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Relative Effects of Eutrophication and Warming on Freshwater Ecosystems Across Ecological Levels

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ABSTRACT

Global change strongly alters biodiversity worldwide, but our ability to predict their consequences for ecosystem functioning remains limited. This lack of knowledge may be attributed to the limited empirical evidence of the simultaneous ecological impacts of global change across multiple ecological levels. Here, we conducted a full factorial experiment to measure the isolated and combined effects of two global change drivers to which freshwater ecosystems are severely exposed: (i) nutrient addition, which mainly affects the lower trophic levels and modifies ecosystems from the bottom of the food chain, and (ii) warming, which primarily affects large organisms at the top of the food chain. We quantified the effects of the two global change drivers at four different ecological levels: community composition (zooplankton and benthic invertebrates), size structure, trophic architecture, and ecosystem functioning. We found that the impacts of treatments varied significantly across different ecological levels. Specifically, community composition was predominantly affected by warming, whereas nutrient addition played a more important role than warming in ecosystem functioning (e.g., primary production and atmospheric CO_2 uptake). More importantly, we found that food webs (described using size spectrum and stable isotope structure) represent an integrative ecological level for capturing the effects of the two global change drivers tested, integrating changes in both community structure and ecosystem functioning. These results provide valuable insights into the responses of aquatic ecosystems to global change and reveal the importance of considering multiple ecological levels to improve our understanding of the processes driving the responses of ecosystems to global change.

1 | Introduction

Global change strongly affects biodiversity through changes in the physiology, phenology, and distribution of organisms (Walther et al. 2002; Parmesan 2006; Scheffers et al. 2016). Freshwater fauna is among the most vulnerable to anthropogenic activities (Vörösmarty et al. 2010; Dudgeon 2019), with at least one-quarter of freshwater species being endangered of extinction (Sayer et al. 2025). Yet, freshwater ecosystems play a critical role in important ecological functions such as the carbon cycle and climate regulation (Lynch et al. 2023). However, predicting how changes in biodiversity induced by human activities affect ecosystem functioning remains difficult (Wieczynski et al. 2021). To date, most studies have focused on quantifying responses at the individual and population levels, while investigations into the consequences for energy flows in ecosystems are still limited (Montoya and Raffaelli 2010; van der Putten et al. 2010). While species richness, evenness, and composition are important facets of biological diversity, interactions among organisms are crucial determinants of the goods and services supported by biodiversity (Guimaraes 2020; Nagelkerken et al. 2020). Therefore, there is an important need to understand how the functional roles of organisms modulate ecosystem responses to global change (Duncan et al. 2015; Maureaud et al. 2019).

Trophic cascade is a key mechanism by which species loss can affect ecosystem functioning (Terborgh and Estes 2013). Emblematic examples of trophic cascades in freshwater ecosystems include the replacement of benthic algae and macrophyte beds by phytoplankton in lakes and rivers in response to the removal of a top-predatory fish, the largemouth bass *Micropterus salmoides* (Power et al. 1985; Carpenter et al. 2001). This can result in a gradual shift from clear to turbid water, with important consequences for ecosystem functioning such as nutrient cycling (Jeppesen et al. 2007). Conversely, changes in ecosystem functioning can occur from the bottom to the top of the food chain. For example, increasing nutrient levels can increase the biomass of primary producers ("green" pathway) or detritus ("brown" pathway) and influence carbon storage (Lourenço-Amorim et al. 2014; Ferreira et al. 2015). Importantly, these changes in energy fluxes within ecosystems can occur without significant shifts in biodiversity, largely due to the stabilizing properties of organisms, such as functional redundancy or consumer's plasticity (Naeem and Li 1997; Yachi and Loreau 1999; Miner et al. 2005). Examining the internal properties of food webs as a part of community structure should therefore help us to better understand the consequences of environmental changes for ecosystem functioning (Woodward 2009; Thompson et al. 2012; La Pierre and Hanley 2015).

Eutrophication, that is, the addition of nutrients from agricultural or domestic runoff, increases the abundance of primary producers beyond the transformation capacity of higher trophic levels and is widely recognized as one of the most significant global change drivers acting on freshwater ecosystems (Smith et al. 1999). Eutrophication generally alters the carbon cycle by increasing the carbon dioxide uptake by primary producers, but it also increases the supply of labile organic matter in the bottom sediment and promotes anoxic conditions, leading to higher methane emissions, a highly potent greenhouse gas (Beaulieu et al. 2019; Grasset et al. 2020; Sun et al. 2021; Colas et al. 2021). Furthermore, eutrophication rarely acts in isolation and often co-occurs with other drivers of global change (Dudgeon 2019). These include climate warming, which primarily affects consumers by decreasing their fitness and biomass (Binzer et al. 2012). More specifically, warming can shift the community size spectrum towards dominance of smaller individuals (Daufresne et al. 2009). Such changes are likely to impact the entire food web, as it is strongly size-structured in aquatic ecosystems through a pyramid of biomass (Woodward et al. 2010; Dossena et al. 2012; Trebilco et al. 2013). Consequently, warming can influence the top-down control of freshwater communities, with a decrease in predator abundance and reduced trophic cascade efficiency (Petchey et al. 1999; Kishi et al. 2005; Jeppesen et al. 2014). Therefore, eutrophication and warming represent potentially antagonist forces acting on the bottom-up and top-down controls of freshwater ecosystems (La Pierre and Hanley 2015; Binzer et al. 2016). However, little is known about the interactions between warming and nutrient addition across multiple ecological levels (Cross et al. 2015).

The objective of the present study was to assess the response of freshwater ecosystems to warming and eutrophication at four different ecological levels: community composition, size structure, trophic architecture, and ecosystem functioning. Using a full-factorial mesocosm experiment, we exposed freshwater ecosystems to nutrient addition (eutrophication) and a +4°C heat wave (warming). We predicted that the intensity of the responses to the two treatments would differ between the four ecological levels, as they may affect the top and bottom of the food chain differently (Ledger et al. 2012; Binzer et al. 2016; Lemmens et al. 2018). Specifically, we expected that (i) nutrient addition would increase bottom-up forces by significantly increasing the abundance of primary producers, primarily affecting functioning; (ii) warming would reduce the top-down force by excluding large species and reducing predator abundance, primarily affecting community composition; and (iii) food web structure, measured by size spectrum and trophic architecture (Simmons et al. 2021), would respond similarly to both treatments, as it integrates changes in both bottom-up and top-down forces. We aimed to provide valuable predictive insights into how ecosystems respond to global change across multiple ecological levels in the context of multiple stressors (Woodward et al. 2010; Stewart et al. 2013; McMeans et al. 2016). In particular, identifying the ecological processes at community level that can either amplify or mitigate these effects is crucial for understanding their consequences for ecosystem functioning (Goldenberg et al. 2018).

2 | Materials and Methods

2.1 | Experimental Design

The experiment was conducted in a set of 24 mesocosms (170 cm diameter and 100 cm high) located in Moulis, France (Richard et al. 2025; Figure 1a). It followed a full-factorial design with four treatments, each replicated six times: (i) control ("C"), (ii) nutrient addition ("N"), (iii) warming ("W"), and (iv) nutrient addition + warming ("NW"). Treatments were assigned to mesocosms using a spatially heterogeneous and symmetrical design (Figure 1b). In early October 2020, the bottom of the mesocosms was covered with a thin layer of inert, dry gravel and filled with filtered water (sand and UV filtration) from the nearby stream Lèze. In addition, a hollow brick (60 × 20 × 30 cm) and two brooms were placed in the center of each mesocosm to increase habitat heterogeneity. Inoculation started in November 2020 with the introduction of natural communities from surrounding gravel pit lakes (Raffard et al. 2023; Závorka et al. 2020). Specifically, sediment, periphyton, phytoplankton, and zooplankton were sourced from two different gravel pit lakes. Periphyton was scraped from submerged littoral substrate, while phytoplankton and zooplankton were collected using nets of 20 and 80 μm mesh size, respectively. From April to early July 2021, a mix of benthic macroinvertebrates was introduced twice a month. Macroinvertebrates were collected with a 500 μm mesh surber net from surrounding gravel pit lakes, from dead arms of the downstream part of the Garonne and the Ariège rivers, and the nearby stream Lèze (details in Table S1). These sites

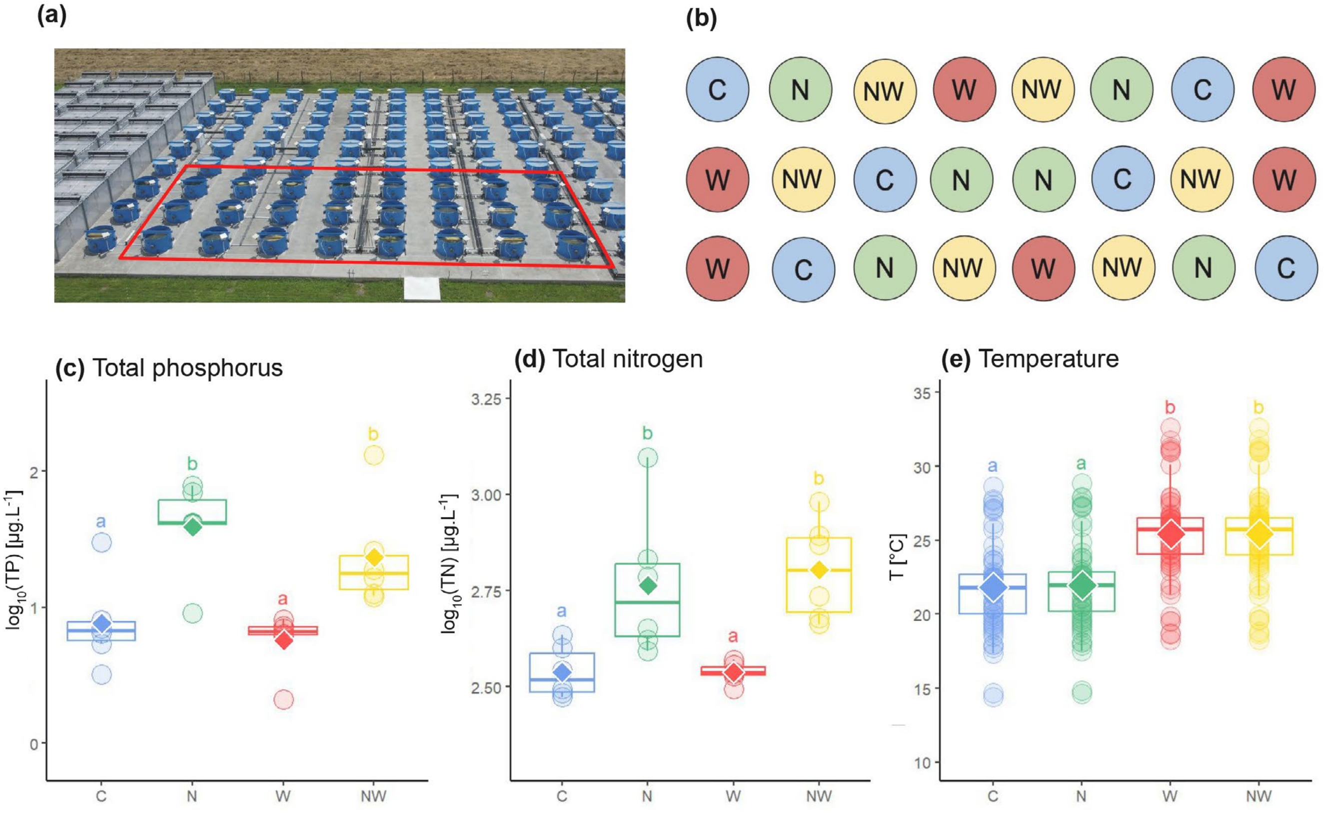

FIGURE 1 | Mesocosm platform used in this experiment (red line) (a) and treatment design (b) colored by treatments: Control (C) in blue, nutrient (N) in green, warming (W) in red, and nutrient + warming (NW) in yellow. Total phosphorus (c) and nitrogen (d) concentrations in the water column at the end of the experiment and mean daily water temperature during the experiment (e). Lozenges represent the mean values for each treatment, and different letters indicate significant differences (pairwise *t*-test, $p < 0.05$).

were selected to capture a broad gradient of hydromorphological and environmental conditions to maximize the diversity of organisms and their tolerance to temperature and eutrophication level. In addition, all mesocosms were left fully open to allow aerial insect colonization before and during the experiment. From April 2021, 20 g of dried poplar leaves (*Populus nigra*) were added monthly to each mesocosm to mimic natural inputs of allochthonous subsidies. Additionally, two macrophyte (*Elodea canadensis*) bunches of five (±1) g wet mass, collected from local ponds, were added into each mesocosm in early July. However, macrophytes exhibited little to no growth during the experiment and were therefore excluded from subsequent analyses.

Experiment was conducted in the summer period, maximizing ecological dynamics and processes. Specifically, treatments were applied for 9 weeks from July 21, 2021, to September 20, 2021. Nutrient addition (N) was performed by weekly adding 150 mg of phosphate (KH_2-PO_4 form) and 1.9 g of nitrogen (NH_4-NO_3 form) to each N and NW mesocosm. At the end of the experiment, total phosphorus concentrations differed significantly among treatments ($F_3 = 9.063$, $p < 0.001$), with mean concentrations in the N and NW being three to four times higher than in C ($47 \pm 24\,\mu g\,L^{-1}$ for treatment N and $36 \pm 47\,\mu g\,L^{-1}$ in NW vs. $10 \pm 9\,\mu g\,L^{-1}$ in C; see Figure 1c). These concentrations are in the range of the values observed in small and shallow oligotrophic and eutrophic lakes found locally (Colas et al. 2021). Total nitrogen concentrations also differed significantly ($F_3 = 8.540$, $p < 0.001$) and were twice as high in the N and NW treatments than in the C treatment ($0.63 \pm 0.32\,mg\,L^{-1}$ in N and $0.66 \pm 0.19\,mg\,L^{-1}$ in NW vs. $0.35 \pm 0.05\,mg\,L^{-1}$ in C; see Figure 1d). The heat wave of the warming treatments (W and NW) consisted of increasing water temperature by 4°C above the average temperature of three control mesocosms using three 600 W titanium heaters placed at the center of the water column in each mesocosm. We selected +4°C to represent a realistic warming anomaly during summer heatwaves in southwestern France, as observed for instance in the summer 2022 (Ibebuchi and Abu 2023; Martins et al. 2024). All heated mesocosms were maintained at the same temperature throughout the experiment (mean 25.4°C ± 3.5°C), whereas unheated mesocosms (C and N treatments) had a mean temperature of 21.8 (±3.4°C), with a significant difference between treatments ($F_3 = 27.138$, $p < 0.001$, Figure 1e).

2.2 | Sampling

Zooplankton organisms were sampled by collecting 12 L of water from three different depths (sub-surface, middle of the water column, and near the bottom) at both the center and periphery of each mesocosm using a 2 L Van Dorn sampler. Water samples were then filtered through an 80 µm mesh (KC Denmark, Denmark), and the remaining material was preserved in 50 mL of 70% ethanol. Taxonomic identification was performed to family level for crustaceans and to the genus level for rotifers using an Olympus SZ61 stereomicroscope (4.5× magnification).

At least three 1 mL subsamples were analyzed for each mesocosm, ensuring the identification of more than 100 individuals per mesocosm. A total of 12 taxa were identified, including five crustaceans, four arthropods, and three rotifers. Zooplankton biomass was estimated using body length measurements from the entire zooplankton sample. The body length of all individuals was determined using a high-throughput imaging system (FlowCam-Macro, Yokogawa, USA) with a resolution of 100 pixels mm^{-1} and analyzed with ImageJ software (Collins 2007). In total, 10,275 individuals were measured. As copepod and cladoceran families could not be distinguished in pictures, individual body mass was estimated using length-weight relationships established at the order level (Dumont et al. 1975). For rotifers, a mean body mass was assigned to each genus based on Dumont et al. (1975). For all pelagic dipterans (chaoborids and culicids), a mean dry mass of 30 μg for all individuals (approximately 1 cm: Mährlein et al. 2016) was used. Data on taxonomic identification and body size were then calculated for each mesocosm by extrapolating individuals to the total mesocosm volume (1800 L).

Benthic macroinvertebrates were collected using three artificial substrates per mesocosm. The three substrates consisted of plastic containers (200 × 100 × 30 mm) filled with gravel and placed at the bottom of each mesocosm in June 2021. At the end of the experiment, the artificial substrates were carefully removed, and invertebrates were separated from the substrate using a 500 μm mesh sieve. Additionally, the brick and brooms were removed and rinsed to collect invertebrates. All samples were then fixed in 70% ethanol for subsequent determination in the laboratory. Taxonomic identification and classification were performed at the family level following Tachet et al. (2010) using an Olympus SZ61 stereomicroscope (2× magnification). All individuals were then photographed at a resolution of 30 pixels mm^{-1} and measured individually. In total, 17,314 invertebrates belonging to 16 families were identified and measured individually using ImageJ software (Collins 2007). Total benthic invertebrate abundance was then calculated for each mesocosm by extrapolating the artificial substrate area to the surface area in the mesocosm (2.25 m^2) and summing the number of invertebrates collected from the brick and brooms. The dry mass for each individual was estimated by using the length-weight relationships established by Mährlein et al. (2016), that were mostly available at the genus or species level and possibly missing for some taxa sampled in the mesocosms. Therefore, body mass estimates were estimated using the closest phylogenetic and morphological organisms for which a length–weight relationship was available. For instance, the length–weight relationship of *Gyraulus* sp. was used to estimate the mass of Planorbidae, and the relationship for Ceratopogonidae was used for oligochaetes.

2.3 | Size Structure

We used the size spectrum approach, derived from the biomass pyramid theory, to estimate an integrative proxy of community size structure (Pomeranz et al. 2019; Yvon-Durocher et al. 2011). Based on the negative linear relationship between organism abundance and body size in a *log–log* space, the community size spectrum reflects several important ecological features, including food web carrying capacity, predator–prey interactions, and trophic energy fluxes, with three common parameters: (i) the slope indicates the efficiency of biomass transfer through body size distributions; (ii) the elevation (e.g., the "width" of the pyramid) represents the carrying capacity of the food web; and (iii) the linearity indicates the strength of predator–prey relationships within the food web (Rossberg et al. 2019). We first classified all individual body masses (in μg) into five bins, according to a geometric series of ten (Dossena et al. 2012). Size classes covered a body size range from 10^{-1} to 10^{4} μg (1st: 0.1–1 μg, 2nd: 1–10 μg, ..., 5th: 1000–10,000 μg), encompassing both zooplankton and benthic macroinvertebrates (Mehner et al. 2018). The lower boundary was set after the abundance peak of size distribution resulting from sampling bias of the smallest size classes, and the upper boundary was set to ensure equal representation of the size classes across all mesocosms and avoid empty bins (Dossena et al. 2012). The first two classes were mainly composed of planktonic primary consumers (crustaceans, rotifers). The third class primarily consisted of insects (pelagic predators such as chaoborids, or benthic deposit feeders such as chironomids and annelids) and small isopods (asellids). The fourth class was characterized by benthic organisms and included a wide variety of trophic groups: primary consumers (e.g., baetids), omnivorous taxa (e.g., lymnaea), and mesopredators (e.g., planaria, small odonatan larvae). Finally, the fifth class was mainly composed of the pelagic top predator notonecta, odonatan larvae, and large individuals of lymnaea taxa. We then calculated the variation rate in abundances across each class ($\log_{10}$ of abundance) to determine the size spectrum relationship within each invertebrate community (Brucet et al. 2010). Slope was defined as the estimated coefficient of body size on organism abundance, elevation was calculated as the midpoint height on the *X*-axis to minimize correlation with the slope (Sprules and Barth 2016), and linearity was defined using the R^2 coefficient of the relationship.

2.4 | Trophic Architecture

Stable isotope analyses (δ^{13}C and δ^{15}N) were used to determine the origin of consumed resources and the trophic position of each taxon. Although we aimed to collect an equal number of samples per taxon in each mesocosm, this was not always possible due to high variability in organism abundance, which was sometimes not sufficient for stable isotope analyses. Consequently, we followed Nagelkerken et al. (2020) and created a unique food web per treatment by randomly selecting three replicates of each taxon (producers, consumers, and detritus), attempting to cover all mesocosms within the treatments. The whole body was used for zooplankton, arthropods, and oligochaetes, while the foot muscle was used for gastropods (Evangelista et al. 2019). Individuals preserved in ethanol were rinsed with distilled water and oven-dried for 72 h at 60°C. No specific correction was applied for isotopic signatures linked to alcohol conservation because its effect on δ^{13}C and δ^{15}N for zooplankton and macroinvertebrates is considered negligible (Syväranta et al. 2008). On average, each sample contained three individuals, ranging from one for odonatans to 150 for copepods (see details for all taxa in Table S2). For primary producers, macrophyte samples were collected from the remaining fragments at the bottom of each mesocosm, phytoplankton samples were obtained by filtering approximately 100 L of water through a

20-μm mesh net, while periphyton samples were obtained by scrubbing three tiles (20 × 20 cm) that had been placed in the mesocosm 5 weeks before the end of the experiment. Additionally, we collected some poplar leaves used as allochthonous inputs. All samples were dried and then ground into a homogeneous powder. A total of 183 samples were analyzed at Cornell's Stable Isotope Laboratory (COIL, USA).

The $\delta^{13}C$ values of consumers were corrected ($\delta^{13}C_{cor}$) by scaling the values between 0 (representing the mean signature of allochthonous carbon: poplar leaves) and 1 (representing the mean carbon signature of primary producers: phytoplankton + phytobenthos + macrophytes) in each mesocosm (Jackson et al. 2017). Values were then expressed as a percentage, reflecting the proportion of autochthonous carbon in consumers, ranging from 0% to 100%. Then, the trophic position (TP) of each consumer i was determined using the following Formula (1):

$$TP_i = 1 + \frac{\delta^{15}N_i - \delta^{15}N_{baseline\ i}}{TEF} \quad (1)$$

where 1 is the trophic position of the baseline (detritus or primary producers), $\delta^{15}N_i$ is the stable nitrogen isotope value of individual i, $\delta^{15}N_{baseline}$ is the $\delta^{15}N$ value of the baseline (detritus or producers), and TEF is the trophic enrichment factor of 3.4‰ (Post 2002). Due to the higher enrichment of $\delta^{15}N$ values of primary producers compared to detritus (ranging from 1‰ to 2‰ depending on treatments), we corrected the baseline for each individual i. Briefly, the $\delta^{15}N_{baseline\ i}$ was defined as the predicted $\delta^{15}N$ value following the enrichment estimate between $\delta^{15}N_{detritus}$ and $\delta^{15}N_{producers}$ with the percentage of resource use found with the $\delta^{13}C$ value of the individual i (details available in Figure S1). Based on the trophic positions of all taxa, we estimated the food chain length for each treatment, defined as the average trophic position value of the highest taxa in the food chain (three values per treatment, including all mesocosms). Notonecta was the top predator for treatments C, N, and W, whereas the highest trophic position was represented by Planaria in treatment NW. Finally, we assessed isotopic niche sizes as an indicator of trophic diversity defined as the space occupied by consumers in the bi-plot of resource origin/trophic position (Cucherousset and Villéger 2015).

2.5 | Ecosystem Functioning

A total of six variables related to carbon stocks and fluxes were measured. First, pelagic and benthic primary production was estimated using chlorophyll-*a* (chl*a*) concentrations, measured with a portable fluorometer (Algae Torch and Bentho-Torch; bbe-Moldaenke, Germany). Total chl*a* concentration was determined by absorption at three different wavelengths (470, 525, and 610 nm) to cover the full range of algal classes. Pelagic primary production was quantified as the mean chl*a* concentrations (in $\mu g\,L^{-1}$) from three measurements at different depths (sub-surface, middle of the water column, and near the bottom). Benthic primary production was quantified by measuring chl*a* concentration on three tiles (20 × 20 cm) placed at the bottom of each mesocosm in a heterogeneous pattern 5 weeks before the end of the experiment (Raffard et al. 2023), and calculating their average ($\mu g\,cm^{-2}$).

The decomposition of coarse organic matter was assessed using leaf bags containing 3 g (±0.01) of air-dried senescent poplar leaves enclosed in coarse-mesh (10 mm mesh size) bags. Three leaf bags were deployed in each mesocosm during the last 5 weeks of the experiment to prevent total leaf consumption and empty bags at the end of the experiment (Závorka et al. 2020). At the end of the experiment, all leaf bags were immediately frozen at −20°C, then oven-dried at 60°C for 72 h in the laboratory (after rinsing to remove sediments and any invertebrates) and finally weighed to the nearest 0.01 g. Then, the decomposition rate (expressed in day^{-1}) was calculated per mesocosm following Petersen and Cummins (1974) as:

$$\text{Decomposition rate} = -\frac{\ln\left(\frac{M_f}{M_i}\right)}{t} \quad (2)$$

where M_i is the total initial leaf dry mass of the three bags (in g), M_f is the total remaining dry mass of the three bags (in g), and t is the exposure time in the mesocosms (in days).

The concentration of dissolved organic carbon (DOC, $mg\,L^{-1}$) was measured by filtering 100 mL of mesocosm water through GF/C filters. The samples were immediately stored at 4°C and analyzed within 1 month (Shimadzu TOC-L).

Dissolved gas concentrations were measured on September 20th, prior to other samplings (around 10 a.m., 2 h after sunrise) by equilibrating 430 mL of mesocosm water with 570 mL of ambient air in a 1 L bottle. After equilibration, 40 mL of the headspace was transferred into 12 mL pre-evacuated Exetainers (Labco Limited, UK). The partial pressure (pCO_2 or pCH_4) in the samples was measured by injecting the headspace gas into a Cavity Ring Down Spectrometer (CRDS, Picarro G2201-i; Picarro Inc., CA, USA) equipped with an open-source autosampler (SAM, Saskatoon, Canada). The original partial pressure in the bottle was then calculated using the headspace ratio, the water column temperature, and the air temperature during equilibration, based on solubility constants (Weiss 1974; Yamamoto et al. 1976). The pCO_2 and pCH_4 in the water were expressed as a partial pressure departure (Δp) from the partial pressure in the atmosphere, calculated from 40 mL atmospheric samples taken during equilibration. A positive differential (ΔpCO_2 or $\Delta pCH_4 > 0$) indicates potential gas emissions from the mesocosm to the atmosphere, whereas a negative differential (ΔpCO_2 or $\Delta pCH_4 < 0$) indicates potential gas uptake from the atmosphere into the mesocosm.

2.6 | Statistical Analyses

For each treatment, we determined the taxonomic diversity using the Shannon index, computed with the function *diversity* from the *vegan* package (version 2.6-4; Oksanen et al. 2013) in *R studio* software. To identify the effect of treatments on taxon identity, we performed ordination analysis based on taxonomic dissimilarities using non-metric multidimensional scaling (NMDS) analysis. This analysis was performed with the *MetaMDS* function in the *vegan* package (Oksanen et al. 2013) after applying a Hellinger transformation (Legendre and Gallagher 2001). The values for each mesocosm according to the three variables (diversity and positions on the two NMDS axes) were analyzed using a one-way ANOVA across treatments. In case of significant differences ($p < 0.05$), a pairwise *t*-test was performed to identify which treatments differed from each other with Bonferroni correction (hereafter "corrected"). The contribution of taxa to observed dissimilarities between treatments was determined using the SIMPER procedure with 10,000 permutations (Clarke 1993). Regarding size structure, we calculated one size spectrum per mesocosm, resulting in six replicates for each of the three parameters: slope, elevation, and linearity. Differences in size spectrum parameters between treatments were analyzed using one-way ANOVA. In case of significant differences ($p < 0.05$), we performed a corrected pairwise *t*-test to determine which treatments differed from each other. Differences between treatments in carbon origin were analyzed using a one-way ANOVA on all taxa values for autochthonous carbon. Corrected pairwise *t*-tests were then performed to identify treatment differences. Differences in food chain length were analyzed using the non-parametric alternative to ANOVA (Kruskal–Wallis rank sum test) due to low replication (three values per treatment). A Dunnett test for multiple comparisons was performed to identify which treatments differed from each other. Differences in trophic niche size were analyzed by comparing the overlapping 95% confidence intervals of the standard ellipse area (SEA). Confidence intervals were calculated using 1000 bootstrap runs with the Stable Isotope Bayesian Ellipses method in R (*SIBER* package version 2.1.7; Jackson et al. 2017). To summarize ecosystem functioning, the six measured variables were reduced to two principal components using Principal Component Analysis (*PCA* function of *FactoMineR* package version 2.8; Lê et al. 2008). All variables were primary scaled to give them similar importance and then log-transformed (except DOC and CO_2 emission) to reduce the influence of extreme values and improve normality. PCA axis 1 (explaining 49.7% of variance, eigen value = 2.98) was strongly correlated with five measured variables and revealed a strong gradient of ecosystem primary production (autotrophic processes: Table S3). High values indicated high primary production, high dissolved organic carbon concentrations, CO_2 uptake, but CH_4 release. PCA axis 2 (explaining 26.5% of variance, eigen value = 1.59) was positively correlated with decomposition rate and negatively correlated with CH_4 emissions, reflecting a gradient of aerobic organic matter processing (Table S3). The coordinates of each mesocosm on PCA axis 1 and PCA axis 2 were compared among treatments using one-way ANOVA. A corrected pairwise *t*-test was performed to identify treatment differences on PCA axis 1 ($p < 0.05$).

To compare the strength of the treatment effects across ecological levels, we summarized all response variables for each ecological level using a meta-analysis approach (Osenberg et al. 1997). Specifically, we used the mean effect size for each ecological level, weighting each treatment's effect size per response variable by its variance (Borenstein et al. 2009). Stable isotope standard ellipse area (SEA) was excluded from the calculation of the global effect size of treatments on trophic architecture to avoid bias in the weighted effect size estimation. Indeed, SEA was derived using 1000 simulations (Jackson et al. 2011) and has a reduced variance compared to other variables. We used Hedge's effect size (g) to limit bias due to low replication. Since g values can be either positive or negative, we used their absolute values to ensure consistency in effect size direction (Buoro et al. 2016).

The mean effect size for each ecological level was calculated following the Equation (3):

$$\bar{g} = \frac{\sum (w_i \times g_i)}{\sum w_i} \tag{3}$$

where g_i is the effect size of the ith ecological level, and w_i represents its weight—defined as the inverse of the variance (V_i) as shown in Equation (4):

$$w_i = \frac{1}{V_i} \tag{4}$$

Finally, the confidence intervals were calculated using the mean variance of the effect sizes (Borenstein et al. 2009), as given by Equation (5):

$$\mathrm{IC}_{95} = z \times \sqrt{\frac{1}{\sum w_i}} \tag{5}$$

where z is set at 1.96 for a 95% confidence level.

3 | Results

There was a strong effect of treatments on invertebrate taxonomic composition (Figure 2a). We found significant differences on the NMDS axis 1 ($F_3 = 16.413$, $p < 0.001$), with the W and NW treatments showing higher values than C and N (Figure 3a). Calanoid copepods contributed significantly to these differences, as they were the most abundant zooplankton taxon in the C and N treatments (14–60 individuals L^{-1}) and were almost eliminated in the W and NW treatments (0–2 individuals L^{-1}; Figure 3a; Table S4). Conversely, bosminids, along with several benthic macroinvertebrate taxa such as chironomids, annelids, or baetids, were at least three times more abundant in the W and NW treatments (Figure 3a; Table S4). We found no significant effect of treatments on the NMDS axis 2 ($F_3 = 2.302$, $p = 0.108$, Figure 3b). However, taxonomic diversity was significantly higher in the W treatment than in all other treatments ($F_3 = 11.852$, $p < 0.001$, Figure 3c).

Communities were strongly size structured, with the relationships between abundance and size classes always being significant, except for one mesocosm in the NW treatment ($p = 0.055$). All slopes were negative (Figure 2b), and differed significantly between treatments ($F_3 = 4.640$, $p = 0.013$), with flatter slopes found in the W treatment (Figure 3d). We also found a strong and significant effect of treatments on elevation ($F_3 = 38.035$, $p < 0.001$), with the N treatment showing higher elevations than C and NW treatments, while the W treatment had lower elevations than C and NW treatments (Figures 2b and 3e). However, there was no significant effect of treatments on size spectrum linearity ($F_3 = 2.958$, $p = 0.057$, Figure 3f).

Regarding trophic architecture, stable isotope analyses revealed significant differences between treatments, especially in the contribution of autochthonous carbon to consumers ($F_3 = 22.920$, $p < 0.001$, Figure 2c). The mean autochthony levels in treatments C, W, and NW were 22%, 17%, and 34%, respectively, while it was significantly higher in the N treatment (71%,

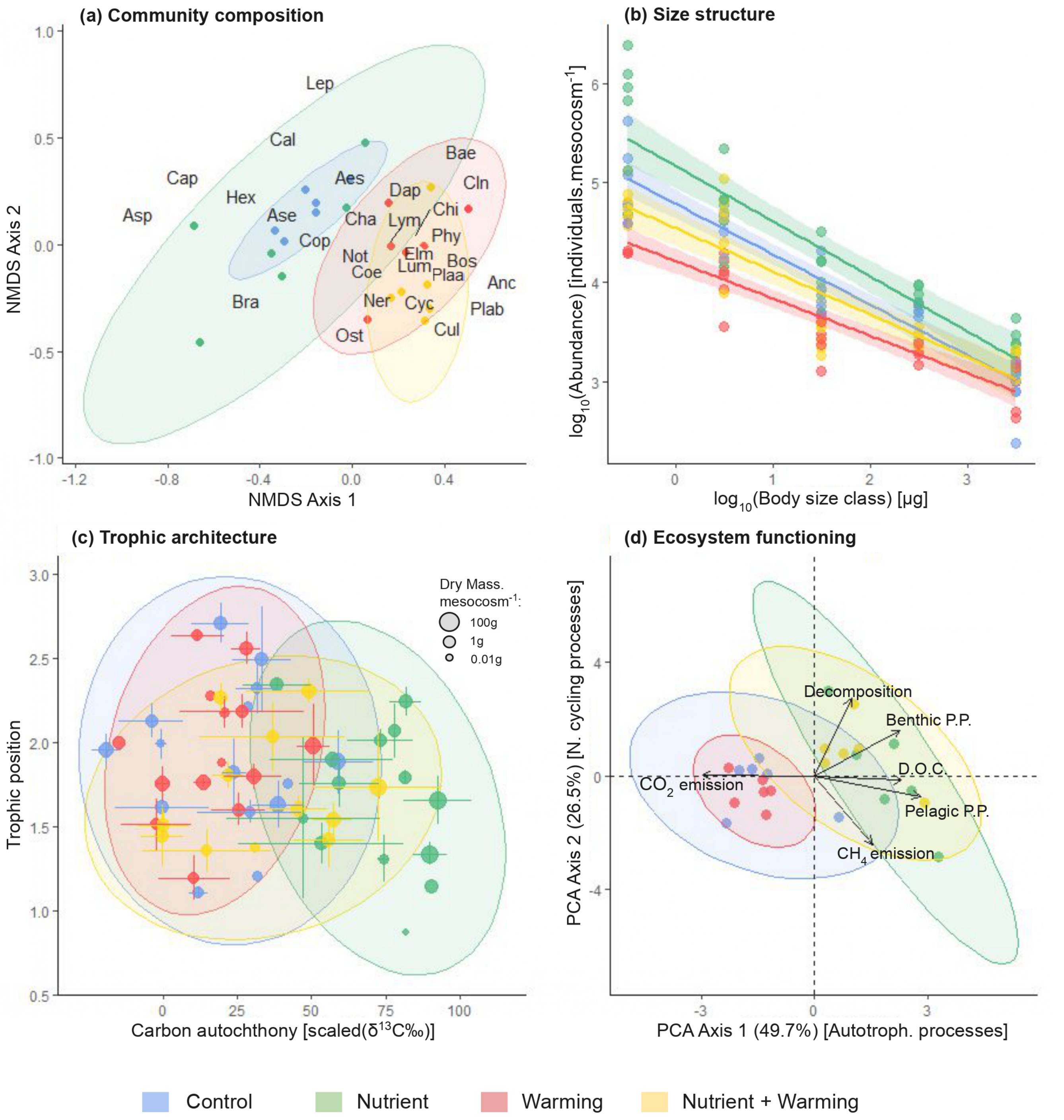

FIGURE 2 | Effects of treatments at each ecological level. (a) Community composition with the first two non-metric multidimensional scaling (NMDS) axes of invertebrate consumers (stress = 0.176). Points represent individual mesocosms, colored by treatments, with ellipses indicating the 95% CI for each treatment. (b) Community size spectrum. Points represent abundances per size class in each mesocosm. Solid line represents the mean size spectrum per treatment (95% CI). (c) Trophic architecture. Each point represents the feeding preference of a consumer, defined by its resource origin (autochthonous/allochthonous) and mean trophic position (±SD). Point size corresponds to the mean abundance of each taxon per mesocosm, with ellipses indicating the 95% CI for each treatment. (d) Ecosystem functioning. The two principal component analysis axes in response to treatments. Each point represents a mesocosm, with ellipses indicating the 95% CI for each treatment. Aes, Aeshnidae; Anc, Ancylidae; Ase, Aselidae; Asp, Asplanchnidae; Bae, Baetidae; Bos, Bosminidae; BPP, benthic primary production; Bra, Brachionidae; Cal, Calanoidae; Cap, Capniidae; CH$_4$ em, CH$_4$ emission; Cha, Chaoboridae; Chi, Chironomidae; Cln, Cladocera nauplii; CO$_2$ em, CO$_2$ emission; Coe, Coenagrionidae; Cop, Copepoda nauplii; Cul, Culicidae; Cyc, Cyclopidae; Dap, Daphniidae; Dec, decomposition rate; DOC, dissolved organic carbon; Elm, Elmidae; Hex, Hexarthridae; Lep, Leptocentridae; Lum, Lumbricidae; Lym, Lymneaidae; Ner, Neretidae; Not, Notonectidae; Ost, Ostracoda; Phy, Physidae; Plaa, Planaridae; Plab, Planorbidae; PPP, pelagic primary production.

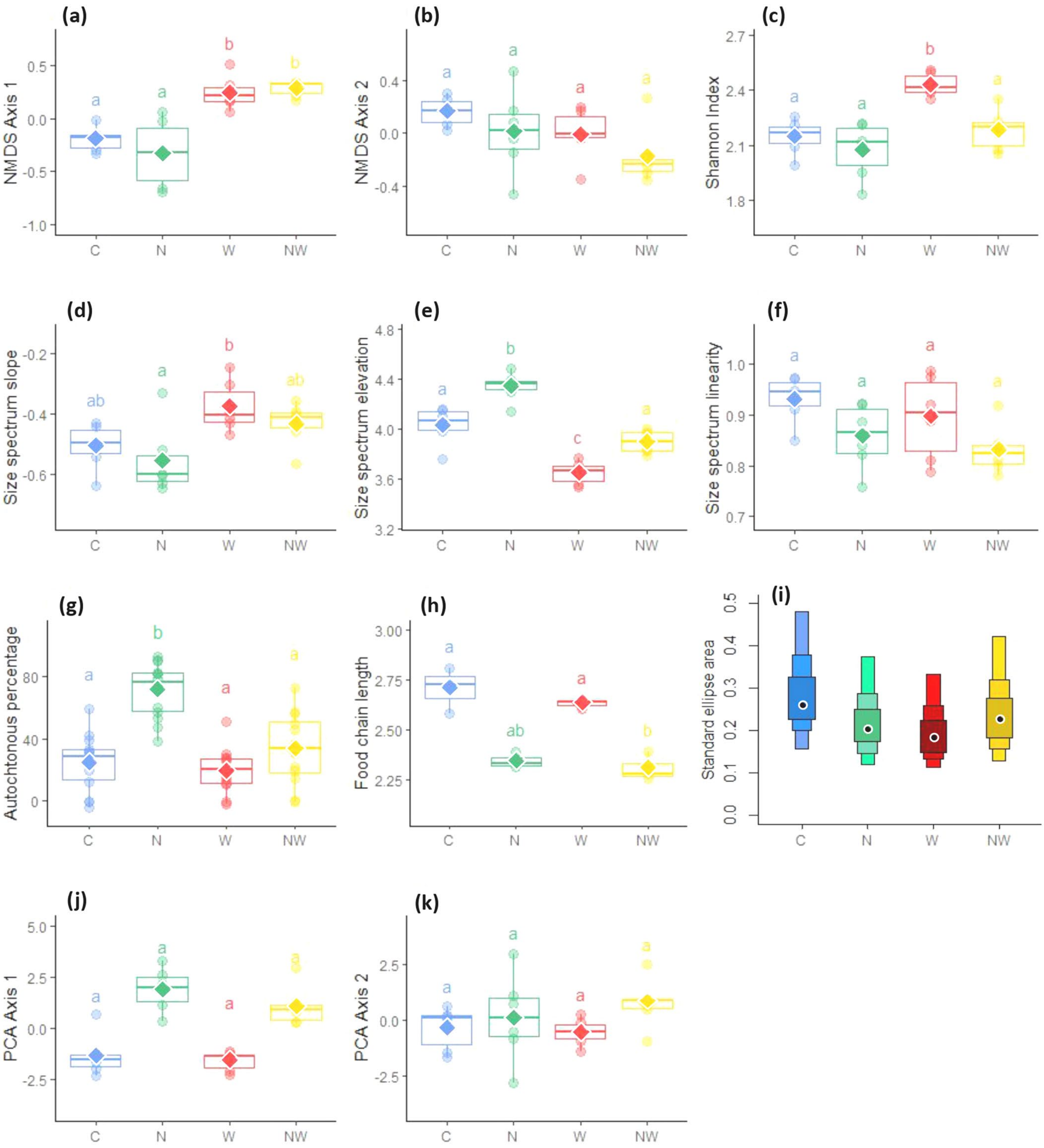

FIGURE 3 | Effects of treatments on community composition (a–c), size spectrum parameters (d–f), trophic architecture (g–i), and ecosystem functioning (j, k). Colors represent different treatments with control (C) in blue, nutrient (N) in green, warming (W) in red, and nutrient + warming (NW) in yellow. For standard ellipse area (i), dots represent the estimated size, and boxes represent the 50%, 75%, and 95% confidence intervals. In other cases, lozenges represent the mean value per treatment, and significant differences ($p < 0.05$) are given by letters.

Figure 3g), reflecting a higher reliance on primary production-derived carbon by consumers. Food-chain length was also significantly affected by treatments ($KW_3 = 8.744$, $p = 0.033$), with food-chain lengths in the NW treatment (2.31) being lower than in C and W treatments (2.71 and 2.63 respectively, Figure 3h). The mean food chain length in the N treatment (2.34) was also lower but did not differ significantly from the other treatments (Figure 3h). Trophic niche size was similar in all treatments (Figure 3i), suggesting that consumers relied on the same diversity of resources regardless of treatments.

Regarding ecosystem functioning, there was a significant difference between treatments on the first PCA axis ($F_3 = 21.411$, $p < 0.001$; Figure 2d). Specifically, the N and NW treatments

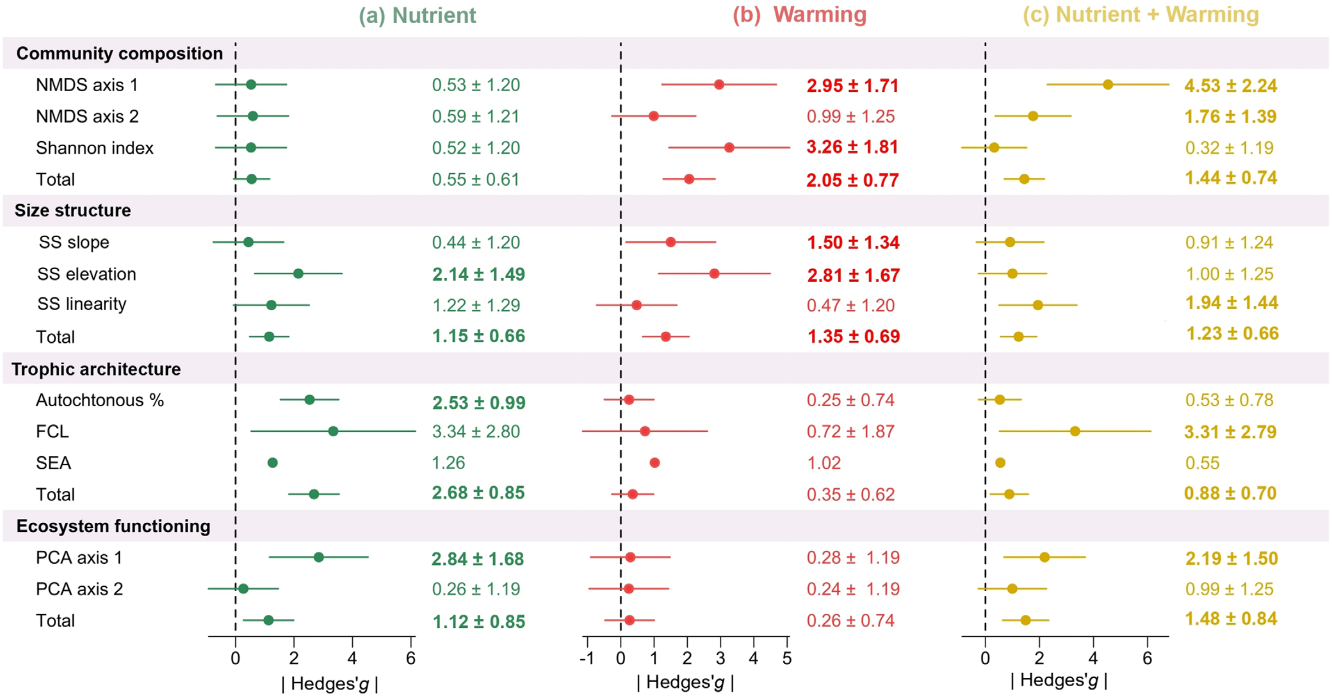

FIGURE 4 | Treatment effects across ecological levels. Total effects represent the weighted mean effect sizes for each ecological level. Significant effect sizes (no overlap of confidence interval with 0) are displayed in bold. FCL, food chain length; SEA, standard ellipse area; SS, size spectrum.

exhibited higher primary production and CO$_2$ uptake than the C and W treatments (Figure 3j). However, there was no significant difference between the treatments along PCA axis 2 (Figure 3k, $F_3 = 1.296$, $p = 0.303$).

Overall, we found that the ecological effects of the treatments varied significantly across ecological levels (Figure 4). Nutrient addition had a strong (>1) and significant total effect on size structure, trophic architecture, and ecosystem functioning, whereas its effects on community composition were not significant (Figure 4a). In contrast, warming had a strong and significant total effect on community composition and size structure, whereas its effects on trophic architecture and ecosystem functioning were not significant (Figure 4b). When nutrient addition and warming were combined, significant total effects were observed at all ecological levels (Figure 4c). More importantly, effect sizes in the combined treatment corresponded to those observed in the individual treatment that produced the greatest effect, except for trophic architecture, where the effect size was three times lower when nutrient addition was combined with warming than applied alone.

4 | Discussion

Ecologists are increasingly challenged to understand the mechanisms driving ecosystem functioning to better assess the full range of impacts induced by global change (Woodward et al. 2010). Moreover, a mechanistic overview of global change drivers at various ecological levels is essential for predicting the impacts of global change on freshwater ecosystems (Tabi et al. 2019). Our study offers novel insights by examining the intensity of ecological impacts from global change drivers at four ecological levels in freshwater ecosystems. In line with our first two hypotheses, we found that the intensity of responses to warming and nutrient addition differed across ecological levels. Specifically, warming outweighed the effect of nutrient addition at the community level, whereas nutrient addition outweighed the warming effect at the ecosystem level. As a result, nutrient addition, combined with warming, induced responses across all ecological levels. Regarding our third hypothesis, we found that food webs, described by size structure and trophic architecture, represented an intermediate ecological level that responded to both treatments in isolation. Specifically, changes in ecosystem functioning due to nutrient inputs were inherently associated with changes in food web properties (size structure + trophic architecture) but not necessarily to changes in community composition or diversity. In contrast, changes in community composition and diversity were inherently associated with changes in size structure but not necessarily with ecosystem functioning. This suggests that warming-induced changes at the community level can be compensated at the ecosystem level, with food webs providing a more integrative overview of the full range of responses of freshwater ecosystems, especially in the context of multiple stressors.

One of the most striking results of our study is the mismatch between community composition and ecosystem functioning. Specifically, we observed that: (i) different taxa can lead to similar ecological functions, and (ii) similar communities can lead to different ecological functions. For example, heterotrophic processes, such as leaf litter decomposition, were similar in the control and warming treatments, despite important differences in invertebrate communities. There is ample evidence that the composition and diversity of macroinvertebrate communities can influence leaf litter decomposition (Jonsson and Malmqvist 2000; McKie et al. 2008; Boyero et al. 2021), making these variables a key component in Biodiversity–Ecosystem Functioning studies in freshwater ecosystems (Woodward 2009). However, the high prevalence of generalist behavior in aquatic consumers often results in inconsistencies between changes in community composition and changes in ecosystem functioning (Woodward 2009). For example, many detritivorous invertebrates can also exhibit facultative herbivory (Ledger and Hildrew 2005). In extreme cases, high diversity of detritivores has been shown to reduce decomposition rates (Creed et al. 2009), suggesting that competition for resources may limit the optimal assimilation of allochthonous inputs in food webs. This highlights the importance of considering trophic interactions in Biodiversity–Ecosystem Functioning studies to disentangle what species are from what they do (Cardinale et al. 2006).

To our knowledge, our study is the first to provide a detailed observation of the response of freshwater ecosystems from community to ecosystems, mimicking a real "trophic biodiversity". We confirmed the ubiquity of generalism in primary consumers but also in predators, which switched to omnivorous behavior as primary producer abundance increased (leading to reduced food chain length). These changes can also be attributed to the improved nutritional quality of primary producers in eutrophic environments (van der Lee et al. 2021). Although trophic redundancy in diet may lead to idiosyncratic relationships in Biodiversity–Ecosystem Functioning approaches, it may also buffer food web perturbations by allowing consumers to switch between green (autochthonous) and brown (allochthonous) pathways. This ensures that the energy transfer to higher trophic levels is maintained even when one pathway is altered without requiring changes in community composition (Woodward 2009; van der Lee et al. 2021; Champagne et al. 2022). Additionally, a rapid food web shift towards the green pathway can enhance a rapid conversion of primary producers, limiting metabolic consequences due to changes in the ratio between producers and consumers in inland waters exposed to nutrient runoff (Grasset et al. 2020). However, nutrient loading in inland waters rarely acts in isolation and is often associated with other global change drivers that can compromise the food-web rewiring (Jeppesen et al. 2009, 2014; Zhang et al. 2021). For example, summer heat waves overlap with cropping periods, and we demonstrated that higher temperatures can compromise the food web's shift towards the green pathway. This highlights the current challenge in predicting ecological responses in the context of multiple stressors, especially if they exert antagonistic effects on the food web (Simmons et al. 2021).

Warming is expected to have a negative impact on large predators and release predation pressure on intermediate consumers (Gardner et al. 2011; Jeppesen et al. 2010). However, our results indicate the opposite, as the proportion of large-bodied individuals was higher under warmer conditions, and the food chain length remained unchanged. This suggests that predator ingestion may have increased sufficiently with warming to meet their metabolic requirements, which in turn could have exerted a stronger top-down control on primary consumers (Kratina et al. 2012; Shurin et al. 2012; Nagelkerken et al. 2020), resulting in a flatter size spectrum slope (O'Gorman et al. 2017). Top predators in our study were mainly black swimmers (*Notonecta* sp.), whose predation pressure could be compared to that of planktivorous fish in invertebrate communities (Arnér et al. 1998). However, these outcomes might differ in the presence of fish because black swimmers are particularly tolerant to warming and low dissolved oxygen levels (e.g., via aerial respiration: Katzenberger et al. 2021), contrary to fish. Heat wave experiments generally lead to significant fish mortality (Moran et al. 2010; Işkın et al. 2020), especially when combined with nutrient addition, which can exacerbate hypoxia (Jeppesen et al. 2021). However, warming experiments conducted within fish thermal tolerance can also increase their top-down control (Kratina et al. 2012; O'Gorman et al. 2023). In general, the effect of warming in regulating primary producers through trophic cascade strongly depends on various factors, including the life-history traits of consumers, habitat connectivity, and food web properties such as food chain length (Hansson et al. 2013; Marino et al. 2018; Ross et al. 2022; O'Gorman et al. 2023). Importantly, increasing predation pressure observed here can represent a transitory state (Hastings et al. 2018) where predators gradually deplete prey populations, compromising their viability in the longer term (Nagelkerken et al. 2020), and results in a steepened size spectrum slope in extended experiments (Dossena et al. 2012). Nevertheless, dynamic models examining the relationship between the duration (or intensity) of warming and the metabolic response of communities at various trophic levels are still lacking (Marino et al. 2018; Rahman et al. 2023). Although the effect of global warming on the intensity of top-down forces through changes in predation pressure depends on environmental context, our results provide a realistic view of how a three-trophic level network can respond to a brief warming event comparable to a heat wave, which does not exceed the thermal optimum of predators. This is particularly relevant for fishless ecosystems, such as headwater streams, high-altitude lakes, ponds, or temporary waters.

In line with our main hypothesis, we demonstrated an interactive effect of treatments across ecological levels. The predominance of top-down controls at the community level is well documented in aquatic ecosystems, where predation pressure often prevails in determining community composition and diversity (Burkepile and Hay 2006; Gruner et al. 2008; Howeth and Leibold 2010; Jeppesen et al. 2010). This predominant role is evident in the majority of experimental studies that manipulate trophic cascades and basal resources (Smith et al. 2010; Lemmens et al. 2018). Our findings support this view as warming increased predation pressure in our mesocosms. On the contrary, it is often reported that changes in the intensity of bottom-up forces have a stronger effect on the quantity of communities rather than their identity (Brett and Goldman 1997; Lemmens et al. 2018). These bottom-up effects have major implications for primary and secondary production as well as associated functions related to carbon storage and flux (Grasset et al. 2020). However, it is important to emphasize the extent to which our conclusions can be applied to larger and natural ecosystems, particularly regarding functioning and carbon fluxes. Several important processes such as interstitial exchanges are difficult to reproduce experimentally and are often underestimated (Mathers and Wood 2016). In particular, organic matter decomposition in anoxic sediment layers can exacerbate methanogenesis (Bastviken et al. 2004; Grasset et al. 2018). In contrast, sediments can act as a temporary sink for nutrients and may equilibrate with lower nutrient concentrations in the overlying water column (Søndergaard et al. 2003), thereby contributing to the buffering of the eutrophication process. However, our study provides a rare contribution by directly comparing the predominance of bottom-up and top-down controls across multiple ecological levels. Specifically, these findings have strong implications for our understanding of how freshwater ecosystems adapt to global change (Cross et al. 2015; Dyer et al. 2015; La Pierre and Hanley 2015), especially as anthropogenic activities are strongly modifying the intensity of bottom-up and top-down forces in ecosystems worldwide (Bunnell et al. 2014; Rosenblatt and Schmitz 2016; Listiawati and Kurihara 2021). Understanding how different ecological levels respond to changes in the intensity of these forces is not only a critical question for ecologists; it is also crucial for predicting how global change may affect ecosystem properties (e.g., species composition and diversity, functioning and services) that are not necessarily interdependent (Rosenblatt and Schmitz 2016).

In conclusion, our study provides new insights into how global change affects community composition, size structure, trophic architecture, and ecosystem functioning. Although apparent changes in community composition can occur rapidly in response to a shift in top-down force intensity, ecosystem functioning responded more rapidly to alterations in bottom-up force intensity. Food web, representing an intermediate ecological level, integrated changes in the intensity of both forces and should be used as a key framework for resolving the idiosyncratic relationships between biodiversity and ecosystem functioning. We encourage future researchers to explore the balance between bottom-up and top-down controls across different ecological levels to enhance our understanding of how these controls mediate the overall response of ecosystems to global change.

Author Contributions

Valentin Marin: conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, writing – original draft. **Fanny Colas:** conceptualization, funding acquisition, investigation, methodology, resources, writing – review and editing. **Stéphanie Boulêtreau:** conceptualization, funding acquisition, investigation, methodology, resources, writing – review and editing. **Julien Cucherousset:** conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and the script required to carry out the analyses and generate the figures can be accessed via the following DOI: 10.6084/m9.figshare.29580620.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:**