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ARTICLE

Patterns and drivers of fish trophic trajectories over time

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Abstract

Biological communities are facing profound upheaval induced by global environmental change. While changes in community composition over time are now well documented, much less is known about whether concomitant shifts in trophic structure also manifest. Here, we leveraged a 10-year dataset of freshwater fish communities and stable isotope compositions in nine lakes to test whether compositional changes (i.e., changes in community structure) and local environmental factors drove trophic trajectories over time. We found marked changes in the trophic structure of fish communities across all lakes, with a general tendency toward narrower trophic niches dominated by trophically redundant species. The variations in trophic trajectories among lakes were primarily linked to differences in the temporal pace and directionality of change. Specifically, lakes exhibiting greater compositional changes displayed more irregularity in their trajectory, and communities dominated by non-native species displayed elevated trophic stability over time. Our findings reveal species turnover as the dominant factor shaping trophic dynamics, through the addition or removal of predatory species and trophic turnover. The trophic stability observed in communities that were already invaded at the start of the study could be driven by their reduced susceptibility to compositional change caused by subsequent invasions. These findings highlight the existence of strong changes in trophic niches and unveil the intricate interplay between compositional changes and biological invasions in governing the trophic trajectories of communities and food web architecture, with subsequent implications for ecosystem functioning.

KEYWORDS
community structure, compositional changes, ecological trajectories, non-native species, stable isotope analyses, temporal dynamics

INTRODUCTION

The rapidity of global change is raising concerns that the rewiring of the Earth's food webs may fundamentally alter ecosystem functioning in the future (Bartley et al., 2019). The rich diversity of food webs across the world (Chase, 2000) has sparked ongoing scientific inquiry seeking to identify the primary drivers of food web structure (Post et al., 2000; Schoener, 1989). Among them, habitat complexity has been identified as a key driver of food web structure (Halaj et al., 2000; Warfe & Barmuta, 2006). For example, more complex habitats have been reported to support lower trophic diversity and network connectance in ecosystems such as mangrove forests or lakes (Leclerc et al., 2023; Nauta et al., 2023). Studies have also shown that ecosystem productivity affects food web structure and food chain lengths (FCLs; Kaunzinger & Morin, 1998; Vander Zanden et al., 1999) through differences in the availability of basal resources (Briand & Cohen, 1987) and trophic transfer efficiency (Schmoker et al., 2016). Despite growing recognition of the dynamism of food webs (Kortsch et al., 2021), most studies have focused on the spatial variability of food webs, overlooking how temporal changes in the structure of biological communities affect food web architecture (Frelat et al., 2022; Polazzo et al., 2022).

Changes in community composition could be responsible for modified ecological interactions (Ponisio et al., 2019), through changes in taxonomic and functional diversity (Lepš et al., 2011) as well as resource availability and utilization (Kato et al., 2003; McMeans et al., 2015; Yletyinen et al., 2016). A well-known example is the reintroduction of wolves (*Canis lupus*) in Yellowstone National Park (USA) which caused a dramatic decrease in elk (*Cervus canadensis*) abundance and, as a result, an increase in the biomass of primary producers, thus reshaping the entire food web (Ripple & Beschta, 2012). Similarly, the introduction of invasive species can lead to profound changes in food web structure through trophic cascades and trophic niche displacement (Cucherousset & Olden, 2011; Jackson, Wasserman, et al., 2017). For example, the invasion of predatory lake trout (*Salvelinus namaycush*) entirely disrupted lake food webs in the Rocky Mountains (USA) through trophic displacement and dispersion (Wainright et al., 2021).

Freshwater communities face escalating pressures from human activities (Easterling et al., 2000; Tickner et al., 2020; Vörösmarty et al., 2010) and both species extirpations and invasions have led to the reshuffling of entire communities (Dornelas et al., 2014; Reid et al., 2019). Freshwater food webs are highly complex, owing in large part to elevated degrees of omnivory and their strong linkage with adjacent terrestrial and marine habitats (Baxter et al., 2005; Woodward et al., 2005), making them especially prone to change over time (Olesen et al., 2010). Nevertheless, our knowledge of the potential association between temporal changes in community structure and the associated food web changes remains limited (Frelat et al., 2022; Polazzo et al., 2022), notably because of sparse monitoring of food web structure over time.

Using recent frameworks developed to analyze ecological trajectories, this study explored whether fish compositional changes (i.e., changes in community structure) or environmental conditions led to predictable changes in trophic (isotopic) structure of gravel pit lakes over a 10-year period. Newly created lakes (Morse et al., 2014), such as gravel pit lakes, provide a unique opportunity to explore ecological trajectories because of the strong dynamics displayed by their ecological communities (Zhao et al., 2016) driven by community assembly and human-assisted colonization of species (Garcia et al., 2023; Paz-Vinas et al., 2021). These findings will help to understand the relationship between changes in community composition and trophic structure and will have important implications in the context of global change because the fluctuations of ecological communities are becoming increasingly frequent and intense (Chang & Turner, 2019; Gaüzère et al., 2015).

MATERIALS AND METHODS

Study sites

This study was performed in nine gravel pit lakes, located in a 450-km^2 area within the central part of the Garonne floodplain in southwest France, which are part of a long-term biodiversity monitoring program (Figure 1) (Alp et al., 2016; Zhao et al., 2016). All lakes had long exceeded the post-dredging filling phase (i.e., all were ≥15 years old) and were disconnected from the hydrological network and other gravel pit lakes. Consequently, variations in dissolved organic carbon (DOC) concentrations during the study period were limited (mean $= 1.48 \pm 1.69$ mg C L^{-1} SD), and trophic status index (TSI) values showed limited variation (mean $= 3.85 \pm 1.52$ SD), suggesting that trophic conditions remained relatively stable throughout the study period. These artificial lakes were selected to provide a gradient of local environmental conditions caused by different (1) levels of ecosystem maturity (Table 1, Colas et al., 2021), with lake age ranging from 15 to 49 years post-excavation at the beginning of the study, which was reflected in a gradient of productivity caused by eutrophication (from mesotrophic to hypereutrophic) and (2) hydromorphologies with differences in shoreline perimeter (from 564 to 4139 m), surface area (from 1.89 to 21.30 ha), and maximum depth (from 2.0 to 5.1 m) (Table 1).

Fish community monitoring

To assess the temporal changes in fish community and trophic structures, the nine lakes were sampled every

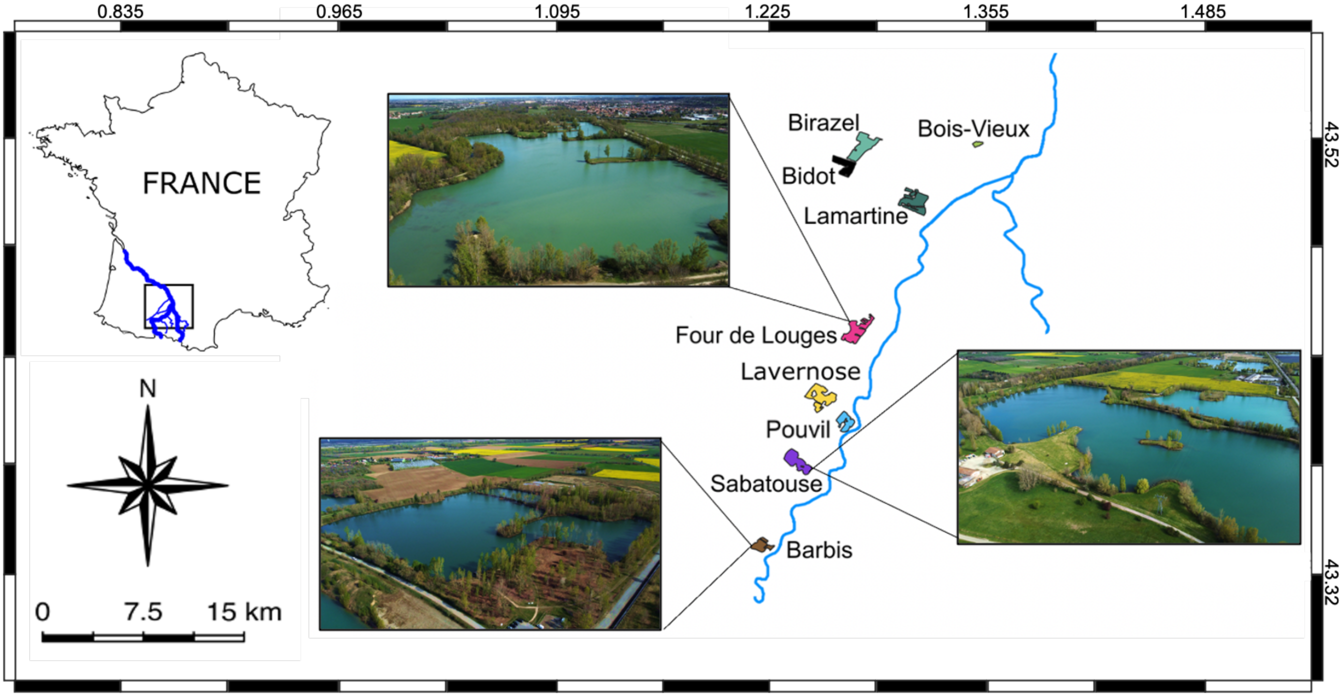


FIGURE 1 Locations of nine studied gravel pit lakes in the central part of the Garonne floodplain, southwestern France. Photo credits: Flavien Garcia.

TABLE 1 Environmental conditions of lakes at the beginning of the study.

Lake name	Excavation date	Surface (ha)	Perimeter (m)	Depth (m)	Trophic status index (TSI)
Barbis	1984	9.10	1617	4.4	55.37 (eutrophic)
Bidot	1993	15.18	2583	2.9	68.97 (eutrophic)
Birazel	1992	20.36	2634	2.6	60.80 (eutrophic)
Bois-Vieux	1963	1.89	564	1.9	64.31 (eutrophic)
Four de Louges	1980	18.77	3922	2.0	61.76 (eutrophic)
Lamartine	1970	21.30	4139	3.0	68.55 (eutrophic)
Lavernose	1992	18.21	2485	3.7	53.36 (eutrophic)
Pouvil	1996	10.39	2199	4.3	48.04 (mesotrophic)
Sabatouse	1997	16.29	2113	5.1	51.79 (eutrophic)

2 years on five consecutive occasions between 2012 and 2022 (except in 2020 due to the COVID-19 sanitary crisis) using the same protocol based on the use of a combination of gill netting and electrofishing (Zhao et al., 2016). Gill nets were deployed ($n = 7 \pm 1$) in the pelagic zone of the deepest area of each lake ($n = 2$ gill nets; mono-mesh size 50 mm and multimesh Pelagic EN 14757), and a set of additional nets was randomly distributed in the littoral zone to represent the different types of substrates and habitats ($n = 4$–6 depending upon lake size; mono-mesh size: 12, 20, 30, and 60 mm; and Benthic EN 14757). Gill nets were installed early in the morning (before 08:00 am) for about 1.5 h. This approach allowed a high density of gill nets, covering all the types of habitats and most fish body sizes, while limiting the associated mortality (Zhao et al., 2016). In addition, electrofishing (EFKO FEG 7000; Germany) was used as a complementary approach to collect fish, including small-bodied individuals, along the shore in shallow and highly structured habitats. This was performed using the point abundance sampling by electrofishing (PASE) approach, which is a cost-effective and nondestructive method to sample different species and life stages of freshwater fish in shallow habitats (Persat & Gordon, 1990). Following Copp and Paul (1995), an average of 27.3 ± 4.8 PASE was used, depending on lake size and perimeter. Each sampled fish

was identified to species and measured to obtain fork length to the closest millimeter. Body mass of each individual was subsequently obtained using length–weight relationships of each species from the study area (Zhao et al., 2016, 2019), and used to estimate species abundance (BPUE, biomass per unit effort). Because the sampling method was similar for each lake across habitats and between years, we expressed the biomass of each fish species by adding the data from the two methods (Zhao et al., 2016) to characterize the temporal dynamics of fish communities.

In total, 23,158 fish belonging to 22 species (including 11 non-native species) were sampled. Species richness of the lakes varied between 4 and 16 fish species throughout the study period (mean = 9 ± 3 SD). Fish communities in the study area were dominated by European perch (*Perca fluviatilis*, 21.48%), roach (*Rutilus rutilus*, 13.14%), and Northern pike (*Esox lucius*, 0.41%) as native species, and pumpkinseed (*Lepomis gibbosus*, 18.48%), Western mosquitofish (*Gambusia affinis*, 23.28%), and Wels catfish (*Silurus glanis*, 10.23%) as non-native species (Appendix S1: Table S1). The main predators in these lakes were Northern pike, European perch, and largemouth bass (*Micropterus nigricans*). Relative abundances of fish species varied over time (Appendix S1: Table S1), with some species becoming less abundant during the study, such as European perch (2012 = 32.52%, 2014 = 17.48%, 2016 = 33.60%, 2018 = 16.70%, and 2022 = 6.67%), and some species increasing in abundance, such as the Western mosquitofish (2012 = 7.08%, 2014 = 16.62%, 2016 = 14.60%, 2018 = 34.41%, and 2022 = 41.70%).

Stable isotope analyses

For a subset of fish captured ($n = 2290$, ranging from 3 to 22 individuals per species in each population to represent the range of size observed), a small fin-clip (pelvic fin) was sampled, rinsed with distilled water, and kept in a cooler for subsequent stable isotope analyses. We selected a similar number of adults, juveniles, and young-of-the-year (YOY) individuals, when available, to maintain a balanced representation of each life stage and each population over time. In addition, benthic invertebrates—mollusks (i.e., Bivalvia or Gastropoda) and Ephemeroptera—were collected for each site to obtain stable isotope baselines and putative resources (Imbert et al., 2024; Jackson, Evangelista, et al., 2017) by using a combination of kick-net, Ekman grabs, and Surber net. Additionally, terrestrial (allochthonous) primary producers (poplar leaves) and aquatic (autochthonous) primary producers—periphyton (using a brush on different littoral rocks)—were collected. In the field, samples were rinsed with distilled water and then kept in a cooler before being processed in the laboratory.

In the laboratory, fish fin-clips, macroinvertebrate samples, and tree leaf samples were oven-dried at 60°C for 72 h. For macroinvertebrates, dried samples were ground by hand using a pestle to obtain a homogeneous powder. Periphyton samples were frozen at −80°C and then freeze-dried for 72 h to obtain a homogeneous powder. Stable isotope analyses of carbon and nitrogen (δ^{13}C and δ^{15}N, respectively) were conducted by the Cornell University Stable Isotope Laboratory (COIL, USA). Overall, we obtained fish stable isotope values (δ^{13}C and δ^{15}N) in nine lakes in 2012, 2014, 2016, 2018, and 2022 (Appendix S1: Figure S1). Examinations of the temporal trends in δ^{13}C and δ^{15}N values for baseline resources (primary producers and benthic invertebrates) indicated that their stable isotope compositions (signatures) were relatively stable over time within each lake, with low interannual variability ($\delta^{13}\text{C} \le 2.21‰$ and $\delta^{15}\text{N} \le 2.09‰$) and no specific trend observed (Appendix S1: Figure S2A,B). Therefore, changes in stable isotope values of baselines were unlikely to drive the changes observed in the trophic trajectories of fish communities.

Lake properties

Several variables representing lake properties, identified as potential predictors of trophic changes, were measured for each lake (Table 2). Habitat complexity was assessed using the shoreline development index (i.e., ratio of the lake shore length to the circumference of a circle with lake area) calculated as $L/\left(2\pi^{0.5} \times A^{d/2}\right)$, where L is the measured shoreline of the lake, A is the area, and d is the shoreline fractal dimension. Here, a d value of 1.17 was used and obtained by regressing shoreline length on the area of the studied lakes (Seekell et al., 2022). Productivity of each lake was estimated based on the TSI (Carlson, 1977) using chlorophyll *a* concentration (AlgaeTorch; BBE Moldaenke), total phosphorus concentration (colorimetric analysis NF EN 6878, expressed in micrograms per liter), and water clarity (Secchi depth). TSI was calculated for each lake using the mean of the values obtained during the five sampling events. Finally, we quantified a level of non-native species dominance according to the proportion of non-native species biomass (BPUE) relative to the total biomass of the community.

Trajectory analyses

To ensure methodological consistency in the analysis of community changes and trophic changes, we used the

TABLE 2 Explanatory (i.e., lake properties) and response (i.e., trophic trajectory metrics based on stable isotope trajectory analysis [SITA]) variables included in this study.

	Metric	Ecological interpretation
Explanatory variables	Shoreline development index	Measures habitat complexity; higher values indicate a more irregular shoreline.
	Trophic status index (TSI)	Estimates lake productivity based on (chl *a*), (total phosphorus), and water clarity; higher values indicate more eutrophic conditions.
	Non-native dominance	Proportion of non-native species biomass relative to total community biomass (BPUE); higher values indicate a more invaded community at the start of the study.
Response variables	*Magnitude*:	
	Trajectory path length (TPL)	High values indicate a strong trophic change (trajectory magnitude) in the fish community over time.
	Net change ratio (NCR)	High values indicate a more regular magnitude (i.e., pace) of trophic change in the fish community over time.
	Direction:	
	Directionality (DIR)	High values indicate a more regular direction of trophic change in the fish community over time (i.e., straight).
	Trophic fidelity (FID)	High values indicate a small deviation from initial state or a recovery pattern toward their initial state after changes.

community trajectory analysis (CTA, De Cáceres et al., 2019) and stable isotope trajectory analysis frameworks (SITA, Sturbois et al., 2022), as they provide a direct and comparable method to measure temporal changes. These frameworks perform geometric analyses in an *n*-dimensional space of resemblance used to quantify trajectory magnitude and direction. Community and trophic trajectory analyses were performed using the R package "ecotraj" (De Cáceres et al., 2019; Sturbois et al., 2021, 2022).

Regarding community structure, we defined the multivariate space of resemblance by creating a matrix of Hellinger distances: Euclidean distances calculated using the Hellinger-transformed BPUE matrix (giving less weight to rare species; Legendre & De Cáceres, 2013; Legendre & Gallagher, 2001). To assess community variations through time (i.e., compositional changes), we calculated the length of community trajectory (trajectory path length [TPL]; see De Cáceres et al., 2019 for detailed formulas) within community ordination space (Appendix S1: Figure S3), which corresponds to the sum of all the segment lengths of the global trajectory (segments are the distance between two consecutive observations). Thus, high values of community trajectory indicate strong changes in community composition.

Regarding the trophic structure trajectory, the trophic ordination space was defined using a principal coordinates analysis (PCoA) based on a matrix of several functional metrics describing the geometric structure of fish communities in the stable isotope space (δ^{13}C and δ^{15}N). These stable isotope metrics included δ^{13}C range, isotopic richness (i.e., Total Area from Layman et al., 2007; Iric), isotopic divergence (Idiv; i.e., tends to 1 when all the trophic entities are located on the edges of the convex hull), isotopic evenness (Ieve; i.e., tends to 1 when trophic entities are evenly distributed in the isotopic space), isotopic dispersion (Idis; i.e., tends to 1 when trophic entities tend to have contrasted stable isotope compositions), and isotopic uniqueness (Iuni; i.e., tends to 1 when most of the trophic entities are isolated in the isotopic space) (Cucherousset & Villéger, 2015). In order to measure the FCL in each food web ($n = 9$ lakes $\times$ 5 years $= 45$ food webs), we first transformed the trophic position of each individual using a baseline transformation (TP; Anderson & Cabana, 2007) and then took the maximum TP (Post, 2002b); following this equation (Equation 1):

$$\mathrm{TP_{sample}} = \mathrm{TP_{baseline}} + \frac{\delta 15\mathrm{N_{sample}} - \delta 15\mathrm{N_{baseline}}}{\mathrm{TEF}} \tag{1}$$

where $\delta^{15}\mathrm{N}_{\mathrm{baseline}}$ was the mean of δ^{15}N values of mollusks (i.e., Bivalvia or Gastropoda) and Ephemeroptera (Imbert et al., 2024). If only one baseline was collected, it was used to calculate $\delta^{15}\mathrm{N}_{\mathrm{baseline}}$. $\mathrm{TP}_{\mathrm{baseline}}$ was 2 and TEF (trophic enrichment factor) was 3.4 (Post, 2002a).

Trophic trajectories of fish communities were evaluated according to the first two dimensions of the aforementioned trophic ordination space, which accounted for 62.3% of the total variance in the stable isotope metrics (Appendix S1: Figure S4). The first dimension (41.3% of the total variance and eigenvalue of 2.9; Appendix S1: Figure S4) was mainly associated with the isotopic uniqueness (25%), isotopic dispersion (22%), and isotopic evenness (19%; Appendix S1: Table S2), reflecting the level of trophic redundancy in the community (cf. Layman et al., 2007). Therefore, fish communities displaying low values along the first dimension had redundant species (i.e., similar isotopic compositions), whereas fish communities displaying high values had unique species. The second dimension (21.0% of the total variance and eigenvalue of 1.47; Appendix S1: Figure S4) was mainly associated with the FCL (27%), isotopic diversity (23%), and the range of δ^{13}C of the fish community (23%; Appendix S1: Table S2), reflecting the trophic niche breadth of the community (i.e., size of the trophic niche). Consequently, fish communities with low values along the second axis had a narrow trophic niche, whereas fish communities with high values had a broad trophic niche.

To assess trophic variations through time, several trophic trajectory metrics describing the magnitude and direction of change were calculated based on the trophic multidimensional space (De Cáceres et al., 2019; Sturbois et al., 2021 for detailed formulas, Table 2): (1) the trophic TPL which corresponds to the sum of all the segment lengths of the global trajectory; (2) the net change ratio (NCR)—defined as the ratio between the overall net trajectory change (NC; difference between the initial and final state) and the TPL—which describes the regularity of trajectory segment magnitude over time; (3) the directionality (DIR) which corresponds to the regularity of trajectory segment angles over time; and (4) the "trophic fidelity" (FID) which refers to the deviation from the initial state (RDT in De Cáceres et al., 2019; Sturbois et al., 2021) with high values of FID indicating a small deviation from the initial state or a recovery pattern toward the initial state after changes. To assess the potential effects of the analytical errors in stable isotope analyses on trophic trajectory metrics, we performed an error propagation analysis using a bootstrapping approach (Appendix S2: Methods).

Community and trophic dynamics analyses

Associations between the trophic trajectory metrics (matrix *Y*) and both the community trajectory metrics and lake environmental characteristics (matrix *X*) were quantified using a redundancy analysis (RDA; Legendre & Legendre, 2012). All variables were standardized prior to the RDA. Both the significance of the global RDA and the variables of the explanatory matrix were tested using the anova.cca function with 10,000 permutations. RDA was performed using the R package "vegan" (Oksanen et al., 2017).

To quantify species turnover over time, we calculated the Jaccard index (*J*), which measures the proportion of shared species between two consecutive time steps relative to the total number of species observed across both surveys (Legendre & Legendre, 2012). The Jaccard index was calculated for each lake separately, and then averaged across all lakes to provide a regional value. To assess the changes in species relative biomass composition in each community, we used the Bray–Curtis dissimilarity index (BC) (Legendre & Legendre, 2012). This metric quantifies differences in species relative biomass between time steps, ranging from 0 (identical composition) to 1 (no shared biomass among species). Jaccard similarity coefficients were calculated using the *betapart* package (Baselga & Orme, 2012) and Bray–Curtis dissimilarity coefficients (based on the species BPUE matrix) were calculated using the vegan package.

Following the same logic as the community-weighted mean δ^{13}C and δ^{15}N, often used in trait-based or isotopic ecology (e.g., Fujii et al., 2023), we computed the community-weighted trophic position (CWTP) for each lake and each year, to assess interannual variability within lakes. CWTP represents the average trophic position of all individuals in the community, weighted by their relative biomass, and was computed as follows (Equation 2):

$$\mathrm{CWTP} = \sum_{i=1}^{n} (\mathrm{TP}_i \times W_i) \tag{2}$$

where TP_i is the trophic position of species *i*, and W_i is its relative biomass within the community. The SD of CWTP within each lake was also computed to estimate the degree of trophic fluctuation over time.

To examine the changes in the contribution of key piscivorous species (e.g., Northern pike, largemouth bass, European perch, pikeperch *Sander lucioperca*, and Wels catfish) to fish communities, we calculated the relative occurrence of piscivorous species (expressed as the number of piscivorous species divided by the total number of species recorded) and relative biomass (i.e., total biomass of piscivores relative to the total biomass of the fish community) at each time step. For each lake, we computed the delta values (i.e., mean annual changes ± SD, expressed as % per year) by comparing each survey with the previous one (e.g., 2014 vs. 2012 and 2016 vs. 2014). Lastly, we calculated the temporal variability of the trophic position ($\mathrm{TP}_{\mathrm{temporal}}$) of piscivorous species for each lake as the mean trophic position and its SD across years. All statistical analyses were conducted using R (version 4.4.1717).

RESULTS

Trophic ordination space and trajectories

All lake fish communities experienced marked changes in their trophic structure over the study period (TPL 7.92 ± 1.20, Appendix S1: Table S3), with strong overall shifts (i.e., Net Change, NC) in all lakes between 2012 and 2022 (Figure 2a). Clear differences in the trophic trajectories between lakes were observed in the trophic ordination space (Figure 2b), especially regarding the breadth of fish trophic niche (first dimension of the trophic ordination space, Appendix S1: Figure S4) and the trophic redundancy of the species (second dimension of the trophic ordination space, Appendix S1: Figure S4). While the trophic structure of fish communities often exhibited a shift from wide (i.e., spread) trophic niches composed of trophically unique species (located in the top right corner of the ordination space; Figure 2a) to narrower (i.e., constricted) niches dominated by redundant species (bottom left corner; Figure 2a)—as observed in Lakes *Pouvil*, *Four de Louges*, or *Bois-Vieux*—this pattern was not universal (Lakes *Barbis* and *Bidot*; Figure 2a,b). Moreover, between-lake differences in trophic trajectory metrics greatly exceeded the variation induced by the analytical error associated with stable isotope analyses (Appendix S2: Results, Figures S1 and S2).

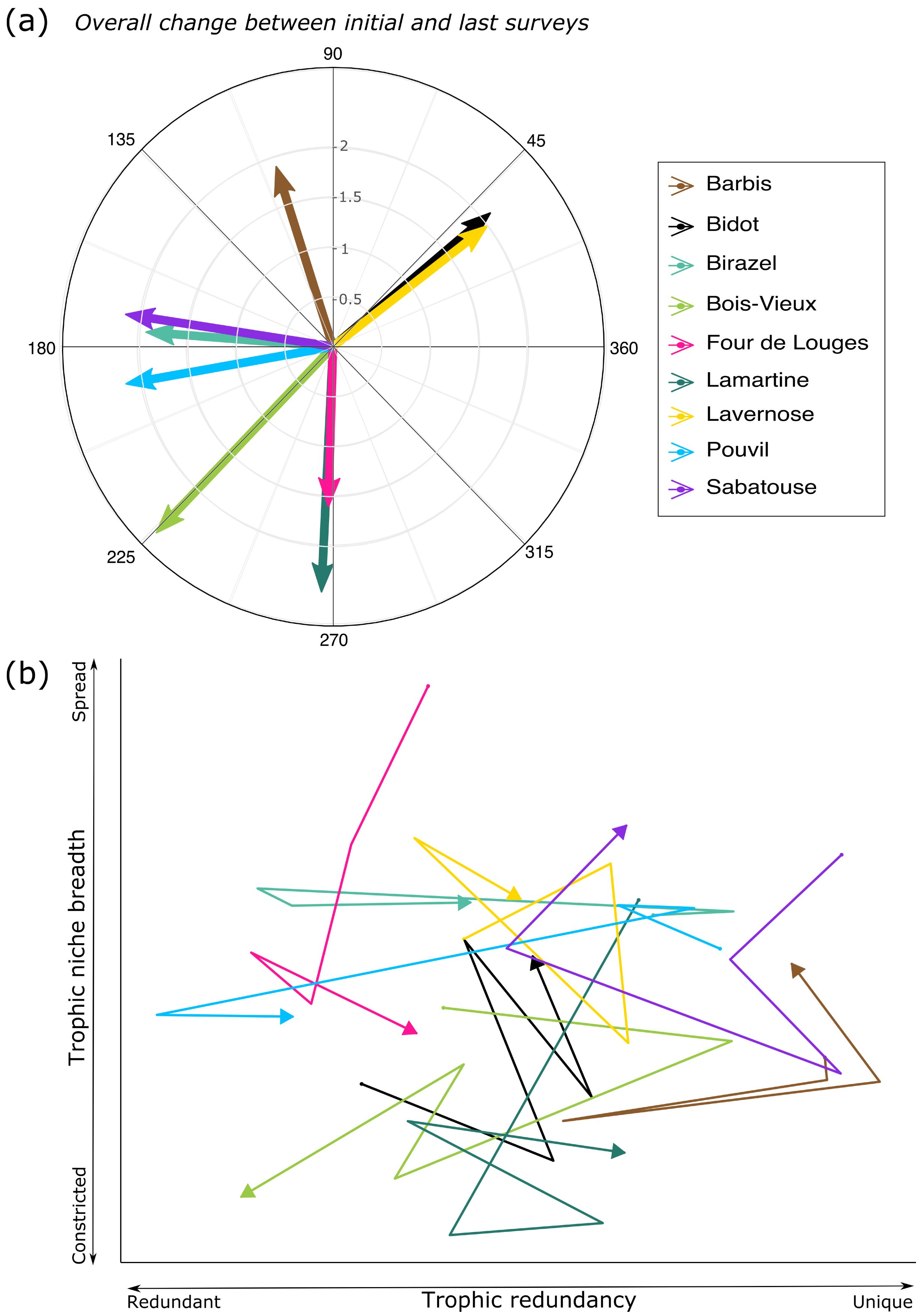
Some fish communities displayed strong regularity in their changes in trophic structure over time, both in terms of magnitude (NCR) and directionality (DIR), indicating a consistent pace and direction of change. For instance, in Lake *Four de Louges*, the trophic structure was initially broad and gradually narrowed during the study period ($\text{NCR} = 0.60$ and $\text{DIR} = 0.55$; Figure 2b). In Lake *Pouvil*, the fish community initially comprised species with unique trophic compositions but became increasingly redundant over time ($\text{NCR} = 0.50$ and $\text{DIR} = 0.31$; Figure 2b). By contrast, some lakes displayed irregular trophic trajectories, characterized by variations in both magnitude and direction. For instance, in Lake *Barbis*, trophic structure changed at an inconsistent pace and in multiple directions ($\text{NCR} = 0.14$, $\text{DIR} = 0.18$), while in Lake *Birazel*, the community transitioned from unique trophic compositions to redundant ones, before returning to its initial state ($\text{DIR} = 0.07$; Figure 2b). Other lakes exhibited trophic fidelity (FID), where communities returned to their original trophic structure after an initial shift. For instance, in Lake *Lamartine*, trophic structure initially changed but ultimately returned to its starting condition ($\text{FID} = 5.71$). Similarly, Lake *Lavernose* followed a circular trajectory over time ($\text{FID} = 1.95$; Figure 2b). Notably, while three out of four possible trajectory patterns were observed, no lake exhibited a trajectory toward the lower right portion of the plot (Figure 2b), that is, a narrow trophic structure composed of trophically unique species.

Predictors of trophic trajectories

Patterns in trophic trajectories were well explained by both community trajectories and lake environmental characteristics (RDA: $F = 2.56$, $R^2 = 0.72$ and $p = 0.04$). Compositional changes and the level of non-native species dominance had an overall significant effect on the trophic trajectories of fish communities ($F > 3.22$ and $p < 0.04$). Community trajectory was negatively associated with NCR and DIR (Figure 3 and Appendix S1: Table S4), indicating that lakes experiencing greater changes in their fish community composition displayed strong irregularity in their changes in trophic structure, both in terms of magnitude and directionality (e.g., Lake *Birazel* and Lake *Barbis*). By contrast, non-native species dominance was positively associated with FID (Figure 3 and Appendix S1: Table S4), indicating that invaded fish communities displayed higher trophic fidelity (e.g., Lake *Bois-Vieux* and Lake *Lamartine*). There was no significant effect of the productivity level of the lake (TSI) and of habitat complexity (shoreline development index) on the trophic trajectories of the fish communities ($F < 1.87$ and $p > 0.19$).

Species turnover and trophic shifts

Species turnover (i.e., changes in species presence/absence) was substantial across lakes, with communities sharing, on average, 69% of their species between consecutive surveys (mean Jaccard index $J = 0.69 \pm 0.08$; Appendix S1: Table S5), indicating a 31% change in species composition over time. Some lakes, such as Lake *Barbis* (mean $J = 0.493 \pm 0.153$), showed strong species turnover, while others, like Lake *Lamartine* and Lake *Bois-Vieux* (mean $J = 0.85 \pm 0.08$ and 0.79 ± 0.06), exhibited greater species persistence. Changes in relative biomass also varied significantly (mean Bray–Curtis = 0.43 ± 0.13; Appendix S1: Table S5), with pronounced shifts in Lake *Barbis* and Lake *Sabatouse* (mean Bray–Curtis = 0.57 ± 0.21 and 0.41 ± 0.21), reflecting major changes in species dominance, regardless of species gains and losses. Conversely, in lakes with high species turnover, such as Lake *Lamartine* and Lake *Bois-Vieux*, biomass shifts were less pronounced (mean Bray–Curtis = 0.43 ± 0.07 and 0.29 ± 0.19). All lakes exhibited substantial fluctuations in CWTP, with a



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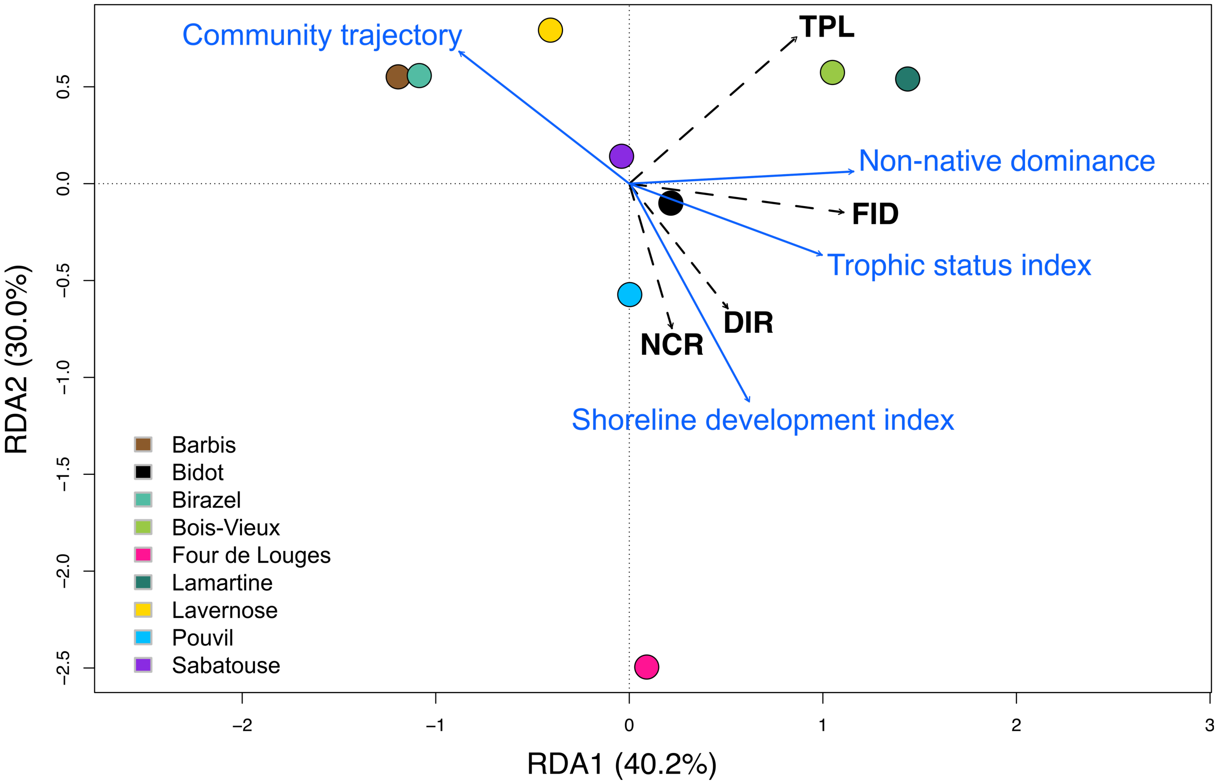

FIGURE 3 Redundancy analysis of trophic trajectory metrics (displayed in black dashed lines; DIR, directionality; FID, trophic fidelity; NCR, net change ratio; TPL, trajectory path length) and potential drivers (compositional changes, non-native dominance, productivity level, and habitat complexity; displayed in blue solid lines) (cf. Table 2 for details). The first and second axes explain 40.2% and 30.0% of the total variance, respectively.

mean SD of 0.33 around the lake-specific means, suggesting that species turnover—in terms of both occurrence and biomass—influenced the trophic structure of fish communities (Appendix S1: Figure S5).

Overall, relative piscivore occurrence increased on average by 1.13 ± 2.64% per year (Appendix S1: Table S6, Figure S6). This trend was observed in Lake *Pouvil* and Lake *Four de Louges* (+3.1 ± 11.7% and +3.8 ± 9.3% per year), driven by the gain of predatory species such as the Northern pike and largemouth bass, alongside the decline of rudd (*Scardinius erythrophthalmus*) and common carp (*Cyprinus carpio*). However, some lakes experienced a decline in the relative proportion of piscivores, including Lake *Sabatouse* and Lake *Barbis* (−2.9 ± 10.1% and −0.8 ± 7% per year), due to gains in low-trophic-level species (e.g., pumpkinseed or Western mosquitofish) and losses of top predators (e.g., largemouth bass and European perch). Similarly, the relative biomass of piscivorous species showed considerable variation (Appendix S1: Table S6, Figure S6), with an average annual increase of 0.03 ± 4.15% (+0.11 ± 16.66% overall). Some lakes, such as Lake *Sabatouse* and Lake *Bidot*, displayed strong increases (+5.4 ± 15.5% and +4.4 ± 43.1% per year), possibly driven by the expansion of top predators (e.g., Northern pike or pikeperch). In contrast, piscivore biomass declined in Lake *Lamartine* and Lake *Pouvil* (−8.6 ± 16% and −1.3 ± 21.8% per year), presumably resulting from reductions in the abundance of European perch and Northern pike, alongside increases in common carp and roach biomasses. These pronounced declines in piscivore biomass were mirrored by drastic declines in CWTP in these lakes ($\text{CWTP}_{\text{Lamartine}} = 4.36 \pm 0.61$ and $\text{CWTP}_{\text{Pouvil}} = 3.52 \pm 0.32$; Appendix S1: Figure S5).

Trophic position temporal trends ($\text{TP}_{\text{temporal}}$) of key piscivorous species were generally stable (Figure 4). For instance, European perch in Lake *Barbis* and Lake

FIGURE 2 (a) Circular plot representing the overall trajectory change for each lake (i.e., NC, net change), with arrows displaying the length and angle of trajectories from 2012 to 2022. (b) Trophic trajectories of fish communities between 2012 and 2022 in the trophic ordination space (trophic redundancy and trophic niche breadth). Each color represents a lake. Each segment of the arrows represents the change between two sampling events.

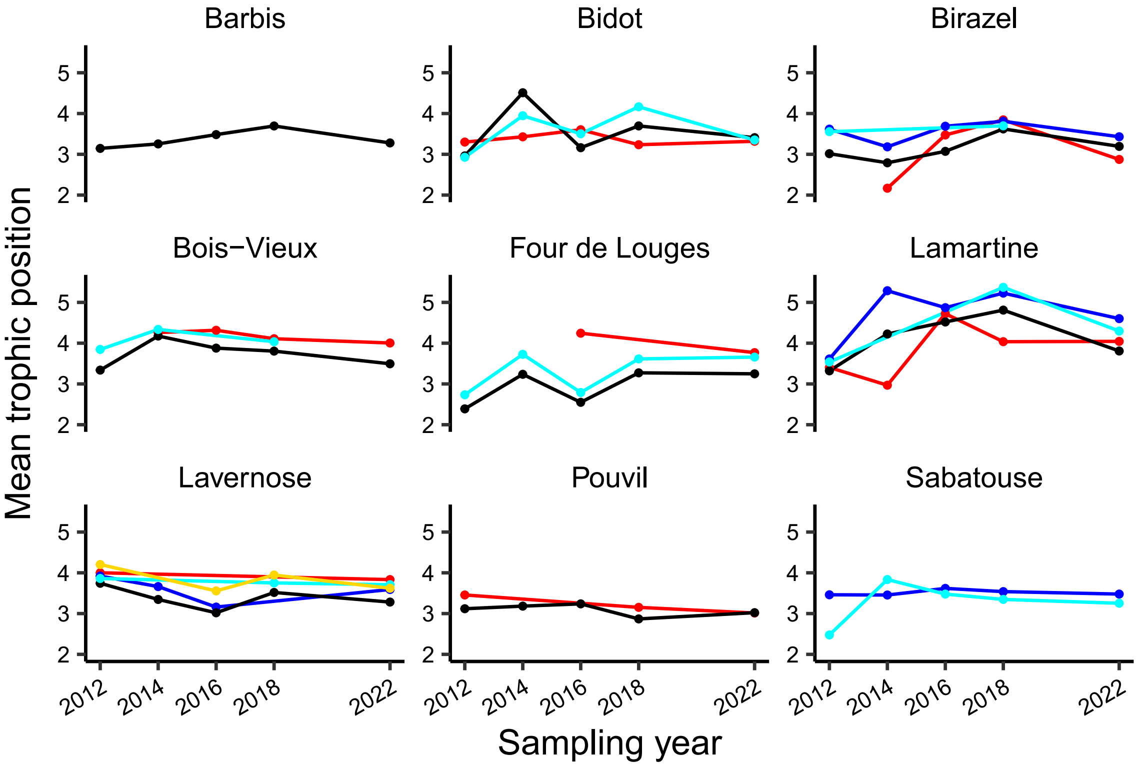

FIGURE 4 Temporal variation in the mean trophic position ($TP_{temporal}$) of five key piscivorous species across the nine studied lakes from 2012 to 2022. Each colored line represents a different species: *Perca fluviatilis* (black), *Micropterus nigricans* (red), *Esox lucius* (dark blue), *Sander lucioperca* (cyan), and *Silurus glanis* (yellow).

Pouvil ($TP_{temporal} = 3.37 \pm 0.22$ and 3.09 ± 0.15, respectively) or largemouth bass in Lake *Bidot* and Lake *Bois-Vieux* exhibited limited variation ($TP_{temporal} = 3.38 \pm 0.14$ and 4.17 ± 0.14, respectively). However, in Lake *Lamartine*, strong variations were observed for several species, such as largemouth bass and Northern pike ($TP_{temporal} = 3.84 \pm 0.67$ and 4.72 ± 0.68), despite limited changes in fork length (Appendix S1: Figure S7).

DISCUSSION

Understanding the role of biological communities in shaping the dynamics of food web structure is paramount for anticipating the consequences of changing biodiversity. Over a decade, trophic structure changes in freshwater fish communities were mainly driven by shifts in community composition and initial non-native species dominance. Trophic changes involved fluctuating isotopic niches of fish communities—in terms of trophic niche breadth and species trophic redundancy—and variable regularity in the magnitude and directionality of shifts over time.

All lakes exhibited strong trophic structure changes of relatively similar magnitudes (TPL). Generally, trophic niches became more constrained—characterized by a longer FCL, reduced isotopic richness, and $\delta^{13}C$ range—and composed of more trophically redundant species over 10 years. Such patterns have been reported from other aquatic ecosystems such as marine and brackish ecosystems (St. George et al., 2024; Yurkowski et al., 2018). Interestingly, despite similar trophic change magnitudes (TPL) and close geographical proximity, lakes exhibited distinct trajectory patterns. The marked differences in trophic trajectories among fish communities suggest the existence of strong local drivers impacting fish communities at the lake level, which, according to our results, are not related to environmental factors such as productivity or habitat heterogeneity. Rather, evidence points to the key role of species composition, including the relative dominance of non-native species, in explaining the differences observed. This aligns with the notion that in ecologically isolated and evolutionarily young ecosystems, such as gravel pit lakes, community composition is a key driver of food web characteristics (Post, 2002a, 2002b).

Communities experiencing significant compositional changes (high community trajectory) displayed strong variability in trophic niche breadth and trophic redundancy over time (i.e., low NCR and DIR). This pattern aligns with findings in freshwater invertebrate communities, where changes in food web topology (connectance and generality) followed compositional shifts induced by pesticides (Polazzo et al., 2022). Here, species turnover—in terms of both occurrence (gain/loss) and biomass (increase/decrease)—emerged as the dominant factor shaping trophic dynamics, likely modifying trophic niche breadth and redundancy. A similar pattern was observed in the Baltic Sea, where the addition of a generalist benthivorous fish and an increase in planktivorous fish biomass enhanced food web connectivity (Olivier et al., 2019). This supports the idea that species turnover drives trophic turnover, with new species occupying different trophic roles (Cuesta Núñez et al., 2023; Törnroos et al., 2019). Specifically, FCL increased in some lakes, driven by the introduction of piscivorous predators (e.g., Northern pike and largemouth bass in Lake *Four de Louges*). This process, known as the mechanism of addition (Post & Takimoto, 2007)—where predator introductions extend food chains—has been observed in various ecosystems, including the San Rafael River (Utah, USA) (Walsworth et al., 2013). Conversely, the broadening of the trophic niche (accompanied by an FCL reduction) was observed only when a strictly piscivorous species was lost (e.g., European eel *Anguilla anguilla* in Lake *Bidot*). Such predator removal is known to shorten food chains (Post & Takimoto, 2007), a phenomenon also documented in marine ecosystems following the decline of top predators such as sharks (e.g., Young et al., 2024). Additionally, increased trophic redundancy was further detected in lakes where species losses were not functionally compensated (e.g., common carp in Lake *Pouvil*), reinforcing the idea that some species occupy unique, irreplaceable trophic niches (e.g., carps in these gravel pit lakes; Imbert et al., 2024). Finally, intraspecific dietary shifts also contributed to trophic changes, as reflected by fluctuating trophic positions of key species (e.g., Northern pike in Lake *Lamartine*), despite stable biomass and body size distributions. In the absence of baseline isotopic shifts, this suggests plastic feeding behaviors in response to resource fluctuations, a phenomenon well documented in freshwater fish (e.g., Falke et al., 2020).

Our investigations also revealed that initially invaded fish communities (i.e., already invaded at the study's onset) tended to exhibit greater trophic stability (high FID) and fewer compositional changes. Existing literature is uncertain with respect to the effects of biological invasions on community stability (Garcia et al., 2022), as invaded communities can be either more or less stable than uninvaded ones (Báez & Collins, 2008; Wilsey et al., 2014), depending on species traits and recipient community (Lockwood et al., 2005; Maron & Vilà, 2001). Evidence from the invasion of a successional plant system suggests that already invaded communities are less susceptible to further invasions (Yurkonis & Meiners, 2004), resulting in reduced changes in species composition and, consequently, limited changes in trophic structure. However, another possible explanation for the stability of highly invaded communities may lie in the role that non-native species play within food webs. For instance, several studies in plant–pollinator systems have shown that highly invaded communities are more stable due to increased connectance (e.g., Campbell et al., 2022; Traveset et al., 2013). Additionally, increasing climatic extremes, particularly heat waves over the past decade, may have influenced community stability. Overall, native species in the study area (e.g., European perch) are physiologically less tolerant than non-native species (e.g., black bullhead *Ameirus melas* and Western mosquitofish) (Cucherousset et al., 2007), which could explain the lower trophic shifts in invaded communities. Contrary to our expectations, neither lake productivity nor habitat complexity showed a significant association with trophic trajectories. For instance, one could have expected eutrophic lakes to exhibit trophic shifts due to the well-documented fluctuations in food web structure caused by cyanobacteria blooms (Han et al., 2021; Van Der Lee et al., 2021). Still, the lack of relationship in our study could be explained by the relatively limited differences in productivity and habitat complexity among the studied lakes, and thus it would be valuable to investigate further across a large environmental gradient of lakes.

In conclusion, this study offers a rare empirical quantification of temporal trophic shifts in fish communities. These trophic changes in isotopic niches of fish communities, especially regarding trophic breadth and species redundancy, could have strong implications for ecosystem functioning and stability (Poisot et al., 2013); for instance, by reducing vulnerability to extinction (Sanders et al., 2018). Our results revealed the critical role of community compositional changes in shaping the regularity of the pace and direction of trophic trajectories. While species turnover remained the primary driver of trophic shifts, our findings emphasize the need to consider both community composition and individual behavioral responses (i.e., diet shift) when assessing food web dynamics. Implications of these findings include a better understanding of the trophic consequences of changing biological communities, which are now ubiquitous across aquatic and terrestrial ecosystems. Food web architecture is strongly linked to ecosystem functioning (Funes et al., 2022) and encourages additional inquiry into the role of ecological trajectories in ecosystem stability.

AUTHOR CONTRIBUTIONS

Flavien Garcia: Conceptualization; data curation; data analysis; formal analysis; investigation; writing original draft; review and editing. **Julian D. Olden:**

Conceptualization; funding acquisition; review and editing. **Anthony Sturbois:** Data analysis; review and editing. **Julien Cucherousset:** Conceptualization; data curation; funding acquisition; review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Garcia et al., 2025) are available in Figshare at https://doi.org/10.6084/m9.figshare.29608436.v2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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