.org/10.57745/OF9WXR>. Fish community data was obtained from the Data portal of the Lake Ecosystems Cluster and can be requested at <https://dataecla.fr/en/contact>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.