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What happens when salinization meets eutrophication? A test using stream microcosms

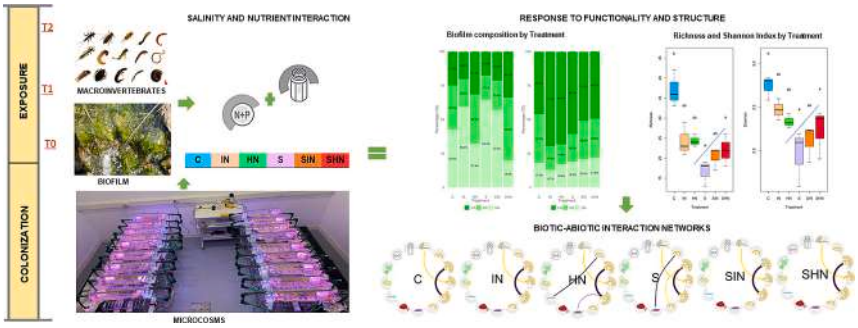
Alvaro Javier Moyano Salcedo [a,b,d,*], Narcís Prat [a], Lluís Bertrans-Tubau [c], Martí Piñero-Fernandez [a], David Cunillera-Montcusí [a,e], Julio C. López-Doval [c], Meritxell Abril [c], Lorenzo Proia [c], Miguel Cañedo-Argüelles [d]

[a] FEHM-Lab (Freshwater Ecology, Hydrology and Management), Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona, Barcelona, Spain
[b] Geohazards and Civil Engineering Research Group, Department of Civil Engineering, Saint Thomas Villavicencio University, C/22 No 1a, 500003 Villavicencio, Colombia
[c] BETA Technological Center, University of Vic–Central University of Catalonia (UVic–UCC), Vic, Barcelona, Spain
[d] Institute of Environmental Assessment and Water Research (IDAEA), CSIC, Carrer de Jordi Girona, 18-26, 08034 Barcelona, Spain
[e] WasserCluster Lunz - Biologische Station GmbH, Lunz am See, Austria

HIGHLIGHTS

- The study explored how nutrient and salt pollution interact in freshwater ecosystems using microcosms with biofilm and macroinvertebrates.
- We found a negative effect of salinity on biofilm function and cyanobacteria.
- We found a strong negative effect of salinity on macroinvertebrate richness and diversity.
- Nutrient addition weakly ameliorated salt toxicity to aquatic macroinvertebrates.

GRAPHICAL ABSTRACT



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ABSTRACT

Nutrient and salt pollution often co-occur in rivers and streams due to human activities (e.g., agriculture, urbanization). Thus, understanding the interactive effects of nutrients and salinity on freshwater ecosystems is critical for environmental management. We experimentally assessed the interactive effects of nutrient and salt pollution on stream microcosms using biofilm and macroinvertebrates as model systems. Six treatments were performed in triplicate: control (C: $N\text{-}NH_4+ = 0.05$; $P\text{-}PO_4^{3-} = 0.037$; $Cl- = 33.5$ mg L^{-1}), intermediate nutrient (IN: $N\text{-}NH_4+ = 0.4$; $P\text{-}PO_4^{3-} = 0.271$; $Cl- = 33.5$ mg L^{-1}), high nutrient (HN: $N\text{-}NH_4+ = 0.84$; $P\text{-}PO_4^{3-} = 0.80$; $Cl- = 33.5$ mg L^{-1}), salt (S: $N\text{-}NH_4+ = 0.05$; $P\text{-}PO_4^{3-} = 0.037$; $Cl- = 3000$ mg L^{-1}), salt with intermediate nutrient (SIN: $N\text{-}NH_4+ = 0.4$; $P\text{-}PO_4^{3-} = 0.27$; $Cl- = 3000$ mg L^{-1}) and salt with high nutrient (SHN: $N\text{-}NH_4+ = 0.84$; $P\text{-}PO_4^{3-} = 0.80$; $Cl- = 3000$ mg L^{-1}). After 14 days of exposure, biofilm chlorophyll-a increased across all

Abbreviations: C, Control treatment; IN, Intermediate Nutrient treatment; HN, High Nutrient treatment; S, Salt treatment; SIN, Salt with Intermediate Nutrient treatment; SHN, Salt with High Nutrient treatment.

* Corresponding author at: Institute of Environmental Assessment and Water Research (IDAEA), CSIC, Carrer de Jordi Girona, 18-26, 08034 Barcelona, Spain.
E-mail address: alvaromoyano@ub.edu (A.J. Moyano Salcedo).

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treatments, with cyanobacteria replacing diatoms and green algae. Treatments with no added nutrients (C and S) had more P uptake capacity than the rest. The indicator species analysis showed 8 significant taxa, with *Orthocladius (Orthocladius) gr. Wetterensis* and *Virganytarsus* significantly associated with the salinity treatment. Overall, salt pollution led to a very strong decline in macroinvertebrate richness and diversity. However, salt toxicity seemed to be ameliorated by nutrient addition. Finally, both structural equation models and biotic-abiotic interaction networks showed that complex biological interactions could be modulating the response of the biological communities to our treatments. Thus, our study calls for species-level assessments of salt and nutrient effects on river ecosystems and advocates for better management of co-occurring pollutants.

1. Introduction

Human activities are increasing the salt concentration of rivers and streams around the world (i.e., freshwater salinization, FS). There is strong evidence that FS can lead to drastic reductions in aquatic biodiversity (Kefford et al., 2006, 2012; Cañedo-Argüelles et al., 2013; Cañedo-Argüelles et al., 2016a, b; Cunillera-Montcusí et al., 2022) and alterations of ecosystem functioning (Herbert et al., 2015; Vendrell-Puigmitja et al., 2022). However, FS often co-occurs with multiple stressors (Kaushal et al., 2022) and the potential interactive effects of salinity and such stressors (e.g., climate change, eutrophication, pesticide pollution) is still poorly understood (Velasco et al., 2018). For example, salt and nutrient pollution are both frequent in rivers and streams subjected to the discharge of urban wastewater and irrigation return flows (Cañedo-argüelles, 2020; Thorslund et al., 2021). Although agriculture is the main driver of elevated NaCl and nitrogen (N) and phosphorus (P) concentrations in rivers and streams (Estévez et al., 2019; Thorslund et al., 2021), wastewater discharge is an important driver of FS when rivers flow through urban areas and most river catchments are impacted by a combination of both activities (Meybeck, 2003; Blaas and Kroeze, 2016; Bhide et al., 2021). Moreover, several industrial processes (e.g., ethanol, agro-food industries) generate by-products that release high concentrations of both nutrients and salts, strongly increasing freshwater and soil salinization (Christofoletti et al., 2013; Marinho et al., 2014). For example, in the ethanol industry, sugarcane vinasse is a massive and continuous by-product with elevated nutrient levels (e.g., pure vinasse has a total N: 639 mg L^{-1}, total P: 150 mg L^{-1}) and salinity (e.g., sodium: 60 mg L^{-1}, conductivity: 8420 μS cm^{-1}) that is difficult to manage and use as fertilizer, potentially affecting the surrounding aquatic and terrestrial biodiversity (Dreux Fraga, 2023). Finally, salt and nutrient load into freshwater ecosystems may vary depending on the agricultural and industrial practices (e.g., irrigation requirements, type of fertilizers), climate and meteorological factors and the efficiency of the wastewater treatment plants (e.g., nutrient and salt removal) (Merchán et al., 2020, Salcedo Moyano et al., 2022).

The vast majority of studies addressing the effects of FS in combination with multiple stressors in rivers have focused on the interaction of salts with temperature (Jackson and Funk, 2019; Serrano et al., 2020; Torregroza-Espinosa et al., 2021), pesticides (Szöcs et al., 2012; Stoler et al., 2017; Dornelas et al., 2021) and metals (Baysoy et al., 2012; Velasco et al., 2018), whereas the interaction between salt and nutrients enrichment has received less attention (Lind et al., 2018; Osburn et al., 2023) and has been much more studied in lakes (Lind et al., 2018; Greco et al., 2023, Wang et al., 2023; Ersoy et al., 2022) than in rivers (Pace et al., 1999; Kurle and Cardinale, 2011). Available studies suggest that both synergistic and antagonistic relationships between nutrients and salts are possible, depending on the tolerance of the community to NaCl and the triggering of cascading effects. For example, in the planktonic compartment, the abundance of algal species may be promoted through the reduction in the abundance of large cladocerans due to salt pollution, leading to an increase in chlorophyll-a concentration (Hintz et al., 2017). At the same time, nutrient pollution promotes algal growth, contributing to increased chlorophyll-a concentration (Carpenter et al., 2001; Dodds et al., 2002; Bennett et al., 2021). As a result, there is a synergistic effect that may promote primary production through a combination of increased resource availability and a relaxation of grazing pressure due to cladocerans loss (Lind et al., 2018; Osburn et al., 2023; Zadereev et al., 2023). However, this might not always be the case, since some groups of planktonic algae are subsidized by the N availability and can withstand wide ranges of salinity (e.g., cyanobacteria) whereas others in the benthic zone (e.g., *Nitella*, *Enteromorpha intestinalis*) do not (Lind et al., 2018; Greco et al., 2023; Borburema et al., 2022). Thus, eutrophication and salinization can also have antagonistic effects on the composition of algal communities. The changes in the trophic structure might have consequences for the entire ecosystem. For example, some planktonic cyanobacteria species are capable of releasing toxins (e.g., *Microcystis aeruginosa*) that make water resources unsafe for animals and humans (Gaillard et al., 2021; Georges Des Aulnois et al., 2019; Osburn et al., 2023).

The changes in primary production can determine the response of aquatic invertebrates, some of which feed on algae, to nutrient and salt pollution. For example, some studies evaluating the interactive effects of chloride (Cl) and nutrients have suggested that the toxic effects of increased salts on aquatic organisms such as copepods and snails may be ameliorated by nutrient enrichment, which increases food availability and consequently the available energy to cope with metabolic demands (Hintz et al., 2017; Lind et al., 2018; Greco et al., 2023, Silver and Donini, 2021). Concordantly, Brown and Yan (2015) showed that cladocerans (e.g., *Daphnia pulex* and *D. pulicaria*) were more tolerant to chloride when higher quality food resources were available (Isanta-Navarro et al., 2021). Also, Greco et al. (2023) suggested that organisms living in lakes with high nutrient concentrations could be more tolerant to chloride due to higher food quality and availability. The few available studies on the interactive effects of salt and nutrient pollution on stream invertebrates offer contradictory information. For example, a decline and shift in benthic macroinvertebrate composition has been documented in sections of the Molco River (Araucanía, Chile) where fish farms discharge their effluents. This phenomenon was attributed to the synergistic effects of nutrient enrichment and salinity, mainly due to the toxic effects of elevated salinity on taxa, and to community drift associated with habitat alteration (Encina-Montoya et al., 2020). On the contrary, some studies suggest that nutrients and salts might have antagonistic effects due to the above mentioned increase in food resources (Braukmann and Böhme, 2011; Schröder et al., 2015).

The aim of this study was to examine the interactive effects of nutrient and salt pollution on stream ecosystems by using microcosms (i.e., small artificial channel systems). These microcosms were used to test three treatments: nutrient addition, salt addition, and nutrient + salt addition. This setup allowed the experiment to be carried out under controlled conditions, including flow rate, temperature, light, nutrient levels, and salt, as performed in similar studies (Cochero et al., 2017; Vendrell-Puigmitja et al., 2022; Bertrans-Tubau et al., 2023). Also, the microcosms were adapted to take into account the geographic scale and the community being assessed, with the aim of addressing certain limitations (Martin, 2001; Menczelesz et al., 2020), although the representation of large-scale conditions remains one of these limitations. Benthic microbial communities dominated by primary producers (biofilms) and macroinvertebrates were focused on due to their importance as ecological indicators of rivers' health and because their interaction

can be affected by both stressors and lead to cascading effects (Pace et al., 1999; Kurle and Cardinale, 2011; Ersoy et al., 2022). Finally, it was hypothesized that: (1) Nutrient addition would increase chlorophyll-a concentration, photosynthetic efficiency and phosphorus uptake rate of biofilm communities due to a subsidy effect. This should have indirect positive effects on aquatic macroinvertebrate richness and abundance as a result of higher food availability; (2) Salt addition would have toxic effects both on biofilms and macroinvertebrates. Also, it would drive significant changes in the structure of both communities; and (3) The interaction between salt and nutrients would have an antagonistic effect on algae and macroinvertebrates, with the former being toxic and the latter subsidizing energy demands associated with osmoregulation.

2. Material and methods

2.1. Experimental design and operating

The study was performed in a set of 18 microcosms consisting of 6-L methacrylate channels (length × width × height 26 × 15 × 17 cm) installed in a temperature-controlled chamber at a constant temperature of 18 °C (Fig. 1). Each microcosm contained 15 stream cobbles (previously scraped and autoclaved), 1 large glass plate (220 cm^2) and 6 small glass plates (9 cm^2) used as substrates for natural biofilm colonization that also provided habitat for macroinvertebrates.

The microcosms were connected to a 5-L tank filled with 3 L of dechlorinated water, with an initial chemical composition of 0.05 mg L^{-1} N-NH_4+, 0.0375 mg L^{-1} P- PO_4^{3-} and 33.5 mg L^{-1} Cl. Water was recirculated in each microcosm by a submerged pump (EDEN 105, Eden Water Paradise, Italy) configured to maintain the same flow rate in each microcosm. The water was completely renewed every 3 days to avoid nutrient depletion. The photo-period was set out at 12 h light: 12 h dark using LEDs (LENB 135-lm, LENB/14.97/11.98). During the experiment, the irradiance reaching the substrata was 12 μmol photons m^{-2} s^{-1}.

Natural biofilms were inoculated in each microcosm to promote colonization. Diatoms and algae communities were obtained by scraping cobbles collected from a section of the Llobregat River at Balsareny (sampling point L68 in Prat and Rieradevall (2006)), Spain. This sampling site was selected because it had already been used in previous experiments exploring the effects of salinization on aquatic macroinvertebrates (Cañedo-Argüelles et al., 2012, 2014). The biofilm samples were collected 7 March 2022 and transported in 5 L bottles to the microcosms within 1 h of collection. To remove organic matter and excess of filamentous algae, the samples were filtered through a 500 μm mesh. Finally, 250 mL of this inoculum was added uniformly to each channel, and this procedure was repeated each time water was renewed during the colonization period. The colonization period lasted for three weeks, during which photosynthetic efficiency became appreciable (i.e., measurements indicating chlorophyll presence and biofilm maturity). Throughout this period, the photosynthetic activity and community composition of the biofilm was monitored and measured by means of the analysis of fluorescence response using Benthotorch (BTo-09-048 GPS bbe Moldaenke) and MiniPAM (Pulse Amplitude Modulated) chlorophyll fluorimeter (Heinz Walz GmbH) to assess its adaptation to each microcosm. Aquatic macroinvertebrates were collected at the same sampling point (L68) at the end of the biofilm colonization period (From 7 to 25 March 2022) by kicking all available habitats and using a hand net of 250 μm mesh size. They were transported inside coolers to the microcosms also within 1 h of collection. Each cooler was filled with river water collected at the sampling point. Finally, a 500 mL aliquot of the macroinvertebrate sample was collected from a tray where the community had been homogenized by gently agitating the water. This community sample was collected using a calibrated jar and inoculated into each microcosm. The colonization phase of macroinvertebrates overlapped with the final week of the three-week biofilm colonization period. During a 48 h period, we conducted observations to confirm the establishment and acclimatization of the benthic community within each microcosm (e.g., distribution of taxa within preferential habitats, low mortality and drift).

After the colonization and conditioning of the community, the exposure period started with the addition of salt and nutrients to each microcosm. The salt concentration was chosen at two different levels: low, corresponding to the average minimum concentration of the Llobregat River in the study section (ACA, 2023), and high. This higher salinity has been widely reported in freshwaters (Thorslund et al., 2021), especially within the study area where rivers and streams have high salt concentrations associated with the dissolution of salts that naturally occur in rocks (Prat and Rieradevall, 2006). Furthermore,

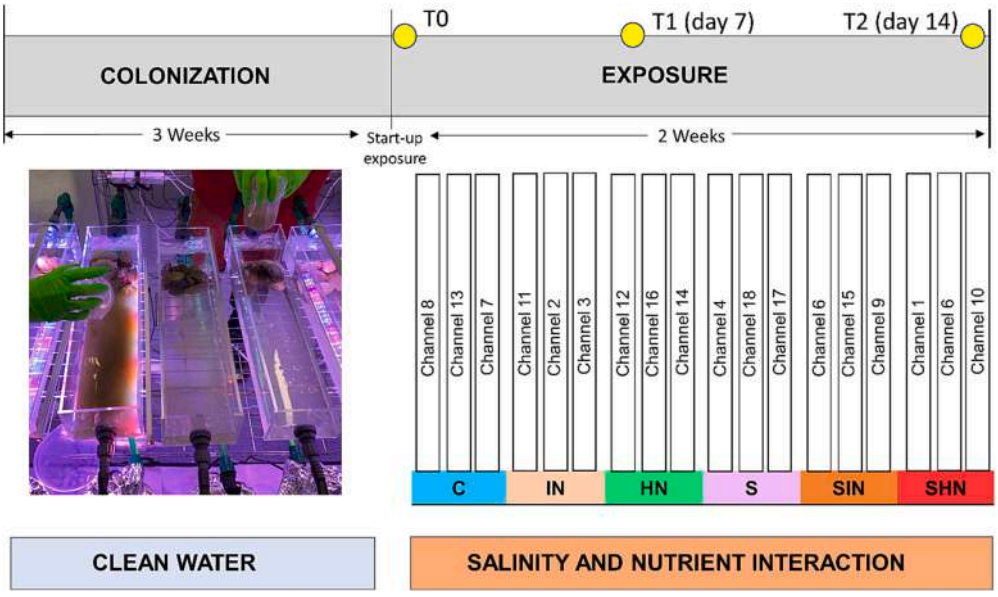

Fig. 1. Experimental design and sampling times (yellow circles) during the exposure period. The biofilm community was measured at T0, T1 and T2. The macroinvertebrate community was inoculated at the start of the exposure period (T0) and collected for identification at the end of the experiment (T2). Control treatment (C), salt (S), intermediate nutrients concentration (IN), high nutrients concentration (HN), salt treatment in combination with intermediate nutrients concentration (SIN) and salt treatment in combination with high nutrients concentration (SHN).

previous studies conducted using mesocosms and communities collected from the same river have consistently shown that a concentration of 3 g L^{-1} NaCl is sufficient to induce significant changes in aquatic macroinvertebrate communities (Cañedo-Argüelles et al., 2012, 2014).

Nitrogen and phosphorus concentrations mimicked those of streams affected by wastewater treatment plant discharges within the study area (Lorenzo Proia, personal communication based on water quality monitoring data collected by the BETA research center). The control was related to the average nutrient levels upstream the WWTPs, intermediate nutrient concentrations corresponded to sites located around 20 and 40 m downstream of the WWTP, and the high nutrient concentrations corresponded to the discharge point of the WWTPs.

The experimental design included 6 treatments in triplicate: control treatment (C: N-NH_4+ = 0.05; P-PO_4^{3-} = 0.037; Cl- = 33.5 mg L^{-1}), intermediate nutrient concentration (IN: N-NH_4+ = 0.4; P-PO_4^{3-} = 0.271; Cl- = 33. 5 mg L^{-1}), high nutrient concentration (HN: N-NH_4+ = 0.84; P-PO_4^{3-} = 0.80; Cl- = 33.5 mg L^{-1}), salt (S: N-NH_4+ = 0.05; P-PO_4^{3-} = 0.037; Cl- = 3000 mg L^{-1}), salt treatment in combination with intermediate nutrient concentration (SIN: N-NH_4+ = 0.4; P-PO_4^{3-} = 0.27; Cl- = 3000 mg L^{-1}) and salt treatment in combination with high nutrient concentration (SHN: N-NH_4+ = 0.84; P-PO_4^{3-} = 0.80; Cl- = 3000 mg L^{-1}). The experimental water used in the microcosms was dechlorinated tap water with high nitrate and nitrite concentrations (3.7 ± 0.2 N-NO_3- and < 0.1 ± 0.1 N-NO_2- mg L^{-1}). The biofilms and macroinvertebrate communities were exposed to the treatments during 14 days (From 25 to 7 April 2022) and the treatments were randomly distributed across the microcosms (Fig. 1).

2.2. Physical and chemical water conditions

Dissolved oxygen (DO) concentration and saturation, temperature, pH, and conductivity were measured directly in the microcosms using sensor probes (YSI professional plus, YSI Incorporated, USA). Also, triplicate water samples for each treatment (one random sample per treatment) were collected 3 times a week after each water change and filtered through a 0.22 um nylon filter (Merck) to analyze nutrient concentrations. Water samples were frozen immediately and kept at −20 °C until analysis. Finally, N-NH_4^+ and P-PO_4^{3-} were analyzed following APHA (1992).

2.3. Biofilm sampling

Biofilms were sampled immediately before (T0) and 7 (T1) and 14 (T2) days after nutrient and salt addition. At each biofilm-sampling day, one random small glass plate (9 cm^2) was collected from each microcosm and scraped using a blunt spatula. Aliquots of 10 mL of biofilm were then sub-sampled to analyze chlorophyll-a concentration and ash-free dry mass (AFDM). Chlorophyll-a concentration and AFDM samples were stored at −20 °C until analysis.

2.3.1. Chlorophyll-a concentration and AFDM

Chlorophyll-a was measured using spectrophotometric techniques following standard methods (APHA, 1992). To calculate AFDM (ash-free dry mass), the biofilm suspension was filtered through filters (0.7 μm pore size), then dried for 72 h at 60 °C and combusted at 550 °C for 4 h obtaining algal dry mass (DM) and finally AFDM (1 g dry mass ≈ 0.9 g AFDM).

2.3.2. Photosynthetic efficiency and community composition in the biofilm

The photosynthetic efficiency (Yeff) was measured with a Mini-PAM (Pulse Amplitude Modulated) chlorophyll fluorimeter (Heinz Walz GmbH). The main photosynthetic groups' densities (diatoms, cyanobacteria and green algae) covering the colonized glass plates were measured using BenthoTorch probe (BTo-09-048 GPS bbe Moldaenke).

2.3.3. Phosphorus uptake rate of biofilm

Biofilm phosphorus uptake rate was determined directly on the colonized glass plates in each microcosm measuring the temporal decay of phosphorus in water after a controlled spike (Proia et al., 2017). The initial phosphorus concentration was determined, and the corresponding amount was added in each channel to quadruple the background concentration. Then, the biofilms were incubated under these conditions for 240 min and water was sampled in 10 mL tubes at 0, 120, and 240 min after the addition through a 0.22 um nylon filter (Merck) and stored at −20 °C until analysis. The biofilm phosphorus uptake rate was calculated as:

$$U = \frac{Po - Pf}{AxTf}$$

where P0 = the initial mass of P after the spike (μg); Pf = the final mass of P at the end of incubation (μg); A = the area colonized by biofilm (cm^2) and Tf = the time of incubation (h).

2.4. Sampling of macroinvertebrates

Macroinvertebrates were sampled from each microcosm at the end of the experiment by emptying the microcosms and scraping and washing all artificial substrates. The resulting sample (which contained water, sediment and algae) was filtered through a 250 μm mesh and preserved in 90 % ethanol at −5 °C. Then, at the laboratory, macroinvertebrates were sorted and identified at the genus level following Tachet et al. (2000), except for Chironomidae which were identified to the genus/species level using local taxonomic keys (Prat et al., 2014) because of being the dominant group in terms of relative abundance.

2.5. Data analysis

All statistical analyses were performed in R (R Core Team, 2002) and the nomenclature proposed by Muff et al. (2022) was used to report our results in the language of evidence (very strong evidence: P Value between 0.0001 and 0.001; strong evidence: P value between 0.001 and 0.01; moderate evidence: p value between 0.01 and 0.05; weak evidence: p value between 0.05 and 0.1; little or no evidence p value between 0.1 and 1). Two-way ANOVA was used to assess biofilm both the structural parameters (i.e., chlorophyll-a concentration, AFDM, and relative composition and abundance of each algal group) and functional parameters (i.e., photosynthetic efficiency, nutrient uptake capacity) across treatments. First, all interactions (e.g., time:salinity:nutrients) were examined. Then, in the absence of a strong relationship, variables without supporting evidence were systematically removed from the analysis to streamline the model, ultimately arriving at a representation of the most important interactions (e.g., Time + Salinity+Nutrients). In cases where moderate to strong differences were observed based on the two-way ANOVA model (P value <0.05), pairwise comparisons were performed using the Bonferroni test.

Macroinvertebrate richness and Shannon diversity indices were calculated using the "vegan" package (Oksanen et al., 2009) and differences between treatments were analyzed using the same procedure (two-way ANOVA + Bonferroni test). An Indicator Species Analysis (IndVal) was performed to identify indicator taxa for each treatment using the "labdsv" package (Roberts et al., 2023). Non-metric multidimensional scaling (NMDS) was used to visualize differences in community composition between treatments (Oksanen et al., 2009), and these differences were tested through an ADONIS test using the "labdsv" package (Roberts et al., 2023).

A structural equation model (SEM) was built to assess the interactions and effects between salinity, nutrients, algal communities and macroinvertebrates at the end of the exposure period using the "lavaan" package. SEM is based on the variance-covariance matrices between predictor and response variables and interactively assesses direct and

indirect causal pathways using correlations between these variables and their statistical significance (Grace, 2006; Frainer et al., 2014). The model contained 198 sampling units which included all sampling events (i.e., six treatments × three replicates × average of three sampling times for biofilm per replicate treatment; T1, T2 and T3) and 11 variables: salinity, nutrients, chlorophyll-a, photosynthetic yield, P-uptake rate, the concentration of cyanobacteria, diatoms and green algae, and the abundance, richness and Shannon diversity of macroinvertebrates. Before building the model, variables with a Spearman correlation higher than 0.9 were excluded (Taylor, 1990). Salinity and nutrients (i.e., sum of concentration of N-NH_4+ and P-PO_4^{3-} mg L^{-1}) were set as the predictor variables.

Finally, the interaction strength between the different taxa (focusing on those associated to any of the treatments according to IndVal analysis) in relation to abiotic variables was assessed using biotic-abiotic interaction networks (BAINs). The global interaction network of the experiment was obtained, and it was modulated by each treatment to compare their structure (i.e., number and strength of links; Hernández-Carrasco et al., 2023). BAINs were calculated using mixed graphical models (mgm; Haslbeck and Waldorp, 2020; Momal et al., 2020), which used a sparse penalized maximum likelihood estimator (LASSO) GLM to generate undirected graphs based on the distribution between variables without any previous assumptions about their dependencies (Ohlmann et al., 2018; García-Girón et al., 2020; Haslbeck and Waldorp, 2020). Since the aim was to describe the main BAIN structure for each treatment and not to focus on its predictive strength, cross-validation was employed as the procedure for selecting the tuning parameter (lambdasel = "CV"), allowing for a less restrictive selection of significant interactions. The mixed graphical model was moderated according to the six treatments, and the corresponding conditioned BAIN was obtained for each treatment.

3. Results

During the colonization period, pH, conductivity, DO and temperature remained stable with no differences between microcosms (Table S1). Once the exposure period started, there was no evidence of variability in DO, water temperature and pH, but conductivity changed as expected with the addition of salts (Table S2, Table S3).

There was very strong evidence (two- way ANOVA, P value <0.001, Table S4) that the chlorophyll-a concentration in the biofilms increased progressively during the exposure period in T0-T2 and T1-T2 (Fig. 2, pairwise comparison Table S5). At the end of the exposure time (T2), IN and SHN had the highest (T2, Max = 0.10 μg cm^{-2}, Min = 0.02 μg cm^{-2}) and lowest (T2, Max = 0.04 μg cm^{-2}, Min = 0.004 μg cm^{-2}) concentrations of chlorophyll-a, respectively. There was no evidence of changes in chlorophyll-a influenced by nutrients and salinity across treatments (Table S4).

AFDM increased throughout the experimental period in C channels (T0 = 0.38 ± 0.06 mg cm^{-2}), reaching a concentration of 0.77 (± 0.14) mg cm^{-2} by the end of the experiment (T2). In S, IN and SIN treatments there was also a steady mean increase of AFDM, whereas in HN and SHN it increased from T0 to T1 but then decreased from T1 to T2 (Fig. 2). Two-way ANOVA showed very strong change in AFDM during the

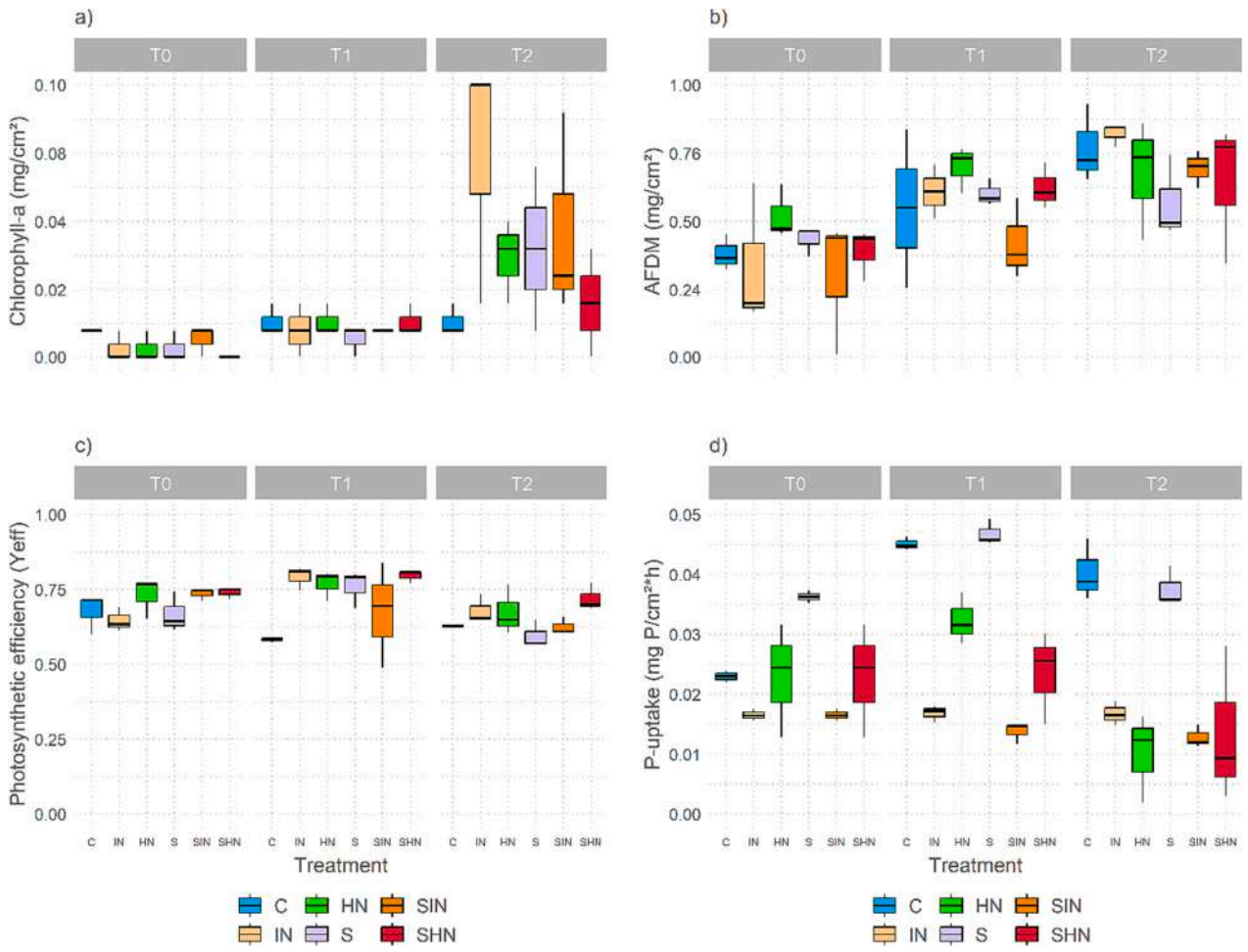

Fig. 2. Changes in the biofilm functioning during the exposure period for each treatment. a) Chlorophyll-a concentration; b) Ash-free dry mass (AFDM) c) Photosynthetic efficiency (Yeff); d) Phosphorus uptake rate.

exposure time (Table S6) for both T0-T1 and T0-T2 (pairwise comparison, Table S7). In spite of these differing trends, there were no significant differences in AFDM among salinity and nutrients levels (Table S6).

Yeff of the biofilm did not change strongly in the control treatment during the exposure period (Fig. 2). After 7 days of exposure (T1) Yeff increased in the IN, HN, S and SHN, whereas it decreased in C and SIN (Fig. 2). At the end of the exposure period (T2) Yeff decreased in all treatments except the control (C). The lowest Yeff was observed in the S treatment followed by SIN (Fig. 2). Also, there was no evidence of a change in Yeff due to salinity and nutrients across the treatments (Two-way ANOVA, Table S8).

P uptake rate showed a decrease in all treatments compared to the C at T2 (Fig. 2). Overall, the addition of nutrients, including the interactive salt-nutrient treatments (IN, HN, SIN, and SHN), resulted in a decrease in P uptake by the end of the experiment, whereas the treatments without nutrient addition (C and S) showed an increasing P uptake capacity from T0 to T2 (Fig. 2). According to two-way ANOVA, there was a very strong change in biofilm P uptake rate over time (T0-T1 and T1-T2) influenced by nutrients (P value <0.001, Table S9, Table S10, Table S11). Moreover, pairwise comparisons from the two-way ANOVA P uptake model further demonstrated differences in P uptake based on nutrient and time combinations (Table S12). Salinity did not have a strong effect on P uptake, as all low nutrient treatments (C and S) had high P uptake. The highest P uptake for both low and high nutrient concentrations treatments (C, S, HN, SHN) was found at exposure time T1. Contrarily, P uptake did not experience strong temporal fluctuations in the intermediate nutrient treatments (IN, SIN).

The biofilm community was mainly composed of green algae in C (42 %), IN (60 %), S (64 %) and SIN (57 %), while diatoms dominated in HN (37 %) and SHN (46 %) at the beginning of the experiment (T0, Fig. 3, Fig. S1). However, over time (T0-T2 and T1-T2), the biofilm community showed very strong changes (P value <0.001, two-way

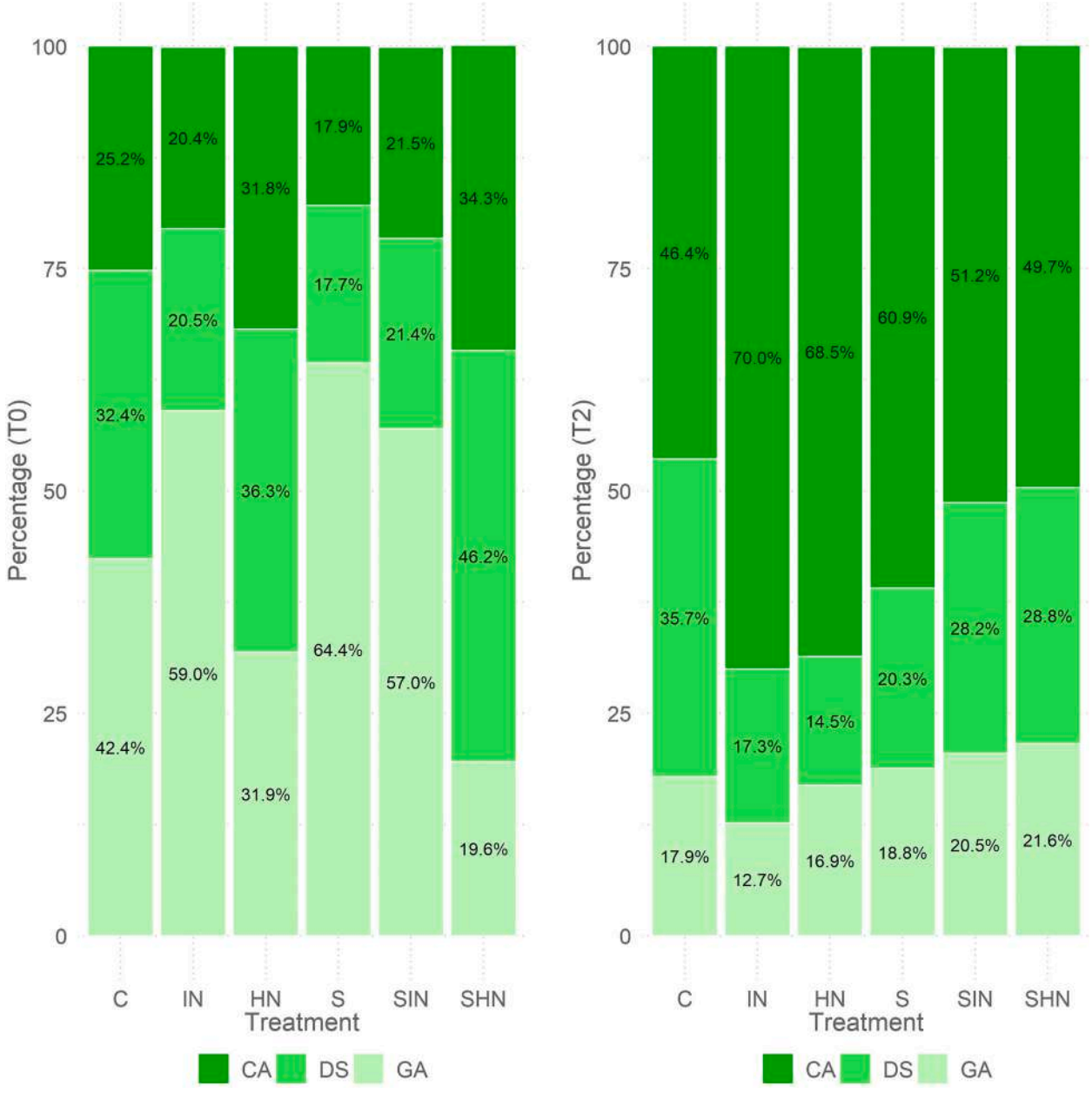

Fig. 3. Plot representing biofilm community composition at the beginning and end of the exposure period (T0 and T2) of each treatment. CA: Cyanobacteria, DS: Diatoms and GA: Green Algae. a) C: Control, b) IN: intermediate nutrients, c) NH: high nutrients, d) S: salt, e) SIN: salt in combination with intermediate nutrients and f) SHN: salt in interaction with high nutrients.

ANOVA, Table S13. Table S14), with cyanobacteria becoming dominant in all treatments (T2, Fig. 3). Pairwise comparisons showed that CA strongly differed from DS and GA in T0 and T1 when compared to T2 (Table S15). We found no evidence of differences in biofilm assemblages based on nutrient and salinity concentrations (Table S13). Although cyanobacteria were most abundant in the nutrient treatments (IN and HN, Fig. 3), they also dominated in the salt treatments (e.g., 61 % in S at T2). Also, in the salt treatments S and SIN green algae showed the greatest reduction (e.g., from 64 % in T0 to 19 % in T2 in the S treatment), whereas diatom concentrations weakly increased (e.g., from 21 % in T1 to 28 % in T2 in the SIN treatment) (Fig. S1). In contrast to S and SIN, there was a decrease in diatom concentration in SHN from T1 (46%) to T2 (29%), while green algae concentrations remained fairly constant along time (Fig. 3, Fig. S1).

Macroinvertebrate richness and abundance were dominated by chironomids (Fig. S2, Table S16), with small representation from other families such as *Baetidae, Oligochetae* and *Caenidae* (Table S16). The macroinvertebrate richness and Shannon diversity index were higher in the C than in the rest of the treatments (Fig. 4). The salinity (S) treatment showed the lowest values for both macroinvertebrate richness and diversity (Fig. 4). Macroinvertebrate richness showed a very strong change as a result of salinity (P value <0.001, two-way ANOVA, Table S17, Table S18), with moderate evidence of interaction between nutrients and salinity (Table S19). At the same time, Shannon diversity showed a very strong decrease in response to salinity (P value <0.001, two-way ANOVA, Table S20), but weak evidence of interactive effects between salinity and nutrients (Table S21). The decline in richness and Shannon diversity with salt addition seemed to be ameliorated by nutrient addition, since both increased along the nutrient addition gradient (from S to SIN and SHN; Fig. 4).

Eight macroinvertebrate taxa strongly associated with two different treatments were detected according to the IndVal analysis (Table S22). The predatory chironomids *Ablabesmyia* and *Conchapelopia* were found exclusively in C, whereas the chironomids *Cricotopus bicinctus* and *Virgatanytarsus* were exclusively found in S. The MDS and ADONIS analyses showed a strong dissimilarity between treatments in terms of community composition, with S, SIN, and SHN being the most different to C (Fig. S3; Table S23).

The SEM analysis (CFI = 0.90, RMSEA <0.05) (Fig. 5) revealed a strong negative effect of salt addition on cyanobacteria and the diversity and richness of aquatic macroinvertebrates, and a positive effect on macroinvertebrate abundance (Fig. S2) that was mainly related with an increase in *Orthocladius* (*Orthocladius*) gr. *wetterensis*, *Tanytarsus* and *Virgatanytarsus* (Table S24, Table S25). On the contrary, nutrients showed a weak to moderate positive effect on the concentration of all algal groups and on the richness, diversity and abundance of macroinvertebrates, and they had a strong positive effect on the photosynthetic yield. Therefore, nutrients and salt addition showed antagonistic effects on the concentration of the different algal groups and on the macroinvertebrate richness and diversity, but the effect of nutrients was

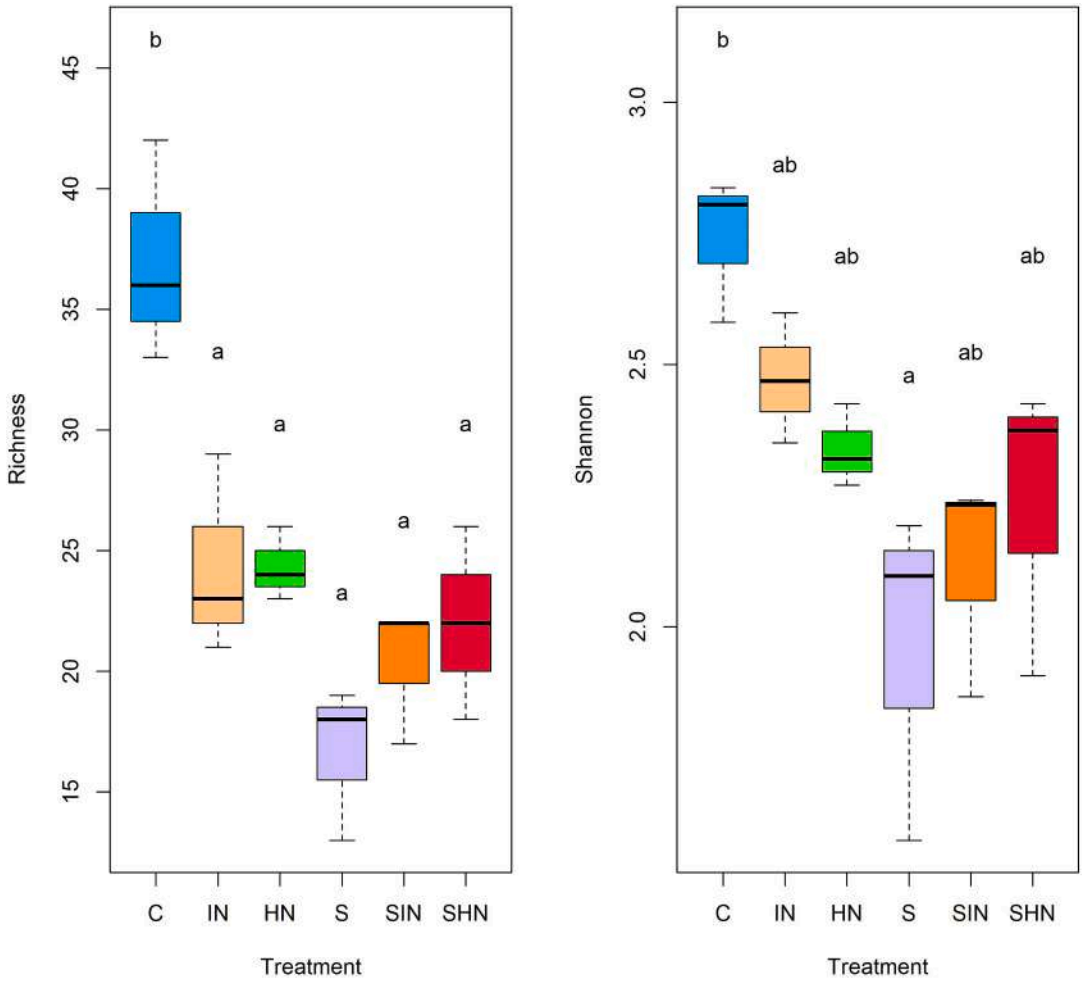

Fig. 4. Boxplot of the macroinvertebrate richness and Shannon diversity for each treatment at the end of the experiment: control treatment (C), salt treatment (S), intermediate nutrients concentration (IN), high nutrients concentration (HN), salt treatment in combination with intermediate nutrients concentration (SIN) and salt treatment in combination with high nutrients concentration (SHN). Differences between treatments are according to Bonferroni tests are shown with letters (i.e., different letters imply strong differences).

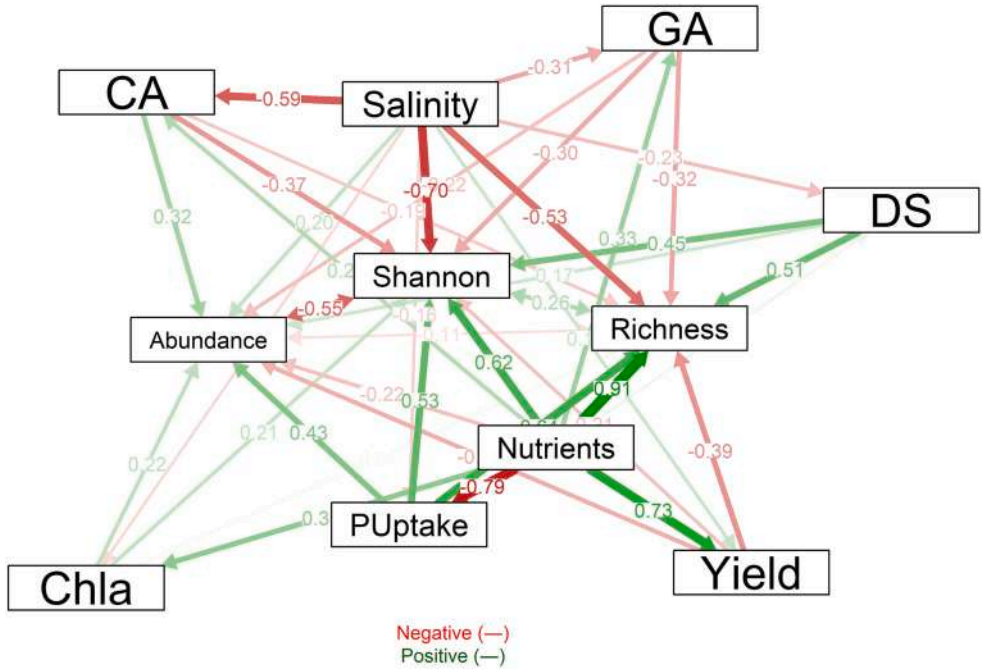

Fig. 5. Structural equation model showing the effects of nutrient and salt addition on the biofilm and aquatic macroinvertebrate communities. Salinity: salinity (mg L^{-1}); Nutrients: N-NH_4+ and P- PO_4^{3-} (mg L^{-1}); Chla: chlorophyll-a concentration (μg cm^{-2}); Yield: photosynthetic efficiency; PUptake: Phosphorus uptake (mg P $cm^{2}*h^{-1}$); DS: diatom concentration (μg cm^{-2}); GA: Green algae concentration (μg cm^{-2}); CA: Cyanobacteria concentration (μg cm^{-2}); Richness: taxa richness of aquatic macroinvertebrates; Shannon: Shannon Diversity of aquatic macroinvertebrates. Abundance: abundance of aquatic macroinvertebrates (total number of individuals). The red and green lines indicate negative and positive relationships, respectively. Model fit indices were set at CFI $\geq$ 0.90 and RMSEA $\leq$0.05.

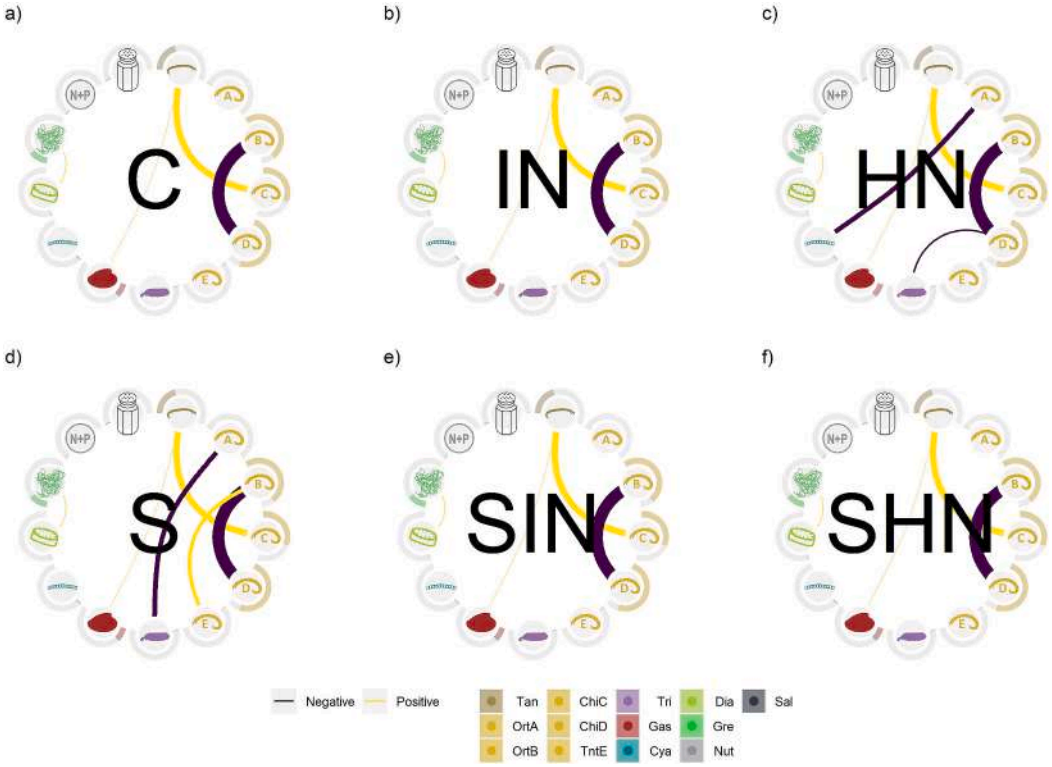

Fig. 6. Biotic-abiotic interaction networks corresponding to the conditioned main model for each experimental treatment: control treatment (C), salt (S), intermediate nutrients concentration (IN), high nutrients concentration (HN), salt treatment in combination with intermediate nutrients concentration (SIN) and salt treatment in combination with high nutrients concentration (SHN). Network nodes corresponds to the taxa strongly associated to treatments according to IndVal analysis, the concentration of the different algal groups and the abiotic variables: Tan (*Conchapelopia* sp.), OrtA (*Cricotopus bicinctus*), OrtB (*Orthocladius* gr. *wetterensis*), ChiC (*Phaenopsectra* sp.), ChiD (*Polypedilum* sp.), TntE (*Virgatanytarsus* sp.), Tri (*Hydroptila* sp.), Gas (*Bacillus* sp.), Cya (Cyanobacteria), Dia (Diatoms), Gre (Green Algae), Nut (Nutrient addition), Sal (Salt addition). Colored links indicate the sign of the covariation value (blue = negative, red = positive). The complete BAIN including all samples can be found in Fig. S4.

rather weak.

The global BAIN (i.e., including all the treatments) detected two interactions between some of the selected Chironomidae species (Fig. S4 and Table S26) indicating that covariation of the selected species was mostly explained by biotic interactions (all biotic-abiotic interactions are presented separately from Fig. S5 to Fig. S10). Once the model was conditioned for each one of the six treatments, the two main interactions were preserved along all the treatments (Fig. 6 and Table S27), but the model detected additional interactions for the HN and the S treatments (Fig. 6 C & D).

4. Discussion

Overall, it was found that nutrient addition strongly reduced the P uptake by the biofilm whereas salt addition had a strong negative effect on the richness and diversity of aquatic macroinvertebrates, with some taxa such as *Orthocladius* (*Orthocladius*) gr. *wetterensis* becoming clearly dominant. Although there was weak evidence of interactive effects between nutrients and salinity at the concentrations used in this study, the toxic effects of salt addition on aquatic macroinvertebrates seemed to be ameliorated by nutrients in a concentration-dependent manner (i.e., the higher the nutrient concentration the higher the ameliorating effect). Also, after natural succession, nutrients seemed to promote cyanobacteria growth, whereas salt seemed to prevent it, thereby suggesting potential interactive effects on algal communities that deserve further attention.

Nutrient addition was primarily responsible for the increase in chlorophyll-a concentrations, as shown in previous studies (Dodds et al., 2002; Dodds and Smith, 2017). However, it should be noted that this increase may be limited at high nutrient loads (Bennett et al., 2021), as it happened in our study (i.e., chlorophyll-a was much higher at intermediate than at higher nutrient concentrations). Our results suggest that while nutrient addition can promote chlorophyll-a concentration, it may also limit it during cyanobacterial blooms (Kane et al., 2014; Xu et al., 2015). This may be attributed to factors other than N limitation, as indicated by the N:P ratio (i.e., N:P ratio close to 5:1 in HN), such as the presence of biofilm communities that do not respond to variations in N and P levels, possibly due to nutrient saturation or other associated factors (e.g., limited available light, alteration of herbivores) (Bennett et al., 2021).

Furthermore, since cyanobacterial species are often dominant during blooms, it is possible that some of these species do not contain as much chlorophyll-a as other algal groups (Torregroza-Espinosa et al., 2021). Our results suggest that nutrients and salinity could have antagonistic effects on the composition of the biofilm. Cyanobacteria clearly became dominant along time in all treatments (including control), however its growth was promoted by nutrients and prevented by salts (i.e., the salt addition treatments had lower cyanobacteria biomass than the control treatment at the end of the study). It is important to note that dominance of cyanobacterial species could have strong implications for the entire aquatic ecological network because of the release of cytotoxins, which may affect other species, human health, and limit river uses (Gaillard et al., 2021; Osburn et al., 2023).

The shift in dominance from green algae to cyanobacteria found in our study could be related to a competition for resources (Vendrell-Puigmitja et al., 2022; Kimambo et al., 2019). However, the fact that only the biomass of the main algal groups was measured limits our ability to understand the effects of nutrients and salts on community composition, since the response to salt and nutrient addition might be species-specific. For example, there are different species within each algal group (i.e., cyanobacteria, diatoms, and green algae), with some species being able to tolerate high salinities (Arnott et al., 2023; Balycheva et al., 2023) and accumulate high concentrations of nutrients (Ardón et al., 2021; Bennett et al., 2021). Based on our results (e.g., photosynthetic efficiency increased along the nutrient addition gradient in the salt treatments) and previous studies (Li et al., 2021; Osburn et al., 2023; Arnott et al., 2023), it is hypothesized that nutrients might help some algal species to cope with salt stress by making more energy available. However, this might not always be the case. For example, *Aphanizomenon*, a genus of freshwater cyanobacteria, was sensitive to salt stress regardless of nitrogen availability in a previous study (Osburn et al., 2023). These changes in biofilms may not only have direct effects on various species, such as macroinvertebrates (Kurle and Cardinale, 2011), thereby disrupting the dynamics of subsequent trophic levels (Pace et al., 1999), but may also have far-reaching effects on various aspects, such as the decomposition of organic matter and changes in the carbon cycle, which are essential for the maintenance of ecosystem services (Pettorelli et al., 2018; Berger et al., 2019).

The macroinvertebrate communities in our study were dominated by Chironomidae. This is consistent with previous mesocosm studies performed in the region (Cañedo-Argüelles et al., 2012; Cañedo-Argüelles et al., 2014), and it is very likely related to the high dominance of the group in the studied streams and the adaptation of Chironomid species to experimental conditions (which might be stressful to some sensitive groups with specific habitat requirements such as EPT taxa). This group is not only abundant, it is also rich in species and therefore covers wide environmental gradients and represent multiple ecological traits (Cañedo-Argüelles et al., 2016a, b; Armitage et al., 2012; Serra et al., 2017). Taking this into account, the decision was made to identify Chironomidae at the genus/species level, which is rarely done in ecological studies involving aquatic macroinvertebrates (Bazzanti et al., 2008; Cañedo-Argüelles et al., 2016a, b). It was found that different Chironomidae taxa strongly responded to the treatments, with a replacement of taxa that could be partly driven by trophic interactions. This aligns with previous studies at the global (Serra et al., 2017; Martins et al., 2021; Hampel et al., 2023) and at the Spanish level (Bonada et al., 2006, 2007; Cañedo-Argüelles et al., 2012; Prat et al., 2013; Munne et al., 2021), which have identified chironomids as the main indicators of the ecological status of rivers. Another abundant group, Oligochaeta, showed a high tolerance to salt and nutrient pollution, also aligning with previous studies (Blinn and Ruiter, 2006; Wallace and Biastoch, 2016; Paul et al., 2018; Edegbene et al., 2023).

The low abundance of predatory chironomids (< 5 %, Table S24) exclusively associated with the control treatment (e.g., *Ablabesmyia* and *Conchapelopia*), suggests that they were affected by both nutrient and salt addition. Concordantly, several studies have found that these taxa were highly sensitive to salt pollution (Marshall and Bailey, 2004; Cañedo-Argüelles et al., 2012; Rico-Sánchez et al., 2022) and some studies have associated *Ablabesmyia* and *Conchapelopia* with low-intermediate nutrient concentrations (e.g., $N\text{-}NH_4^+ < 0.25$ mg L^{-1}) and low conductivities (273 μS cm^{-1}; 75 μS cm^{-1}, respectively) (Cañedo-Argüelles and Rieradevall, 2009; Rossaro et al., 2022). The reduced presence of predatory chironomids in the microcosms rules out the possibility of top-down control on the rest of the subfamilies (*Orthocladiinae*, *Chironominii* and *Tanytarsinii*) (Sánchez-Montoya et al., 2007; Cañedo-Argüelles et al., 2016a, b). The abundance of non-predators such as the tribe *Tanytarsinii* and the subfamily *Orthocladiinae* (total abundance >50 % and 38 %, respectively, Table S24) highlights not only the wide range of nutrient and salinity conditions that they can tolerate (Prat et al., 1983), but also the importance of these subfamilies in Mediterranean streams (Munoz and Prat, 1994). Also, factors such as lack of top-down control, plasticity in feeding habits and adaptation to artificial habitat conditions could partly explain the observed abundances (Rodríguez-Lozano et al., 2014; Rodríguez-Lozano et al., 2016). For example, previous studies have reported that the abundance and diversity of taxa such as *Tanytarsinii*, which exhibit a filter-feeding strategy and can become collector-gatherers under low or no current conditions, were unaffected by salt pollution (Marshall and Bailey, 2004). Also, *Tanytarsinii* show a preference for inhabiting the sides or bottom of cobbles and some species even construct tubes from small grains of sand or organic material for shelter (Puntí et al., 2009; Serra et al., 2017), providing additional protection from predators and

adverse environmental conditions (Caro-Borrero and Carmona-Jiménez, 2018). In the case of scrapers, strong reductions in abundance and diversity have been reported at salinities above 1500 mg L^{-1} (Marshall and Bailey, 2004). This is consistent with the reduction in Orthocladiinae taxa (except for *Orthocladius* (*Orthocladius*) gr. *wetterensis*) in the salinity treatments in our study (Table S5).

The reduction in macroinvertebrate richness and diversity caused by the salt treatment is in line with previous studies (Kefford et al., 2012; Cañedo-Argüelles et al., 2013; Feld et al., 2023). However, the toxic effect of salt addition was ameliorated by nutrient addition in a dose-dependent manner. Nutrients might have compensated for the toxic effects of salt addition on the biofilm, ultimately favoring macroinvertebrate richness and diversity. Our results do not strongly support this hypothesis (i.e., only cyanobacteria biomass and photosynthetic efficiency showed responded strongly to our treatments), but a deeper analysis of the algal communities at the species level would be needed to accept it or reject this hypothesis. For example, an increase in algal community diversity could mean a greater quantity and better quality of resources for macroinvertebrates, thereby increasing their fitness and their tolerance to salt stress (Guo et al., 2016; Isanta-Navarro et al., 2021). Although preferences may vary among subfamilies depending on their traits (e.g., feeding modes), high-quality green algae have been reported as the most important food source for all stream macroinvertebrates, followed by diatoms and cyanobacteria (Krivosheina, 2008; Guo et al., 2016). Indeed, the quality of the feeding resources can modulate salinity tolerance (Isanta-Navarro et al., 2021), with primary producers' quantity and quality being key for consumers' performance under salinity stress (Torres-Ruiz et al., 2007; Torres-Ruiz and Wehr, 2010; Guo et al., 2016).

Finally, our BAIN analysis suggested an increase in biotic interactions in the salt and high nutrient treatments. This means that species interactions could be playing a role in the response of the macroinvertebrate communities to our treatments. Concordantly, Arnott et al. (2023) found that differences in community composition could partly explain the differences in the sensitivity to salinity of zooplankton species of aquatic communities to salt and nutrient pollution. Also, Moniruzzaman et al. (2021) showed that community composition and biotic-abiotic interactions influence species segregation and aggregation, as well as the adaptation of a species to a particular set of conditions and resources in its environment and the life strategies of aquatic species. In fact, there are many studies showing that species interactions may be an important factor modulating the response of aquatic biodiversity to pollution (Clements et al., 2012; Gessner and Tlili, 2016). We encourage future studies to manipulate trophic interactions under experimental conditions to further explore the potential modulating effect of trophic interactions on the sensitivity of aquatic biodiversity to nutrient and salt pollution. Also, we call for more studies addressing not only the interaction between salts and nutrients resulting from several activities (e.g., agriculture, ethanol industry), but also their combined interaction with other commonly co-occurring pollutants such as pesticides (Schäfer et al., 2011; Markert et al., 2022; Dreux Fraga, 2023).

5. Conclusions

This study provides insights into the responses of algae and macroinvertebrates to the combined effects of salt and nutrients in Mediterranean river ecosystems. Nutrient addition increased chlorophyll-a levels, primarily due to cyanobacterial proliferation, but this increase was limited under nutrient saturation conditions. Nutrient addition affected P uptake by the biofilm, whereas salinity negatively impacted the diversity and richness of the entire aquatic macroinvertebrate community but favored the abundance of resistant chironomid taxa. Although there was weak evidence for an interactive effect between nutrients and salinity, the toxic effects of salt addition on aquatic macroinvertebrates appeared to be mitigated by nutrients in a concentration-dependent manner (i.e., higher nutrient concentrations resulted in stronger mitigating effects). This mitigation could be related to the recovery of green algae and diatom groups. Overall, nutrients promoted algal growth while salt appeared to inhibit it, suggesting potential interactive effects that deserve further attention through biofilm species-level analysis. At the same time, biofilm response may have had direct effects on macroinvertebrate communities, as greater food variety and quality may provide more energy to withstand the toxic effects of salinity. Finally, our results indicate that the feeding quality and preferences of macroinvertebrates and potential ecological interactions among different trophic levels could be key to understanding the effects of nutrients and salinity on the evaluated communities. These findings highlight the complexity of ecological responses to nutrient and salt pollution and have important implications for the management of the freshwater salinization syndrome.

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CRediT authorship contribution statement

Alvaro Javier Moyano Salcedo: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft & editing, Visualization, Project administration. **Narcís Prat:** Macroinvertebrate identification, Formal analysis, Investigation. **Lluís Bertrans-Tubau:** Conceptualization, Methodology, Investigation. **Martí Piñero Fernández:** Conceptualization, Methodology, Investigation. **David Cunillera-Montcusí:** Formal analysis, Investigation, Writing – review. **Julio C. López-Doval:** Methodology, Investigation, Writing – review. **Meritxell Abril Cuevas:** Conceptualization, Methodology, Investigation, Writing – review. **Lorenzo Proia:** Conceptualization, Methodology, Investigation, Writing – review. **Miguel Cañedo-Argüelles:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – final draft & editing, Visualization, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.168824.

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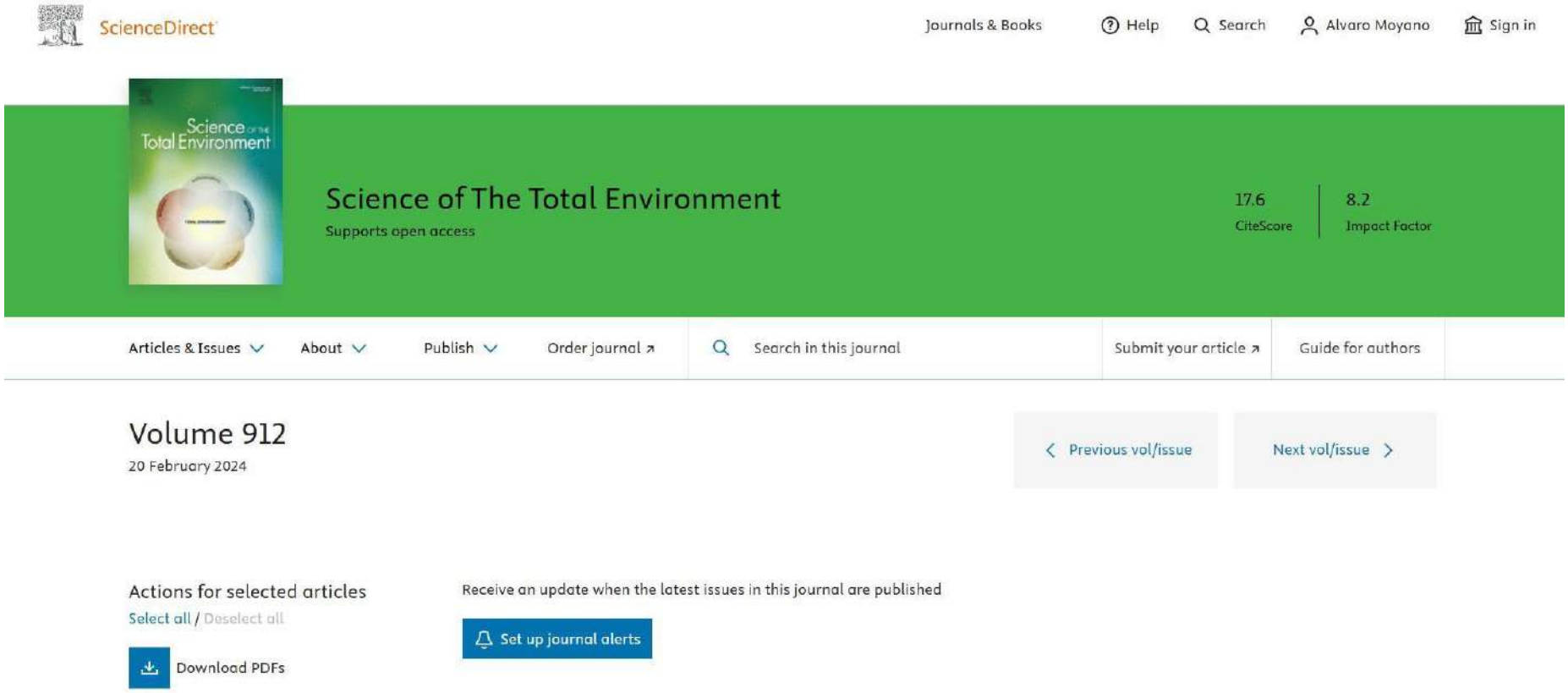

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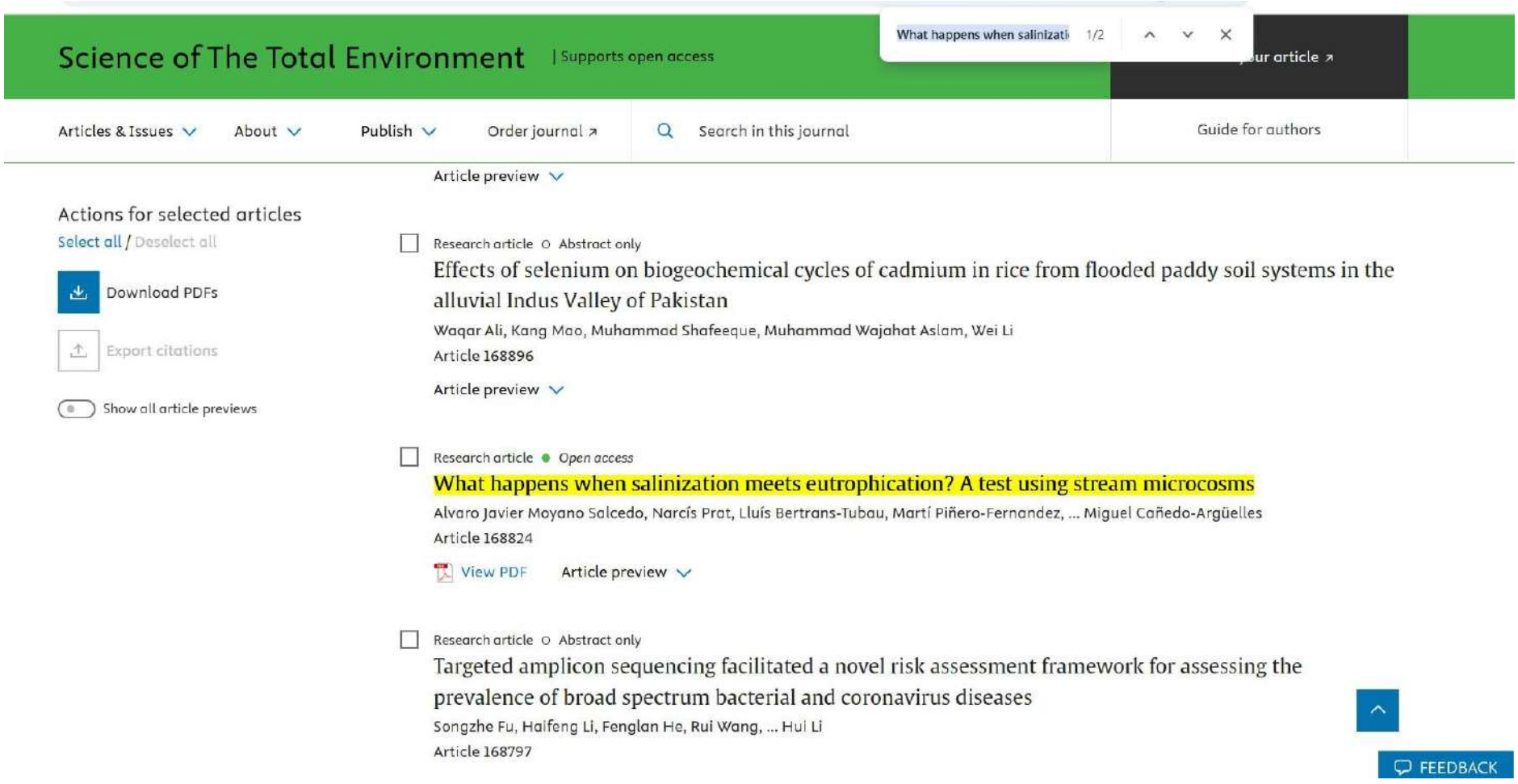

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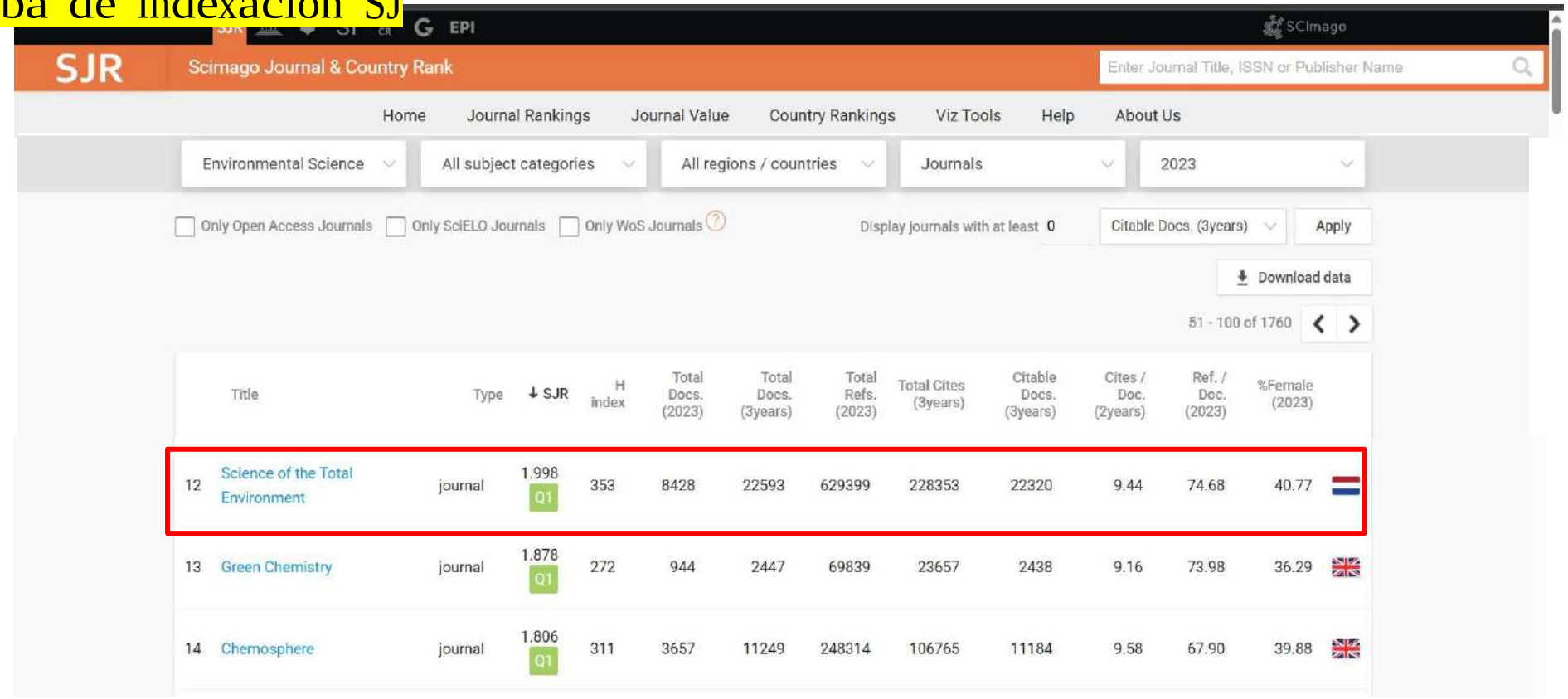

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13	Green Chemistry	journal	1.878 Q1	272	944	2447	69839	23657	2438	9.16	73.98	36.29
14	Chemosphere	journal	1.806 Q1	311	3657	11249	248314	106765	11184	9.58	67.90	39.88

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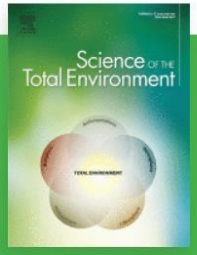

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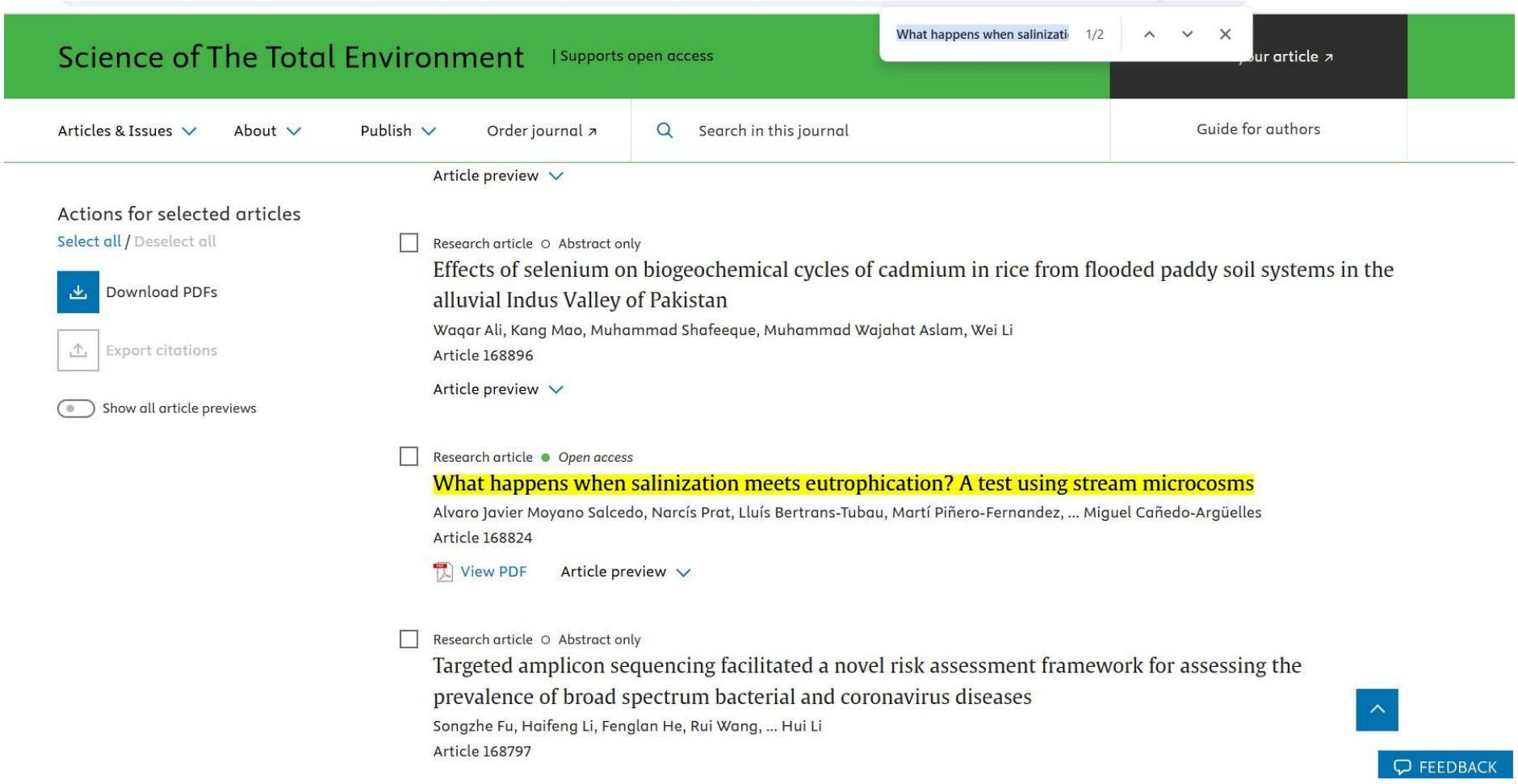

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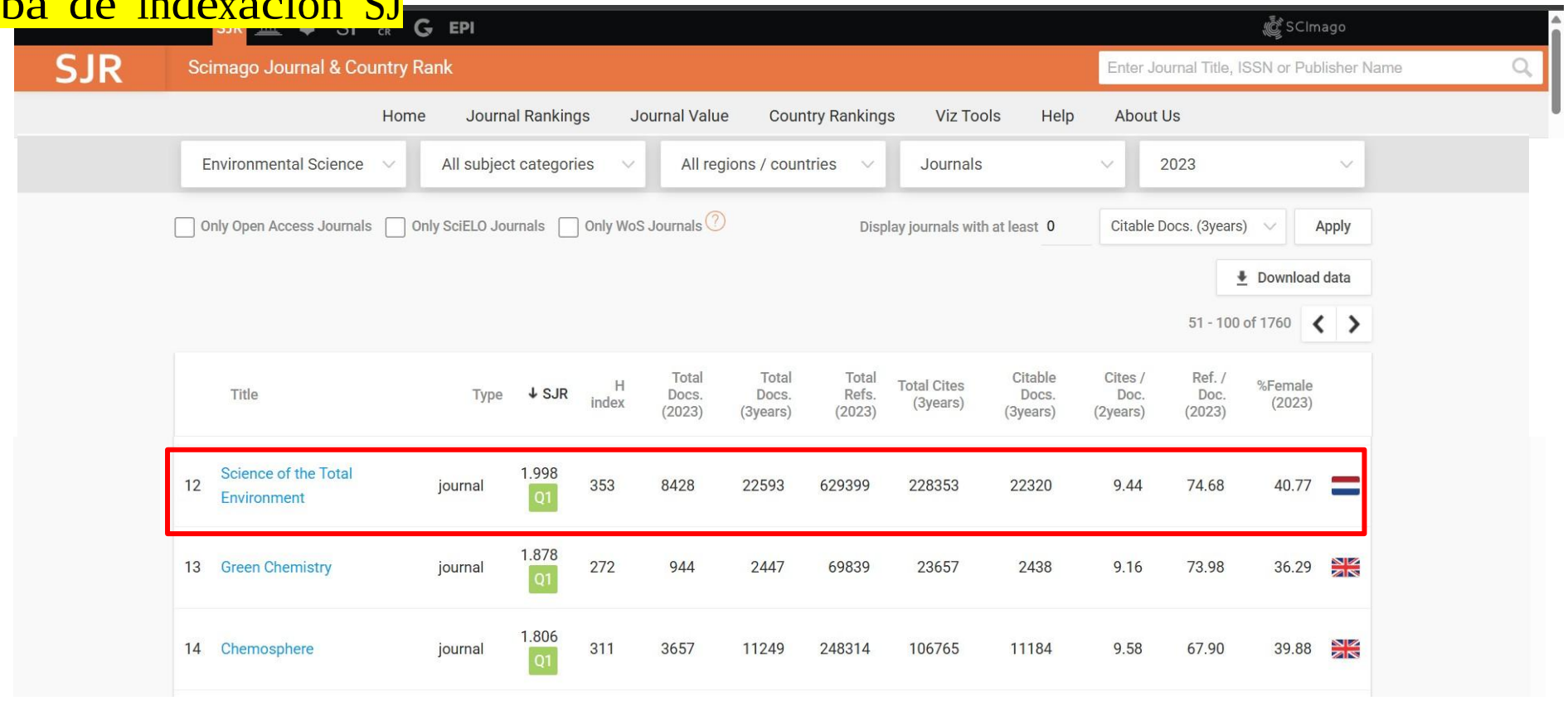

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