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Fish invasion restructures freshwater food webs, facilitating new invasions over three decades

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Although biological invasions are a well-known driver of biodiversity loss in freshwaters, their impact on the structure of aquatic food webs remains relatively poorly investigated. This study examined changes in aquatic community networks driven by biological invasions in the lower Po River Basin, Italy, over the past 3 decades. Using network analysis of fish and macroinvertebrate communities at early (before 1991) and late (after 2009) stages of the invasion, we reveal a significant simplification of the structure of the food web, characterized by reduced species richness and fewer connections, as well as a shift from balanced community control to predominantly bottom-up forces in the late invasion stage. Environmental data showed a shift towards turbid, hypoxic conditions consistent with bioturbation and vegetation loss caused by invasive carp. Native predators such as *Esox cisalpinus* were replaced by tolerant non-native invertivorous fish species and predators such as *Silurus glanis*, indicating trophic reorganization. Canal size influenced invasion outcomes; large canals experienced the greatest species loss, likely due to size-refuge effects reducing top-down control. Asymmetrical trophic interactions and redundancy analyses further support the dominance of bottom-up effects in late-stage communities. These findings align with the invasional meltdown hypothesis, whereby one invader facilitates others, thereby amplifying ecosystem disruption. Despite limitations in the available data, including the absence of pre-invasion baselines and estimates of basal biomass, our results emphasize the advantage of using ecological network analysis with biomonitoring. Our results also highlight the urgent need for long-term data to inform conservation strategies.

KEYWORDS

biological invasion, food web, freshwater, grass carp, invasional meltdown

1 Introduction

Aquatic biodiversity is under severe threat from a multitude of human-caused pressures, including the fragmentation of rivers due to dam construction, widespread habitat deterioration, climate change, and the introduction of non-native species (NNS; [Dudgeon, 2019](#)). The interaction between these pressures can enhance the severity of aquatic ecosystem changes ([Dudgeon, 2019](#)). For example, the increased temperature of the Barents Sea due to climate change has enhanced the presence of species from the Atlantic Ocean, resulting in food web restructuring with newly arrived fish species, such as haddock, taking on a central position in the food web ([Jordán et al., 2024](#)).

Thus, the introduction of NNS is a strong driver of ecological change with important effects on the entire community, especially when they become invasive (Gallardo et al., 2016). Once introduced to a new environment, NNS can establish self-sustaining populations, spread, and become invasive, thereby posing a significant threat to native species and the integrity of ecosystems (Reid et al., 2019). Freshwater fish are among the most frequently introduced taxa in Europe, driven by economic, recreational, and accidental factors (García-Berthou et al., 2005; Nunes et al., 2015). For example, angling and sport fishing promoted the continental introduction and spread of the rainbow trout (*Oncorhynchus mykiss*) and the common carp (*Cyprinus carpio*) (Clavero and García-Berthou, 2006; Vilizzi, 2012). Other examples include the topmouth gudgeon (*Pseudorasbora parva*) from Asia and the channel catfish (*Ictalurus punctatus*) from North America, both introduced accidentally or deliberately across Europe (e.g., Gozlan et al., 2002; Haubrock et al., 2021a). Notably, this group includes highly successful invaders listed in the 100 of the World's Worst Invasive Alien Species [e.g., the common carp; Lowe et al. (2000)] or designated as invasive alien species of Union concern (EU Regulation 2016/1141), such as the black bullhead *Ameiurus melas* and two species of mosquitofish *Gambusia affinis* and *Gambusia holbrooki*. Furthermore, some species native to specific European river basins became invasive following translocation to new basins within the continent (e.g., Pofuk et al., 2017). This is the case of the wels catfish (*Silurus glanis*), native to Central and Eastern Europe, which has become a significant invader in basins across Italy and Spain (Encina et al., 2024; Milardi et al., 2022), as well as the European barbel (*Barbus barbus*), the pikeperch (*Sander lucioperca*), or the common bream *Abramis brama* (Antognazza et al., 2023; Glamuzina et al., 2017; Pofuk et al., 2017).

In Italy, more than 36 non-native fish species have been detected among a total of 98 fish species sampled in Italian watercourses, with the Po River Basin identified as a hotspot of fish invasion (Gavioli et al., 2022; Milardi et al., 2018; 2020). In the lower Po River Basin, the grass carp (*Ctenopharyngodon idella*) and the wels catfish have become established and are driving the decline of native fauna and ecosystem change (Castaldelli et al., 2013; Milardi et al., 2019). The grass carp was introduced in the 1980s (Melotti et al., 1987) into the Ferrara Province, where it has established self-sustaining populations through natural reproduction (Milardi et al., 2015). As an ecosystem engineer, this species alters ecosystem function and community structure through consumption of its aquatic vegetation (Dibble and Kovalenko, 2009 and references herein). During its expansion in the Ferrara Province, it reduced native aquatic vegetation coverage in the freshwater canals, subsequently exacerbating eutrophication in the connected coastal lagoon (Milardi et al., 2022). In fact, aquatic vegetation removal drove sediment resuspension and alteration of nutrients dynamics, such as the increase of phosphorus availability and in turn enhancing eutrophication (Richard et al., 1985; Chen et al., 2025).

A critical aspect of the NNS invasions is the alteration of community trophic structure and dynamics through direct consumption, competitive displacement, and cascading indirect effects that reorganize energy flows and niche relationships across multiple trophic levels (Bernery et al., 2022; Sharpe et al., 2023). Some of these effects will cascade through the food web. For example, silver carp (*Hypophthalmichthys molitrix*), a filter-

feeding species native to Asia, consumes large amounts of phytoplankton and zooplankton, leading to the decline of plankton abundance and biomass in US rivers, especially large-body plankton taxa (De Boer et al., 2018; Novak et al., 2024). Furthermore, the presence of NNS may facilitate subsequent invasions further disrupting the native community, as described in the invasional meltdown hypothesis (Simberloff and Von Holle, 1999). While this hypothesis predicts that positive interactions among NNS accelerate the rate of invasion and compound ecological impacts, support for it has largely been restricted to simple, pairwise interactions or small-scale mesocosm experiments (Ricciardi and Simberloff, 2025). Consequently, there is a critical lack of studies addressing the invasional meltdown hypothesis at the whole food web scale in natural systems (Braga et al., 2018). This gap is significant since biological invasions rarely occur in isolation (Ahmad et al., 2025). Furthermore, understanding how invasions restructure food webs is essential for developing effective management and conservation strategies (Vagnon et al., 2022). However, quantifying the magnitude and trajectory of trophic responses following invasion remains challenging due to the frequent absence of pre-invasion baseline data, concurrent environmental changes, and time-lagged community responses that complicate attribution of observed changes to invasion effects (Rennie et al., 2009).

This study evaluates for the first time in the lower Po River Basin (Italy) the food web community change led by NNS. Particularly, the study aims to *i*) construct trophic networks for aquatic communities in canals in both early and late invasion stages, *ii*) evaluate canal sizes' effect on the networks, and *iii*) compare the temporal differences in the food webs using network analysis.

2 Materials and methods

2.1 Study area

The study area is situated within the Ferrara Province (Supplementary Figure S1), in the southern part of the Po River basin (northeastern Italy), an alluvial plain with a flat topography, with altitudes ranging from -3 to 5 m above sea level (Castigliani et al., 1999). The climate of the region is Mediterranean continental, with a mean annual temperature of 12 °C and annual average precipitation of 1,036 mm. The area is characterized by a network of over 4,000 km of canal (channel) system, which are primarily utilized for irrigation and drainage to support agriculture, the predominant land use. The region has become a significant hotspot for biological invasions, experiencing an increase in NNS richness since the late 1970s (Castaldelli et al., 2013). These introductions were mainly driven by recreational angling (e.g., channel catfish) and biological control efforts (e.g., mosquitofish for mosquito control and grass carp for aquatic vegetation management) (Castaldelli et al., 2013; Milardi et al., 2020). While the abundance and biomass trends of these NNS varied according to their lifestyle, size, and origin, most showed a long-term increase (Castaldelli et al., 2013). This spread has led to the decline in native fish populations mainly by direct predation and habitat degradation, a trend that became pronounced after 2009 (Castaldelli et al., 2013; Gavioli et al., 2018).

2.2 Data collection

To assess the long-term impacts of non-native fish species, our data collection referred to two distinct time periods: the early invasion stage (ES) and the late invasion stage (LS). Within this temporal framework, sampling stations were selected across the canal network to be representative of canals with different widths (Supplementary Figure S1): small canals (SC; less than 10 m wide), middle canals (MC; between 10 and 15 m wide), and large canals (LC; greater than 15 m wide). Fish data for each canal category (i.e., SC, MC, and LC) and time period (i.e., early and late invasion stages) were collected within a long-term official monitoring program. Sampling was conducted in 1991 (i.e., early invasion stage) and 2009 (i.e., late invasion stage) using a unique single-pass method that involved dragging a 25 m seine net (8 mm mesh with a 4 mm cod-end) toward a stationary blocking net that spanned the entire width of the channel. All captured fish were identified to the species level according to Gandolfi et al. (1991) and Kottelat and Freyhof (2007), counted, measured (LT to nearest mm), and weighed (to nearest 0.1 g). Using this data, we obtained species-level abundance and biomass data for fish. For a more detailed description of the sampling method, see Castaldelli et al., 2013.

To obtain data for canal food webs encompassing also macroinvertebrate data representative of each fish sampling location, a literature survey on Scopus was conducted. The search was performed on 2 June 2025, using the search string “Po basin” OR “Ferrara” AND “biomass*” OR “abundance*” AND “canal*” OR “freshwater*” AND “macroinvertebrate*” OR “benthos” in title, abstract and keywords of the manuscript. This search returned 1 publication (i.e., Fornaroli et al., 2019) which did not cover the study area. Consequently, macroinvertebrate occurrence data for SC, MC, and LC in early and late invasion stages were derived from gray literature (Supplementary Table S1) and cross-referenced with diet items reported on FishBase (Froese and Pauly, 2024) and in Gandolfi et al. (1991). All community data were compiled into binary food webs with presence/absence of trophic interactions (unweighted networks). Environmental data for monitoring locations representative of each canal were collected during the official monitoring program of the Regional Environmental Protection Agency of Emilia-Romagna (ARPA) using standard sampling methods across the entire study period. The primary water quality parameters considered in this study are water temperature (T; °C), dissolved oxygen (O%; %), total suspended solids (TSS; mg·L⁻¹), and nitrate (NO₃; mg·L⁻¹).

2.3 Data analysis

A combination of multivariate and network analyses was performed to reveal changes in community composition and environmental data between *i*) early and late invasion stages, *ii*) canal sizes, and *iii*) shifts in food web structure. Invertebrates (although taxonomically different) have similar functional roles in a food web (e.g., shredders, scrapers). Raw data for invertebrates (as compiled from the literature, Wallace and Webster, 1996) were aggregated by guild to obtain comparable networks. Non-native invertivorous fish species were aggregated into one node (exotic invertivorous fish), while other fish species were left unaggregated.

Networks were symmetrized by taking the sum of the links between each node. Twelve basic global network metrics were computed on the two aggregated networks (see Table 1 for detailed descriptions).

A total of twelve indices: four biological (fish species abundance, fish species biomass, ratio of native to non-native fish species, and macroinvertebrate taxa richness) and eight local network indices were calculated on each aggregated network (Table 1). The biological indices were available only for biomonitoring fish data ($n = 16$ nodes). Trophic level and the omnivory index were calculated using the NetIndices R package (Kones et al., 2009), nDC and nBC were computed using UCINET (Borgatti et al., 2002), and the keystone index following the methodology in Jordán et al. (1999). All statistical analyses were conducted in R version 4.3.2 (R Core Team, 2025). Principal Component Analysis (PCA) was run on the 18 shared nodes found in both the early and late networks (based on ten variables). Two variables (TL, nDC) had normal distributions, whereas all other variables had right-skewed distributions and were log-transformed. Variables were normalized (by subtracting the mean and dividing by the standard deviation) to ensure commensurability.

To further explore how the community and environmental variables changed between early and late invasion stages based on canal size, we performed a similar analysis on a more detailed dataset representing six food webs (Early LC, Early MC, Early SC, Late LC, Late MC, Late SC). Network analysis was similarly run, including the same global metrics and 8 local indices (described above). Finally, multivariate analyses (Redundancy Analysis (RDA) and PCA) were performed to highlight the relationship between community structure (abundance) and all other data groups. Specifically, RDA was run on three separate sets on the fish community abundance and three data groups: 1) food web structure (12 global network indices), 2) the biological variables (2 variables), and 3) environmental data (3 variables). Before the analysis, the species abundance data were Hellinger-transformed and predictors were scaled and centered (Legendre and Gallagher, 2001). Due to the large number of variables of food web structure and the high degree of collinearity, we first performed a Principal Component Analysis (PCA). The first two PC axes (which together explained 88.3% of the variance) were used as explanatory variables in the Redundancy Analysis (RDA). Collinearity was evaluated with Variance Inflation Factor (VIF), and predictors with VIF >7 were excluded from the analysis as they resulted significantly collinear. Redundancy Analysis (RDA) analysis were performed in *vegan* R package (Oksanen et al., 2022).

We also computed the dominant community control (bottom-up vs. top-down links) based on the asymmetrical interactions following methods described in Jordán et al. (2024). This method uses the topological importance (TI) index (Jordán et al., 1999) and computes the asymmetry between each node pair (e.g., TI_{ij} and TI_{ji}). Thus, the resulting asymmetry graph is a subset of all TI interactions that are the most asymmetric (using a 67% threshold, Jordán et al., 2024), meaning that the influence of node i on node j is much greater. By taking the ratio of bottom-up and top-down asymmetrical links in each network, we get a sense of how the community control changed over time in each network.

Finally, PCA was run on all data (eight local network indices computed for each of the six food webs) using PRIMER v7 software (Clarke and Gorley, 2015). The PCA shows overall similarities,

TABLE 1 List of variables used in this study (group, code, description, and references).

Level	Variable code	Variable description	References
Global network	S	Number of nodes in the food web	Dunne, 2009
	L	Number of links in the food web	Dunne, 2009
	AD	Average degree (direct links) in the food web	Borgatti et al. (2002)
	D	Density calculated as $L/(S*(S-1))/2$	Borgatti et al. (2002)
	DC	Degree Centralization quantifies the variation in degree centrality among nodes in a network	Borgatti et al. (2002)
	CL	Weighted overall clustering coefficient quantifies the average clustering of all nodes in the network (weighted by their degree)	Borgatti et al. (2002)
	d	Avg distance (shortest path) between pairs of nodes	Borgatti et al. (2002)
	SW	Small world (CL/d)	Watts and Strogatz, 1998
	Max TL	Maximum trophic level in the food web	Kones et al. (2009)
	Mean TL	Mean trophic level in the food web	Kones et al. (2009)
	Max OI	Maximum omnivory index value in the food web	Kones et al. (2009)
	Mean OI	Mean omnivory index value in the food web	Kones et al. (2009)
Local network	TL	Trophic level	Kones et al. (2009)
	OI	Omnivory index	Kones et al. (2009)
	nDC	Normalized degree centrality	Borgatti et al. (2002)
	nBC	Normalized betweenness centrality	Borgatti et al. (2002)
	K _{bu}	Bottom-up keystone index	Jordán et al. (1999)
	K _{td}	Top-down keystone index	Jordán et al. (1999)
	K _{dir}	Direct keystone index	Jordán et al. (1999)
	K _{indir}	Indirect keystone index	Jordán et al. (1999)
Biological	Abun	Abundance of each taxa (for fish species only)	Survey data
	Biom	Biomass of each taxa (for fish species only)	Survey data
	RatioNE	Ratio of native to exotic (non-native) fish species	Survey data
	MacroRich	Macroinvertebrate taxa richness	Survey data
Environmental	Temp	Water temperature (Celsius)	ARPA survey data
	O%	Dissolved oxygen saturation (as percentage)	ARPA survey data
	NO3	Nitrate concentration (mg/L) of the water	ARPA survey data
	TSS	Total suspended solids (mg/L)	ARPA survey data

dissimilarities of nodes within the six networks and the correlation of ten variables, whereas the RDA shows the relationship between community abundance and all other data groups (environment, food web structure, biological variables).

3 Results

3.1 Early vs. late invasion stages

The resulting networks after aggregation were highly comparable in most global network metrics (Table 2). The ratio

of native to exotic (non-native) fish species (RatioNE) decreased from an average of 1.50 to 0.21, suggesting a major shift in the fish community composition over time. The Small World value also decreased, indicating that the late invasion stage became less natural, having smaller clustering and larger average distance (sign of disturbed networks).

For 18 shared aggregated nodes, the PCA revealed the largest community-level changes from the early to late stage in the following one node: Ecis (based on the ordination distance; Figure 1). This means that the community position of the *Esox cisalpinus* (Ecis) species shifted the most as invasion progressed. Along PC1 axes, the groups of macroinvertebrates (Coll, Inve, Shre,

TABLE 2 Global network metrics of the aggregated networks of the early and late invasion stages.

Global network metric	Early invasion	Late invasion
Nodes	25	25
Links	97	87
Avg degree	7.76	6.96
Density	0.32	0.29
Weighted overall clustering coefficient	0.43	0.34
Avg distance	1.88	2.04
Small world	0.23	0.17
Ratio of native to exotic species	1.50	0.21

Zoop) and the groups of different fish (Caur, Cyca, Sery, Lasp, and Laul) show clear separation from each other (but are tightly clustered within their respective groups. *Anguilla anguilla* (Aang) is found separately from the main fish group. The wels catfish (*Silurus glanis*; Sgla), the grass carp (*C. idella*; Cide), and the

Phytoplankton (Fito) were distinct from all other nodes (positioned farthest from the rest of the points). PC1 represents a clear hierarchical axis (explaining 47% of the variance) including higher trophic level (TL), omnivory index (OI). Biomass and abundance were less informative here as they were only available for fish. On the opposite side of PC1, larger bottom-up (K_{bu}) effects group invertebrates, macrophytes (Macr), and detritus (Detr). PC2 describes secondary indices (explaining 31% of the variance), such as direct and indirect effects (K_{dir} , K_{indir}) and centrality indices (nDC, nBC; Figure 1).

Moreover, we found that the top 5 nodes changed between stages (Supplementary Table S2). Based on nBC (nodes serving as “bridges” in the network), the top five nodes were Predators, Collector, Macrophytes, Zooplankton, Shredders (in the early stage), and Exotic invertebrates, Zooplankton, Macrophytes, *S. glanis*, Shredders (in the late stage). Thus, four groups did not change their importance. Predators were more important in the early stage, but over time, the Exotic invertebrates and *S. glanis* nodes became more important in the late stage. Based on nDC (nodes with many direct connections), the top 5 nodes were: Predators, Collector, *E. cisalpinus*, *Anguilla anguilla*, *Micropterus salmoides*, *Perca fluviatilis*, *S. glanis* (the last 4 nodes having the same value) (in

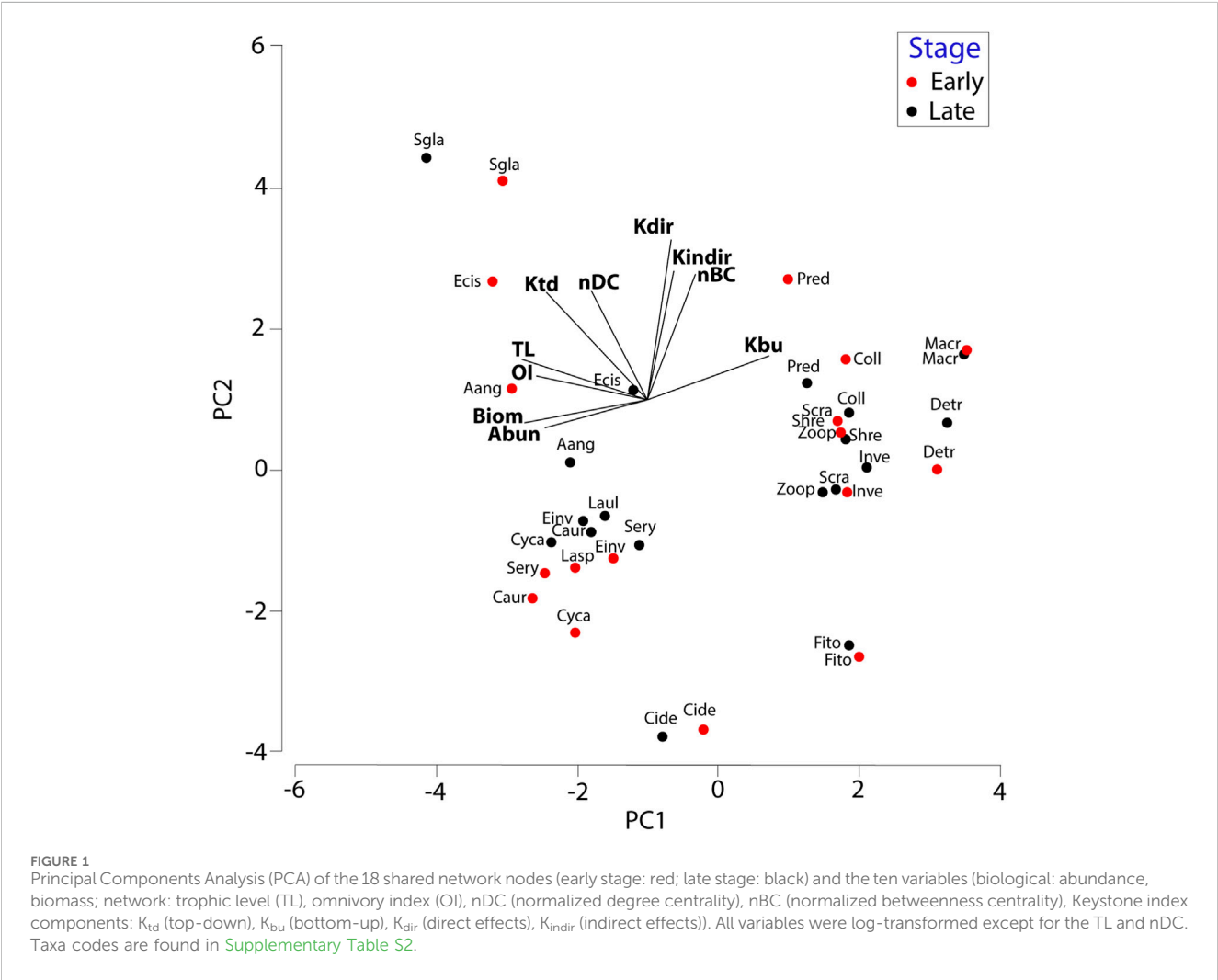


TABLE 3 Results for early and late invasion stages separated by channel size (LC = large channel; MC = medium channel; SC = small channel). Variables are grouped by environmental, global network structure, and biological variables. The most asymmetrical links (based on 67% threshold) are listed in the last two rows, encompassing the asymmetry graph (Figure 2).

Data group	Variable	Early invasion			Late invasion		
		LC	MC	SC	LC	MC	SC
Environmental	Temp (°C)	15.4	17	15.6	16.2	16.4	15.8
	O%	77.3	80.9	73.7	7.8	10.8	7.9
	TSS (mg/L)	28.7	37.7	34.2	40.2	44.4	42.1
Global network	Nodes	25	24	24	21	22	23
	Links	85	79	87	52	57	67
	Avg degree	6.800	6.583	7.250	4.952	5.182	5.826
	Deg Centralization	0.19	0.304	0.273	0.224	0.252	0.158
	Density	0.283	0.286	0.315	0.248	0.247	0.265
	Weighted overall clustering coefficient	0.376	0.383	0.436	0.360	0.372	0.195
	Avg distance	1.987	1.989	1.913	2.314	2.190	2.115
	Small world	0.189	0.193	0.228	0.156	0.170	0.092
	Max TL	4.360	4.589	4.589	4.559	4.658	4.323
	Mean TL	2.753	2.846	2.846	2.766	2.759	2.729
	Max OI	0.281	0.442	0.442	0.250	0.321	0.374
	Mean OI	0.096	0.114	0.114	0.086	0.087	0.110
Biological	Ratio of native to exotic fish species	1.28	1.14	1.14	0.18	0.18	0.08
	Macroinvertebrate richness	23.00	28.00	26.00	11.00	12.00	32.00
Asymmetry graph	1 st	Macr - Cten	Macr - Cten	Macr - Cten	Coll - Caur	Macr - Cten	Macr - Cten
	2 nd	Zoop - Fito	Zoop - Fito	Zoop - Fito	Macr - Cten	Zoop - Fito	—

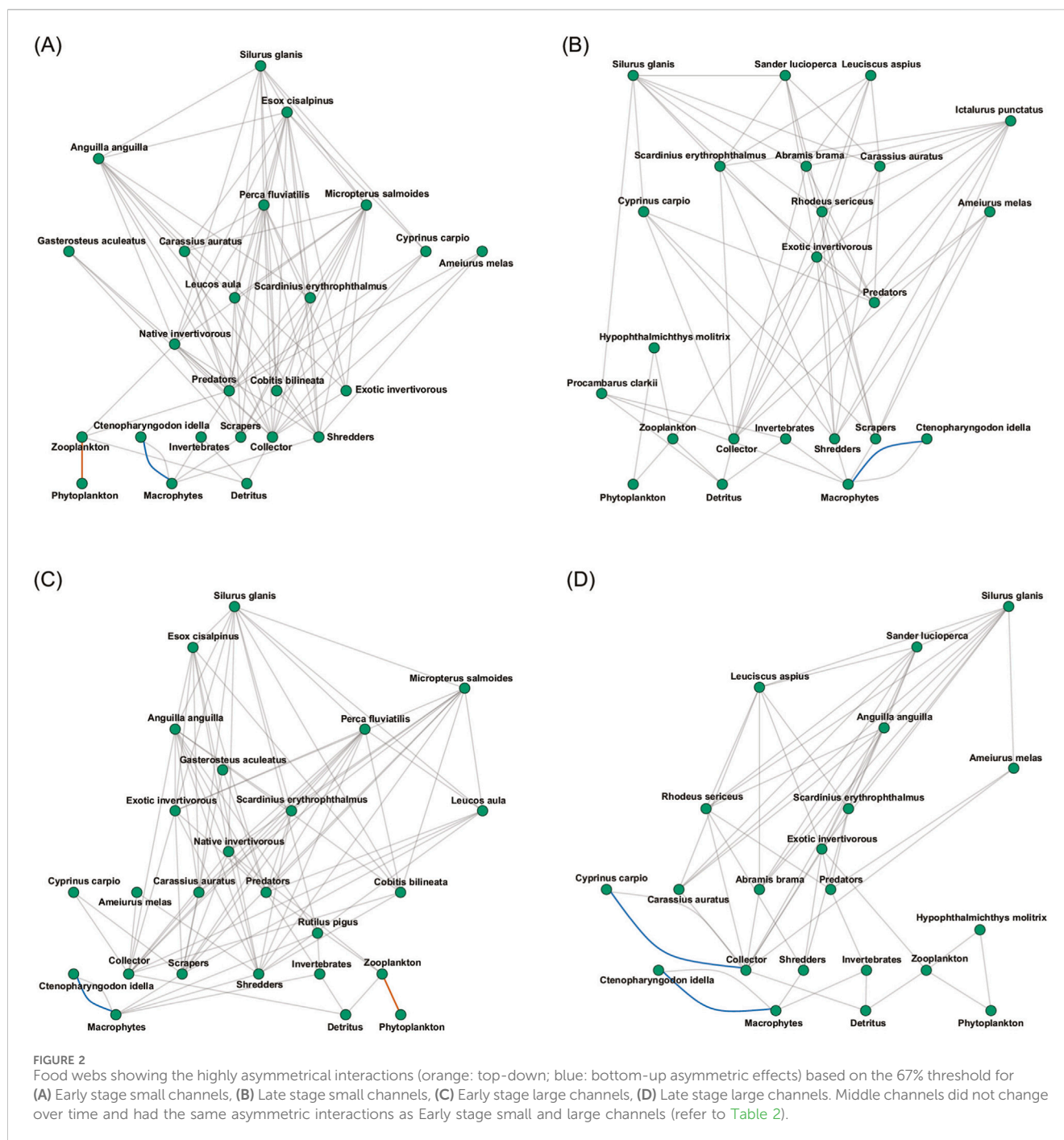
the early stage), and *S. glanis*, Exotic invertivores, *Anguilla anguilla*, Collector, Predators, *Rhodeus sericeus* (the last four having the same value in the late stage) (Supplementary Table S2). Most groups were the same, but, for example, *E. cisalpinus* was more important in the early stage, while again, *S. glanis* and the Exotic invertivores group in the late stage. Thus, according to both indices, *S. glanis* and the Exotic invertivorous fish nodes were central in the late invasion stage.

3.2 Invasion stages by canal size

In the more detailed global network analysis by canal size (Table 3), the LC showed the largest change in terms of overall species loss (from early to late invasion stage). Overall, the number of nodes and links were greater in the early stage (in all canal sizes) as compared to fewer nodes and links in the late invasion stage, evident also in the smaller average degree (fewer direct links per node in the late stage). Other global metrics did not change substantially between the canal sizes (Table 3), except for SC. SC only lost one node overall (but many links), also the overall clustering coefficient changed from being the highest to the smallest of all canals. The ratio of native to exotic species also changed the most drastically in the SC (so the composition of the community changed the most in the SC,

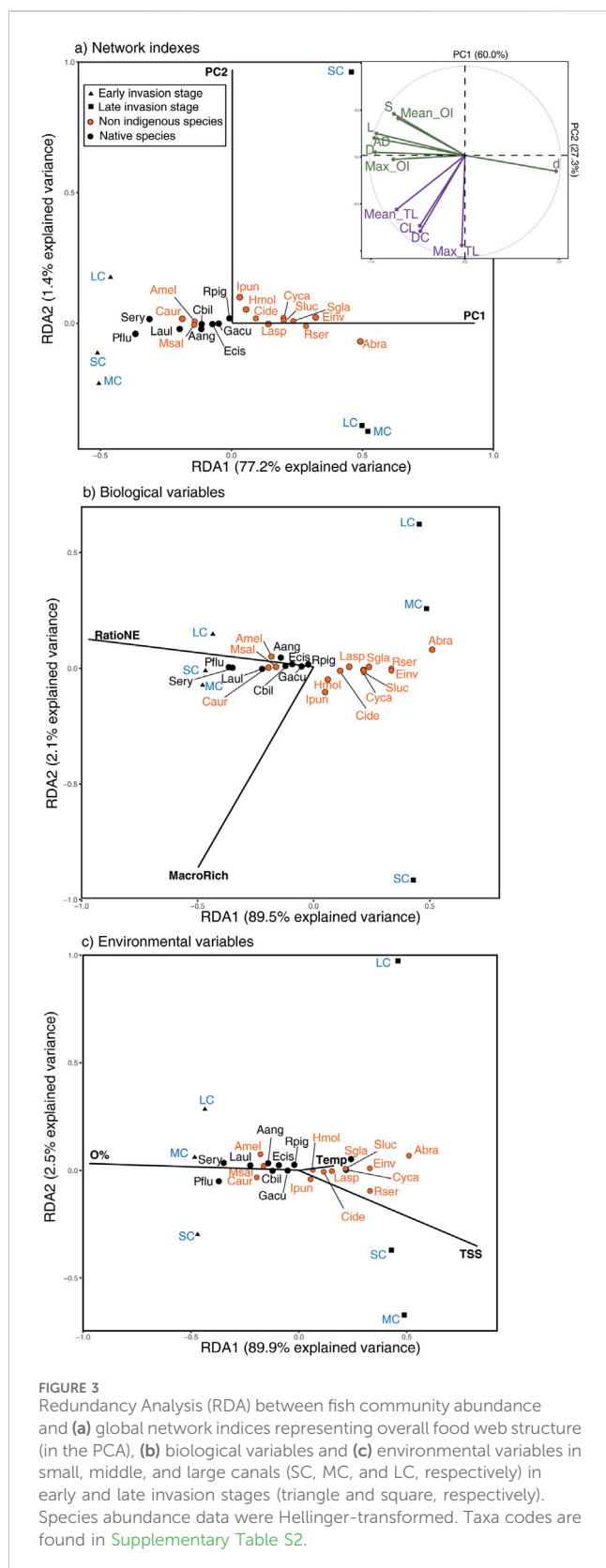
(Table 3; Supplementary Table S3). This is also supported by the small world metric, which indicated that the early invasion networks were more natural networks (tighter clustering, smaller distance) than in the late stage (Table 3).

Based on the local (node) level analyses, we found more details on how these communities changed by canal size over time due to increased pressure from invading NNS. By quantifying the most asymmetrical links (TI asymmetry), we found two links (Macrophytes - *C. idella*; Zooplankton - Phytoplankton) were consistently asymmetrical (>67% threshold) in all canals (except in the late stage LC where the Collector - *C. auratus* link was more asymmetrical) (Table 3; Figure 2). In the early invasion stage, the different canal sizes were similar (having the same two asymmetrical links), but in the late invasion stage, the different canals were more different (late LC and late SC changed). The community control (based on the ratio of top-down to bottom-up asymmetrical links) was the same in the two stages of MC (1 top-down, 1 bottom-up), but changed in the late LC (2 bottom-up) and late SC (1 bottom-up) (Figure 2). Thus, while the early invasion stages and the late MC were overall more balanced (with 1 top-down and 1 bottom-up asymmetrical effects), the late invasion stages for the LC and SC were dominated by bottom-up control. Here, too, most community changes were detected in the LC and the SC canals (reflecting the results of the global network analysis).



RDA revealed a clear separation between early and late stages of invasion based on environmental variables, network indices, and biological variables (Figure 3). Among network indices, the first two axes explained 77.26% (RDA1) and 1.48% (RDA 2) of the variance (Figure 3a). RDA 1 accounted for PC1 which was influenced by network size and connectance metrics (i.e., Mean_OI, S, L, AD, D, Max_OI, and d), distinctly separating early and late invasion communities. Whereas RDA 2 accounted for PC2, primarily driven by trophic level and centrality metrics (i.e., Mean_TL, CL, DC, and Max_TL), further distinguishing fish communities along the canal size (Figure 3a). Among biological variables, RDA1 and RDA2 account for 89.5% and 2.1% of the explained variance,

respectively (Figure 3b). The RatioNE and MacroRich were higher in the early invasion stage canals (Figure 3b). Among environmental variables, the two axes explain a substantial portion of the total variance (89.9% for RDA1 and 2.5% for RDA2), with early invasion stage associated with high O% and late invasion stage associated with high TSS (Figure 3c). In the PCA by canal size (Figure 4), groups appeared separated based on trophic hierarchy. PC1 axis (explaining 44% of the variance) separated groups (Detr, Macr) driven by bottom-up effects (K_{bu}) from top-down groups having large biomass and abundance (e.g., Sgla). The PC2 axis (explaining 31% of the variance) represents the direct (nDC, K_{dir}) and indirect (nBC, K_{indir}) network connections. Similar



to Figure 1, some groups were nicely clustered for all canals (Detr, Macr). Here too, the invertebrate nodes (e.g., Coll, Zoop) were clearly separated from the fish nodes (e.g., Cyca, Cide) along PC1. The Fito group was clustered separately. The Sgla were most

different from the rest of the fish species (driven by larger nDC and K_{td} values). Most of the non-native cyprinids (e.g., Cara, Cyca, Abra) are grouped together in lower K_{dir} , nBC , and K_{indir} values. A distinct separation between the early and late invasion stages of Sgla, Aang, Einv, and Pred was evident, despite variations in canal size.

4 Discussion

4.1 Overall food web changes

This study provides the first comparison of aquatic food webs in the lower Po River basin across different stages of biological invasion (i.e., early and late invasion stages), revealing a profound and progressive community and ecosystem transformation. Our primary finding is a strong change in the aquatic community, with the drastic decline in the abundance and species richness of native species between the early and late invasion stages. At the same time, the overall food web became significantly less complex and diverged from its natural state, as evidenced by key global network metrics. This simplification of community structure is a well-documented consequence of biological invasions, which can alter ecosystem structure and function by disrupting co-evolved interactions (Ricciardi et al., 2017). Furthermore, it reflects the global phenomenon of biotic homogenization, where unique assemblages are replaced by widespread, generalist species (Toussaint et al., 2016), resulting in shorter, less connected networks (Carvajal-Quintero et al., 2024). This process not only reduces local diversity but erodes ecosystem resilience, increasing susceptibility to further disturbances (Rolls et al., 2023). Our results are consistent with other systems in which invaders have led to ecological restructuring. For example, the introduction of invasive predators such as the lake trout *Salvelinus namaycush* in the northern Rocky Mountains (United States) has been shown to increase the dietary variability of native fish and displace them from their food sources, thereby altering the structure of macroinvertebrate communities (Wainright et al., 2021). Similarly, the introduction of omnivorous invaders like goldfish (*Carassius auratus*) is documented to cause food web collapse, reduce consumer diversity and a shift from macrophyte-dominated to phytoplankton-dominated systems (Lejeune et al., 2024). A comparable shift was observed with another cyprinid, the common carp, in Medina Lake, matching the loss of benthic energy pathways found in our study (Rodríguez-Pérez et al., 2016). Furthermore, the wels catfish, an invasive predator and a key species in our study, was shown to be directly responsible for the alteration and homogenization of the fish community following its expansion in an Iberian reservoir (Orduna et al., 2022) and southern France (e.g., Panfili et al., 2024). These patterns extend beyond fish species, for example, the case of the red swamp crayfish (*Procambarus clarkii*) which was found to act as a keystone species, simplifying food web complexity by decoupling native trophic links and channeling energy primarily toward detrital pathways in Guadalquivir marshes of southern Spain (Geiger et al., 2005). The progressive simplification of the food web from the early to late stages of invasion, results in a community structure with reduced resilience to subsequent disturbances and impaired ecosystem functionality. This result is of particular concern as food

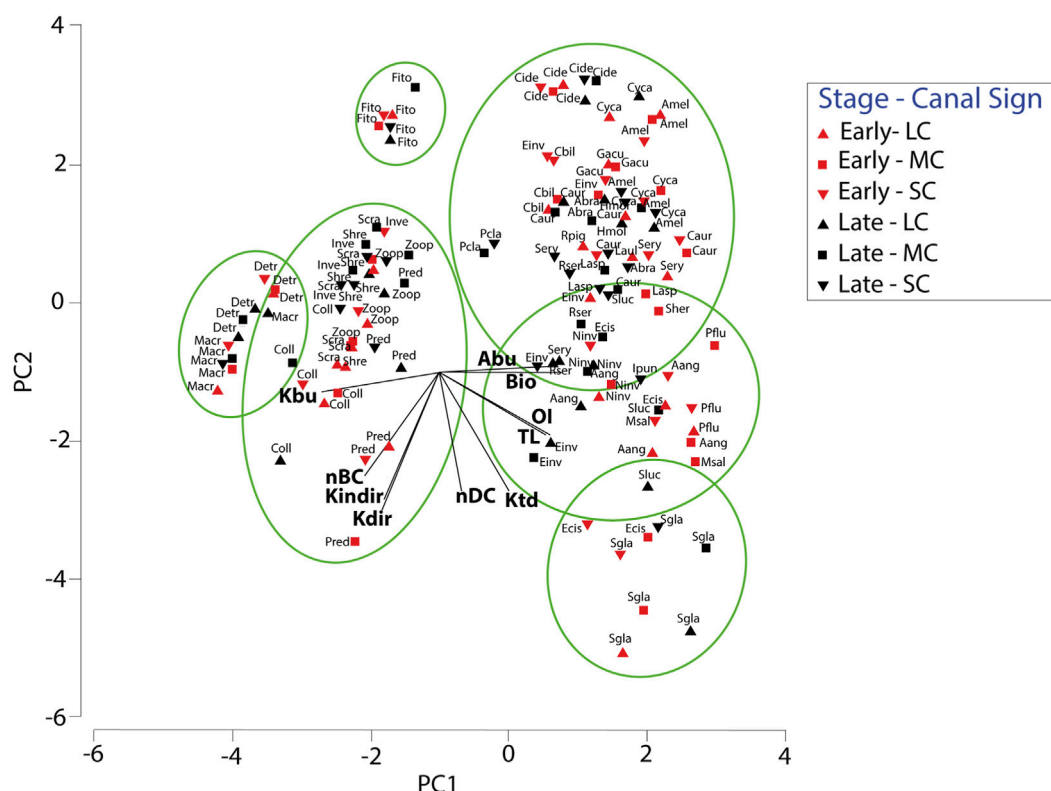


FIGURE 4
Principal Components Analysis (PCA) by channel size (including all nodes) and the ten standardized variables (see detailed list in Figure 1; Table 1). Species are grouped based on clusters having an Euclidean distance of 3.2 (green circles). All variables were log-transformed except for the TL and nDC. Taxa codes are found in Supplementary Table S2.

web simplification is likely to be exacerbated by the concurrent pressures of global warming (Bonnaffé et al., 2024).

4.2 The role of invasive cyprinids

A key mechanism driving this transformation appears to be linked to the increase of invasive cyprinids, which are recognized as ecosystem engineers. Although its direct trophic links were limited, the grass carp likely was a driver of such aquatic community change since its proliferation led to the extensive depletion of aquatic vegetation with cascade effects on water quality, macroinvertebrate and fish communities (Milardi et al., 2022). However, its influence was recognized in the present study only as an asymmetrical relationship, as it acted as a dominant structuring agent with few reciprocal direct effects from the native food web. The depletion of aquatic vegetation by grass carp led to a cascade of effects in the canals, evident in the late invasion stage supported by changes measured in abiotic variables and the community. Specifically, the combined effects of macrophyte disappearance and bioturbation by other invasive cyprinids (e.g., common carp) have likely driven a regime shift towards a turbid, hypoxic state as supported by higher total dissolved solids and lower dissolved oxygen saturation, documented in the late invasion stage. In these altered conditions, native species were the first to suffer; for example,

native invertivores like the tench (*Tinca tinca*), which preys on phytophilous macroinvertebrates, were almost entirely lost. Carps, especially the common carp, are benthivorous species that alter sediment leading to increase of water turbidity (Nieoczym and Kloskowski, 2014; Qiu et al., 2019). Similarly, grass carp was found to completely consume the available aquatic macrophytes and in turn lead to increase of turbidity and decrease of oxygen concentration (Lembi et al., 1978; Pápalová et al., 2009). Turbidity posed a significant challenge in aquatic environments by reducing visibility and hindering the hunting efficiency of visual predators and consumers (e.g., Ferrari et al., 2010). Beyond these predator-prey alteration, turbidity also degrades habitat structure by reducing growth of submerged aquatic macrophytes through a decreased light penetration (Herb and Stefan, 2003). Such alterations also led regime shift to change in aquatic communities. Similar shifts from from macrophyte to algal dominance, as, triggered by grass carp, have been observed in both mesocosm experiments (e.g., He et al., 2024) and other invaded regions (e.g., Maceina et al., 1992; Wittmann et al., 2014). Furthermore, such altered environmental conditions likely create a positive feedback loop that facilitates the success of tolerant NNS over native fauna, as shown by the progressive increase in NNS abundance observed in our study. This mechanism is in agreement with the invasional meltdown hypothesis (Simberloff and Von Holle, 1999), whereby the establishment of one invader facilitates the success of others, a phenomenon also observed in experimental fish studies (e.g., Crone et al., 2023).

Our analysis by canal size revealed that LC experienced the greatest loss of species. This result is likely driven by body-size refuge; in larger water bodies, non-native carp are able to avoid predation by outgrowing their predators, reducing top-down control and amplifying their detrimental effects on the ecosystem (Castaldelli et al., 2013; Claessen et al., 2002).

4.3 Change in producers and top predators

The eradication of macrophytes by invasive carp shifted basal energy pathways to other possible sources (e.g., detritus or phytoplankton). Although this study did not include biomass measurements of these basal resource due to data unavailability, this inference is strongly supported by the observed environmental shift to a turbid, phytoplankton dominated state, in agreement with other findings in aquatic ecosystems (e.g., Claessen et al., 2002; Qiu et al., 2019).

A significant compositional change in response to altered environmental conditions was also evident among top predators. The replacement of the native pike (*E. cisalpinus*), a visual predator, with the invasive wels catfish can be explained by a filtering effect driven by the altered environment. Pike rely on vision to detect prey, and their foraging efficiency and anti-predator behaviours are significantly compromised in turbid waters (Salonen and Engström-Öst, 2013). In contrast, the wels catfish has developed non-visual predation that allows it to forage effectively in low visibility conditions (Bruton, 1996). Consequently, the shift in top predators is not the result of only competitive mechanisms, but is likely driven by adaptation to the environment, thereby reinforcing the invasional meltdown process.

4.4 Study limitations and future research directions

While our study provides a comprehensive overview of ecosystem change during biological invasion, we acknowledge some limitations due to the data availability. Specifically, our network analyses do not account biomass data for basal producers (e.g., phytoplankton, macrophytes). Furthermore, a pre-invasion baseline, which represents the communities before the establishment of any non-native species, could not be reconstructed due to the scarcity of detailed historical dataset with comparable resolution, across centuries (Haubrock et al., 2021b). The difficulty of obtaining long-term data is a common challenge in ecological research, but it highlights the invaluable importance of continuous environmental monitoring in detecting and understanding future changes.

5 Conclusion

Our study in Po River basin canals demonstrated that biological invasions led to the simplification of the aquatic food web, supporting the invasional meltdown hypothesis in this study area. Specifically, we found a shift from balanced community control to predominantly bottom-up forces in the late invasion

stage involving the grass carp. This shift was characterized by a decrease in macrophytes, native fish species richness and network connectance, driven mainly by the replacement of native predators with other invasive predators such as the wels catfish, exotic invertivorous fish, and by the spread of ecosystem-engineering species, such as the grass carp (Milardi et al., 2020).

In aquatic food webs, hierarchical structure is clearly important and well known, reflected in basic traits such as body size or biomass (e.g., larger consumers eat smaller prey, Brose et al., 2006; Sommer et al., 2018). Here, we showed an example in which long-term monitoring data, including abundance, biomass, and environmental variables, were coupled with the predictive power of network analysis, helping separate fish species from invertebrate groups (along the trophic hierarchy). We support the idea that ecological networks, such as food webs, can be the missing link in biomonitoring science (Gray et al., 2014) and we encourage more studies to bridge this gap.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#), further inquiries can be directed to the corresponding author.

Author contributions

KP: Conceptualization, Formal Analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review and editing, Resources, Validation. AG: Data curation, Formal Analysis, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review and editing, Validation. ML: Resources, Writing – review and editing, Investigation, Data curation. AH: Formal Analysis, Methodology, Visualization, Writing – review and editing. GC: Conceptualization, Funding acquisition, Investigation, Resources, Writing – review and editing, Supervision, Validation.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2025.1727438/full#supplementary-material>

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