

RESEARCH ARTICLE

# Long-term changes to plankton communities in artificially heated lakes

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## Abstract

Increased surface-water temperatures and nutrient enrichment are predicted to alter planktonic communities, impacting biodiversity and ecosystem functioning. While short-term mesocosm studies have reported temperature- and nutrient-driven effects, long-term observations from natural systems remain limited. We studied seasonal plankton communities in 10 lakes in central Poland, five warmed by power plant discharge for six decades and ~2°C warmer (annual mean) than control lakes. Based on environmental DNA (eDNA) relative read abundance, green algae (Chlorophyta) were up to 15% more abundant in heated lakes, while golden algae (Chrysophyceae) were up to 7% more abundant in control lakes. Heated lakes exhibited higher diversity of diatoms, green algae, golden algae, cercozoans, basidiomycetes, and chytrids, especially in summer. Their plankton assemblages were compositionally distinct and showed reduced seasonal variability. Multiple regression revealed that rising temperature, interacting with elevated nutrients, reduced diversity in many plankton groups. Warming favored heat-adapted taxa, driving compositional shifts. By providing insights into the long-term impacts of anthropogenic warming, this study underscores the importance of integrating temperature-nutrient interactions in predicting ecosystem responses to climate change.

Warming and nutrient enrichment are prominent drivers of change in freshwater biodiversity and ecosystem functioning (Alahuhta et al. 2019; Gorman et al. 2024). Globally, freshwater surface water temperatures are rising at 0.34°C per decade, outpacing increases in air (0.25°C) and ocean (0.12°C) temperatures (O'Reilly et al. 2015). In European lakes, the warming rate is 0.58°C per decade, nearly double the global rate (Dokulil et al. 2021). Nutrient concentrations, particularly nitrogen

(N) and phosphorus (P), now exceed natural baselines by over 20-fold in many regions (Heathwaite et al. 1996; Beusen et al. 2022), primarily due to urbanization and agriculture. Phosphorus accumulation has often outpaced nitrogen in human-impacted freshwater systems, altering N:P stoichiometry and further disrupting ecosystem dynamics (Yan et al. 2016).

Warming and nutrient enrichment interact in complex ways, and can be synergistic or antagonistic, depending on ecosystem characteristics and taxa-specific responses (Jackson et al. 2016; Birk et al. 2020). Plankton communities play crucial roles in primary production, nutrient cycling, and food web dynamics. For instance, freshwater phytoplankton fix ca. 1.03 Tg of carbon per day (Sayers et al. 2021) and serve as a key food source for zooplankton, which in turn sustain larger invertebrates and fish (Lomartire et al. 2021). Protists and fungi interact with phytoplankton, zooplankton, and other eukaryotes in symbiotic and parasitic relationships, regulating host abundance, biomass, and energy transfer (Agha et al. 2016; Frenken et al. 2020). Consequently, alteration in plankton diversity caused by warming and nutrient enrichment may cascade through ecosystems, affecting productivity and biogeochemical cycles (Cabrerizo et al. 2024).

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Warming typically reduces phytoplankton richness and evenness, often favoring opportunists, while nutrient enrichment enhances biomass and abundance (Rasconi et al. 2017; Verbeek et al. 2018; Richardson et al. 2019; Morasco et al. 2024). However, excessive nutrients promote harmful algal blooms (Paerl and Otten 2016; Paerl et al. 2018). In zooplankton, warming alone has subtle effects on diversity and abundance (Mckee et al. 2002), but in combination with nutrients, can increase biomass, particularly during heatwaves (Işkın et al. 2020). Phenological shifts may result, with warming advancing and nutrients delaying peak abundances (Feuchtmayr et al. 2010; M. Zhang, Shi, et al. 2021). Additionally, increased predation by higher trophic levels under these conditions can reduce large-bodied zooplankton, decreasing energy transfer efficiency (Özen et al. 2013; Işkın et al. 2020). In microeukaryotes, groups such as nanoflagellates and ciliates often increase in abundance under warm, nutrient-rich conditions (Zingel et al. 2018; Özen et al. 2013).

These ecological responses reflect taxon-specific environmental preferences. Cold-adapted species often decline in warmer environments, while thermophilic and nutrient-tolerant species increase, altering community structure (Nelson et al. 2017; Perrin et al. 2021; Devkota et al. 2024). Bioindicator analyses help identify such changes (De Cáceres and Legendre 2009; De Cáceres et al. 2010; Birk et al. 2012). For example, thermophilic copepods such as *Thermocyclops oithonoides* and *Mesocyclops leuckarti* exhibit prolonged activity and increased peak abundance during warmer summers, likely via additional generations (Nilssen and Wærvågen 2000; Gerten and Adrian 2002; Wagner and Adrian 2011). *T. oithonoides*, being planktonic with a winter diapause, can persist across its broad distribution range during colder periods (Nilssen and Wærvågen 2000; Adrian et al. 2006). The copepod *Acanthocyclops robustus* shows seasonal morphological variations in setae that may enhance its ability to cope with elevated temperatures (Lescher-Moutoué 1996; Gerten and Adrian 2002). Copepod species also differ in trophic preferences: *Thermocyclops. decipiens* and *Thermocyclops. prasinus* thrive in mesotrophic-eutrophic conditions, whereas *Thermocyclops. inversus* and *Mesocyclops. anceps* prefer oligotrophic-mesotrophic habitats (da Silva 2011; Perbiche-Neves et al. 2013). Similarly, warming affects diatom assemblages, promoting *Cyclotella* spp. and reducing heavily silicified *Aulacoseira* and benthic *Fragilaria*, due to reduced ice cover and stronger stratification (Rühland et al. 2008; Reavie et al. 2017; Biskaborn et al. 2021). Among chlorophytes, large species such as *Staurastrum* prefer warm waters, while smaller species such as *Monoraphidium* show mixed responses (Willis et al. 2019; Lürling et al. 2013; Zohary et al. 2021).

Despite these insights, studies often yield contrasting results due to differences in method (e.g., mesocosms vs. field

surveys), target taxa (e.g., phytoplankton vs. zooplankton), and experimental design (e.g., single vs. combined stressors). While mesocosm experiments are valuable (e.g., Piggott et al. 2012; Šorf et al. 2015), their relatively short duration might not capture long-term ecosystem dynamics.

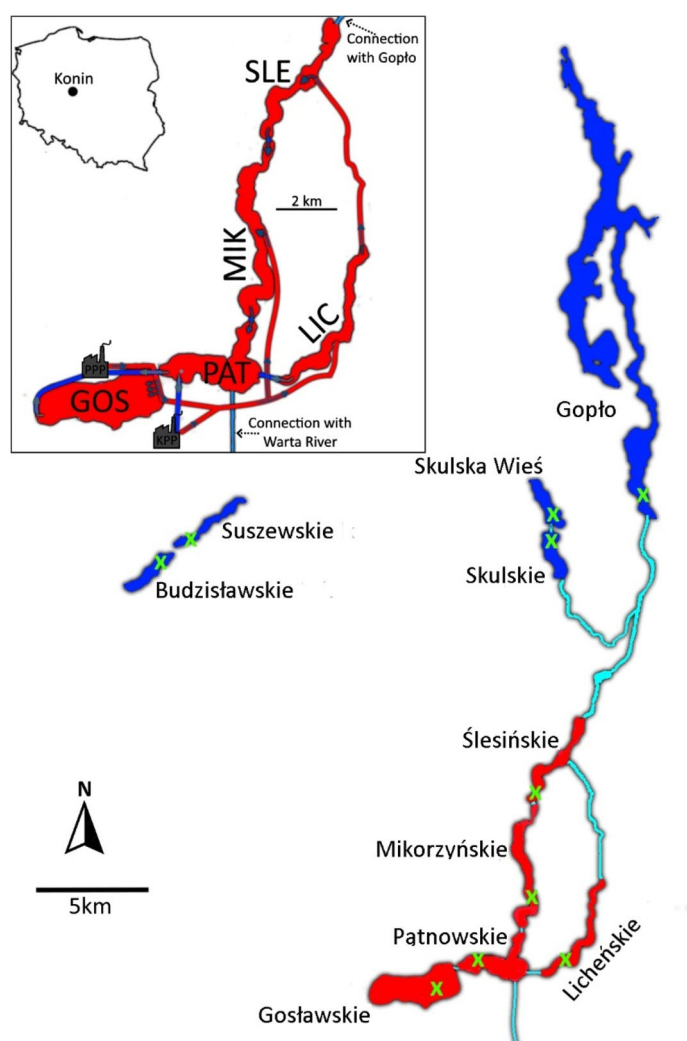
Field surveys of lakes experiencing contrasting temperature and nutrient regimes offer a valuable complementary approach. In central Poland, a unique set of 10 lakes—5 heated by power plant effluents and 5 unheated controls—provides an ideal setting. The heated lakes have been ~2°C warmer on average for over 60 yr (Dziuba et al. 2020), mirroring climate change projections for the end of the 21<sup>st</sup> century (IPCC 2023).

Using eDNA metabarcoding of seasonally collected water samples, we investigated plankton communities in these lakes, focusing on 12 plankton groups. We asked: (i) How do the relative abundance, diversity, and composition of plankton differ between heated and control lakes? (ii) How do warming and nutrient availability interact to influence plankton diversity? (iii) Are there species that exhibit preferences for either heated or control lakes?

## Materials and methods

### Study sites

The study was conducted on 10 lakes near Konin in central Poland (Fig. 1). Five lakes (Gosławskie, Licheńskie, Pątnowskie, Ślesieńskie, and Mikorzyńskie) receive warm water from two lignite-combustion power plants: Konin (established in 1958) and Pątnów (established in 1970). Thermal discharge is year-round, except in Ślesieńskie where it is limited to May to September. These lakes are, on average, ~2°C warmer annually than the five nearby control lakes: Budziślawskie, Gopło, Skulskie, Skulska Wieś, and Suszewskie (Dziuba et al. 2020). Temperature monitoring (2012–2016) consistently confirmed elevated temperatures in heated lakes, particularly at 0–5 m depth in summer and 0–12 m depth in autumn. Long-term temperature records date back to 1965, and winter data to 1995 (Socha and Hutorowicz 2009; Pyka et al. 2013). Heated lakes experience disrupted stratification and minimal ice cover, restricted to stagnant areas (Socha and Zdanowski 2001; Stawecki et al. 2013). During sampling in 2020, no ice was observed; winter air temperatures were ~1°C above the long-term average (Polish Climate Monitoring Bulletin 2020). Thermal effluents are free from chemical pollutants and regularly monitored due to recreational and aquaculture use. However, all lakes are subject to diffuse pollution from agriculture, aquaculture, and urbanization. Lake characteristics and coordinates are detailed in Supporting Information Table S1. With the exception of lakes Suszewskie and Budziślawskie, all lakes are interconnected by channels, enabling species dispersal and migration.



**Fig. 1.** Map of the study area showing the 10 lakes near Konin, central Poland. Heated lakes (red) and control lakes (blue) are marked, with sampling stations indicated by crosses (x). Channels connecting the lakes are shown in aqua blue. The inset provides a zoom-in view of the heated lake system and its location within Poland.

### Sampling

Sampling was conducted in 2020 during winter (January 29–31), spring (May 6), summer (July 27–29), and autumn (October 28–29), resulting in 40 samples across the 10 lakes. Samples were collected above the deepest point in each lake, except for Gopło, where the deepest accessible location was used (Fig. 1). Environmental parameters (temperature, conductivity, pH, total dissolved solids, and oxygen concentration and saturation) were recorded in situ at 1 m depth using a multiparameter probe (YSI Inc). Water transparency was measured using a Secchi disc.

Two liters of surface water were collected for chlorophyll and nutrient analyses, filtered, and frozen on dry ice for transport. Chlorophyll *a* (Chl *a*) and pheopigments were measured following ISO 10260:1992 (<https://www.iso.org/standard/18300.html>).

Nutrient concentrations were determined using a flow injection analyzer (FIA compact, MLE GmbH). Soluble reactive phosphorus (SRP) and dissolved nitrogen forms ( $\text{NO}_2^-$  and  $\text{NO}_3^-$ ) were analyzed after membrane filtration ( $0.45 \mu\text{m}$ , Sartorius), adhering to ISO protocols (ISO 15681-1:2005, ISO 13395:1996, ISO 11732:2005). Total phosphorus (TP) was measured according to ISO 15681-1:2005, using a digestion method adapted from ISO 15681-1:2003. Total nitrogen (TN) was quantified according to ISO 29441:2010.

An additional 2 L of surface water was collected in clean HDPE bottles for eDNA-based plankton analysis. Samples were vacuum-filtered (Whatmann GF/F, 25 mm diameter,  $0.7 \mu\text{m}$  pore size) at 200 mbar. Filters were frozen at  $-80^\circ\text{C}$ , freeze-dried (Alpha 1–4, Martin Christ Gefriertrocknungsanlagen GmbH) for 8 h at  $-45^\circ\text{C}$ , and stored at  $-20^\circ\text{C}$  until DNA extraction.

### DNA extraction, PCR, library preparation, and sequencing

Filters were placed into 2-mL tubes with a stainless-steel bead (5 mm diameter; Qiagen GmbH), covered with TissueLyser (Qiagen), and shaken three times for 90 s at 30 Hz in a mixer mill MM301 (Retsch GmbH). Tubes were briefly centrifuged to collect material into a pellet. DNA was extracted using the NucleoSpin Plant II extraction kit (Macherey-Nagel™), following the manufacturer's protocol. Extracted DNA was stored in TE buffer at  $-20^\circ\text{C}$  until further processing.

Three primer sets were used to target: (i) diatoms and algae, (ii) metazoans and protists, and (iii) fungi including chytrids (Supporting Information Table S2). Polymerase Chain Reaction (PCR) and sequencing steps followed Warter et al. (2024), Beng et al. (2021), and Rajarajan et al. (2025), respectively. Three fungal samples failed PCR despite repeated attempts. Samples were pooled equimolar and sequenced in a single run (300-bp paired-end reads, Illumina MiSeq v3 sequencing kit, 600 cycles) at the Berlin Center for Genomics in Biodiversity Research. Negative controls were included at all stages. Raw data were deposited in the European Nucleotide Archive (<https://www.ebi.ac.uk/ena/data/search?query=PRJEB54709>) via the German Federation for Biological Data service (Diepenbroek et al. 2014).

### Bioinformatics analysis

Primers were removed using Cutadapt 4.1 (Martin 2011). Reads were processed using DADA2 1.24.0 (Callahan et al. 2016) in R 4.2.0 (R Core Team 2022). The analysis script is provided as Supporting Information. Taxonomic assignment of amplicon sequence variants (ASVs) used the Protist Ribosomal Reference database (PR2 4.14.0, Guillou et al. 2013) for DIV4 and EUK15 sequences and the RDP LSU database (Czaplicki 2017) for CHY (fungi). Contaminants were identified and removed by comparing regular samples with negative controls using decontam 1.12 (Davis et al. 2018) in R.

Approximately 6 million reads were obtained, evenly distributed across the three datasets (Supporting Information

Table S3). The DIV4 negative control yielded 2061 reads and three contaminants (*Dinobryon divergens*, *Skeletonema subsalsum*, and Phaeophyceae\_XX). The EUK15 negative control contained 315 reads and 3 contaminants (Pedinellales\_X\_sp., Chrysophyceae\_Clade-F\_X sp., and *Chara* sp.), while the CHY negative control had 420 reads and no contaminants. All identified contaminants and ASVs present in only one sample were removed prior to statistical analysis. Although this may exclude some rare taxa, our focus was on consistently recovered ASVs.

## Statistical analyses

### Environmental differences between heated and control lakes

To disentangle the effect of thermal discharge from seasonal variation, we computed the deviation from seasonal mean temperature by subtracting the average control lake temperature for each season from values recorded in heated lakes.

Correlation among environmental variables was tested using *corrplot* 0.92 (Wei and Simko 2021) in R. For highly correlated variables ( $r > 0.70$ ), the most ecologically relevant was retained (e.g., temperature over conductivity; Supporting Information Table S4). Differences between heated and control lakes were analyzed separately using two-way ANOVA (lake type  $\times$  season) with *rstatix* 0.7.0 (Kassambara 2021) in R. Normality was assessed with the Shapiro–Wilk test and Q–Q plots, while homogeneity of variances was tested using Levene’s test. Data were rank-transformed when assumptions were violated.

### Relative abundance, diversity, and composition of plankton

We analyzed 12 taxonomic groups: Chlorophyta (green algae), Bacillariophyta (diatoms), Chrysophyceae (golden algae), Cryptophyta (cryptophyte algae), Crustacea (crustaceans), Rotifera (rotifers), Ciliophora (ciliates), Dinoflagellata (dinoflagellates), Cercozoa (cercozoans), Chytridiomycota (chytrids), Basidiomycota (club fungi), and Ascomycota (sac fungi). Relative abundance was calculated as the proportion of reads per group relative to the total number of reads in that category (e.g., diatom reads relative to total phytoplankton reads). Effects of lake type, season, and their interaction were tested using beta regression (*betareg* 3.1.4, Cribari-Neto and Zeileis 2010) in R.

Diversity was analyzed using Hill numbers (Hill 1973; Mächler et al. 2021). We used the scaling parameter  $q = 1$ , which balances the contribution of rare and abundant ASVs and corresponds to the exponential of Shannon diversity.

Community composition was based on ASV presence/absence and analyzed via permutational multivariate ANOVA using *vegan* (Oksanen et al. 2023) in R. Similarities among samples were visualized with nonmetric multidimensional scaling of Bray–Curtis distances.

Phytoplankton resource use efficiency was estimated by standardizing Chl *a* concentrations against TP, following Hodapp et al. (2019).

### Effects of warming and nutrients on plankton diversity

To evaluate the influence of lake type, season, and their interaction on plankton diversity (per taxonomic group), a two-way ANOVA (Type II) was applied as in “Environmental differences between heated and control lakes” section. We then constructed generalized linear mixed models including deviation from seasonal mean temperature, SRP, TP, TN, lake area, and depth as fixed effects, with lake and season as random effects. Models were selected using *buildglmTMB* in *buildmer* (Voeten 2020), based on Akaike information criterion. Predictors were standardized prior to modeling using *arm* (v1.13-1; Gelman et al. 2013).

### Species preferences for heated or control lakes

To assess ecological preferences, we calculated the Indicator Value (*IndVal*), Pearson’s phi coefficient of association (*phi*), and Point biserial correlation (*rpb*) using *indicspecies* 1.7.12 (De Cáceres et al., De Cáceres et al. 2016) in R. *IndVal* combines ASV relative frequency and mean abundance; *phi* quantifies the correlation between ASV presence/absence and lake type; and *rpb* quantifies the correlation between ASV abundance and lake type. For fungi, adjustments for unequal sample sizes were applied (i.e., *func* = “*IndVal.g*” for *IndVal* and *func* = “*r.g*” for *phi* and *rpc* indices). Only ASVs identified by at least two of the three indices were retained. The top 10 indicator species per lake type, ranked by the highest *stat* value (as calculated using *IndVal*, *phi*, and *rpc* indices), were visualized with heatmaps (*microeco* 0.11.1 (Liu et al. 2021) in R). Indicator ASVs lacking species or genus assignments underwent additional taxonomic assignment using *metaPR2* 2.0 (Vaulot et al. 2022) and NCBI BLASTN (Johnson et al. 2008), with thresholds of  $\geq 95\%$  identity (genus) and  $\geq 97\%$  (species).

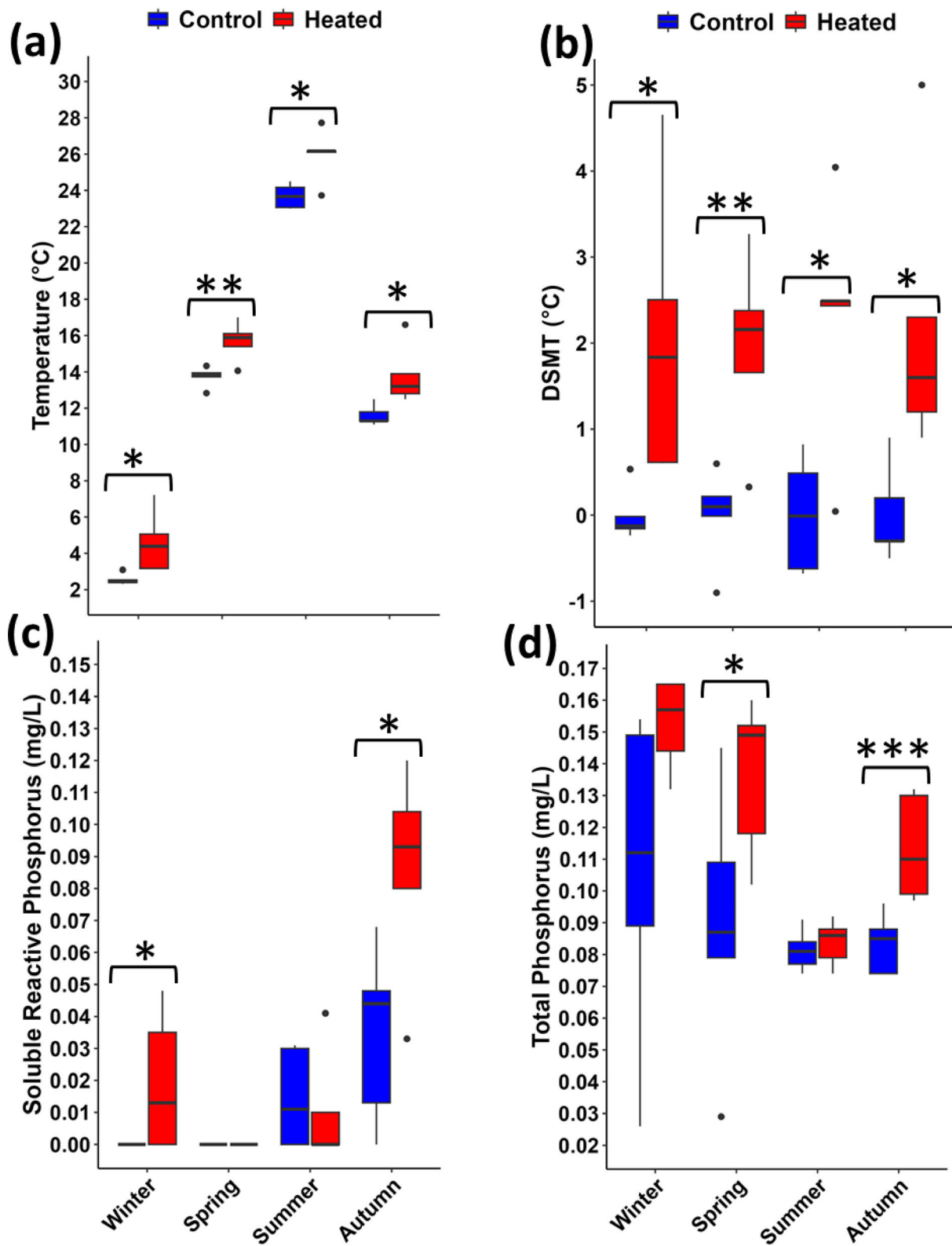
## Results

### Environmental differences between heated and control lakes

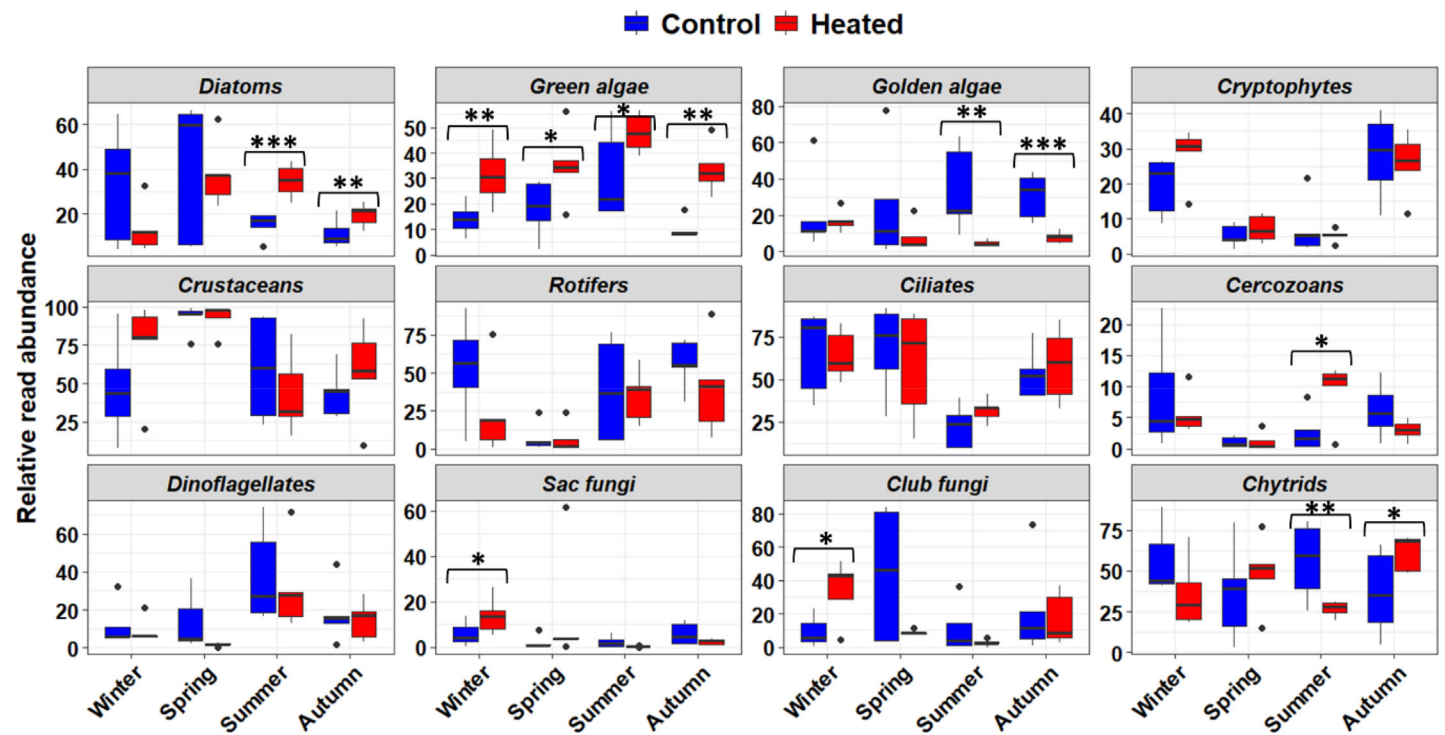
In 2020, heated lakes were on average approximately 2°C warmer than control lakes (Fig. 2a,b; Supporting Information Table S5). They also had higher concentrations of SRP (0.09 mg L<sup>-1</sup> vs. 0.05 mg L<sup>-1</sup>) and TP (0.11 mg L<sup>-1</sup> vs. 0.08 mg L<sup>-1</sup>) (Fig. 2c,d). Total nitrogen concentrations did not differ between lake types (Supporting Information Table S5).

### Plankton relative abundance, diversity, and community composition

The final dataset comprised 1081 ASVs for DIV4, 1444 for EUK15, and 1401 for CHY. Seven of the 12 groups showed significant differences in relative read abundance between heated and control lakes (Fig. 3; Supporting Information Table S6). In heated lakes, relative abundances were higher for green algae (in all seasons), diatoms (summer and autumn), cercozoans (summer), sac fungi and club fungi (winter), and chytrids (autumn). In contrast, control lakes had higher abundances of golden algae (summer and autumn) and chytrids (summer).



**Fig. 2.** Seasonal differences in environmental variables between control and heated lakes. Only variables showing a significant effect of lake type are presented. Boxplots display medians (thick horizontal line) and outliers (black points); DSMT refers to the deviation from the seasonal mean temperature of each lake. Significance codes: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .



**Fig. 3.** Seasonal differences in the relative read abundance of amplicon sequence variant (ASVs) between control and heated lakes across 12 taxonomic groups. Note the different scales on the Y-axes. Boxplots show medians (thick horizontal lines) and outliers (black points). Significant differences between heated and control lakes within each season are indicated by asterisks. Significance codes: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

Plankton diversity also varied by lake type and season (Fig. 4; Supporting Information Table S6). Heated lakes exhibited higher diversity in diatoms, sac fungi, and chytrids (autumn); green algae (winter and summer); golden algae, cryptophytes, cercozoans, and dinoflagellates (summer); and ciliates (winter). Control lakes showed higher diversity of cryptophytes (winter and spring), rotifers (autumn), and sac fungi (summer).

Community composition differed between heated and control lakes for 11 of the 12 groups—club fungi being the sole exception—and displayed strong seasonal variation across all groups (Supporting Information Table S6).

Phytoplankton resource use efficiency was generally lower in heated lakes, particularly during winter, suggesting reduced efficiency of energy transfer from nutrients to phytoplankton biomass (Supporting Information Fig. S1).

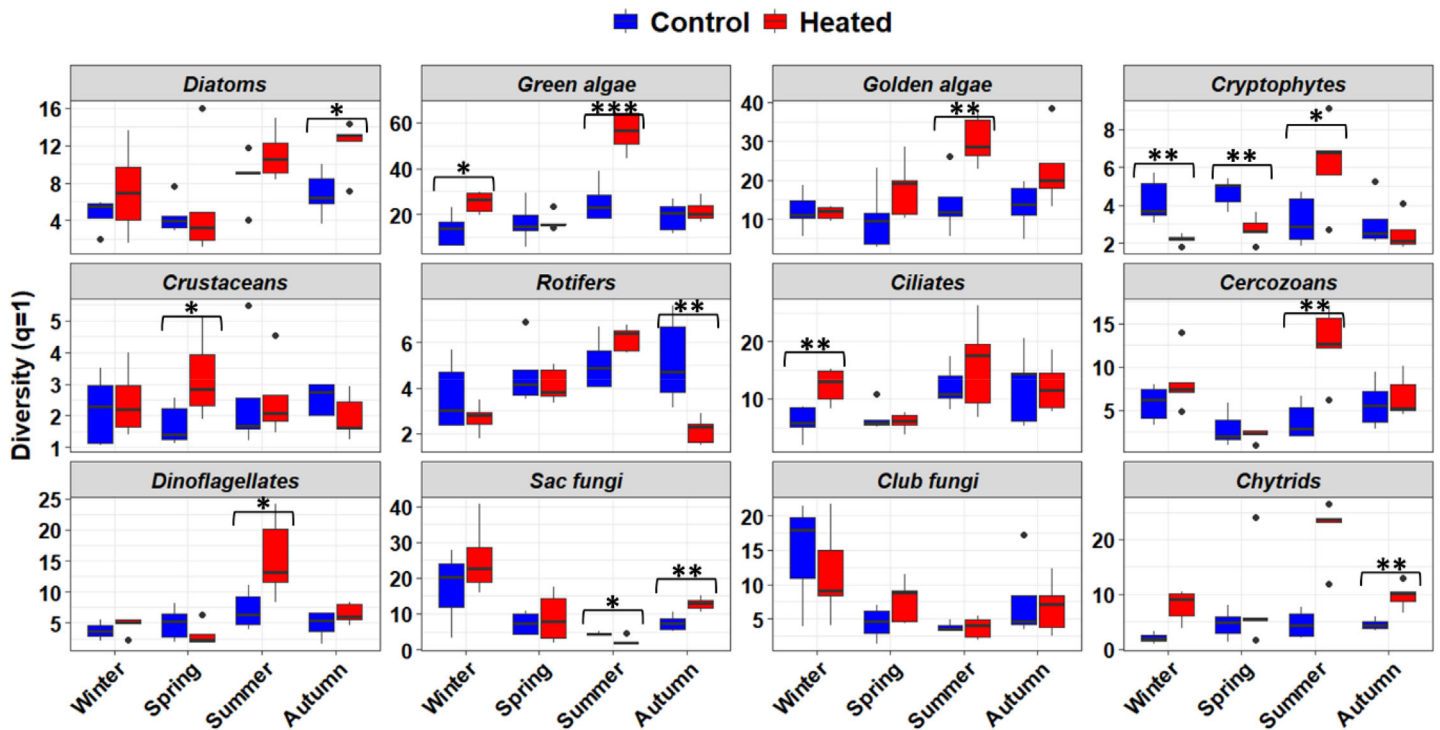
### Impacts of warming and nutrients on plankton diversity

Parsimonious models explained between 7% and 74% of the variance in diversity across plankton groups (Supporting Information Table S7). Warming increased diversity in diatoms, golden algae, cercozoans, club fungi, and chytrids, but reduced diversity in cryptophytes, ciliates, dinoflagellates, and sac fungi. Soluble reactive phosphorus was positively associated with diversity in diatoms, cryptophytes, and chytrids, and negatively associated with ciliates. Total nitrogen was

negatively associated with rotifers, sac fungi, club fungi, and chytrids, but positively associated with crustaceans. Total phosphorus had a negative effect on the diversity of diatoms, rotifers, sac fungi, and club fungi, while enhancing diversity in green and golden algae. Interactions between warming and nutrient enrichment further modulated diversity outcomes. For instance, warming combined with TN significantly impacted diatoms, green algae, ciliates, and chytrids: diversity increased under warming at low TN but declined at high TN (Supporting Information Fig. S2). Similarly, the interaction between warming and TP influenced golden algae, cryptophytes, cercozoans, dinoflagellates, and sac fungi. In most groups, diversity increased under warming at low TP, although sac fungi diversity increased only under high TP conditions (Supporting Information Fig. S3). Additionally, warming and SRP interacted to affect rotifers, with diversity increasing at low SRP and declining at high SRP under warming (Supporting Information Fig. S4).

### Species ecological preferences

A total of 494 ASVs were identified as indicators of lake type. Of these, 404 ASVs (78%) were associated with heated lakes, and 90 ASVs (22%) with control lakes (Fig. 5). Heated lakes were primarily characterized by green algae (30% of indicator ASVs), followed by chytrids (15%), and diatoms (11%), with other groups contributing between 0.2% and



**Fig. 4.** Seasonal differences in diversity between control and heated lakes. Diversity is expressed as Hill numbers of order 1 ( $q = 1$ ), which account for amplicon sequence variant (ASV) frequencies by balancing the contribution of rare and abundant taxa, and are equivalent to the exponential of Shannon diversity. Note the different scales on the Y axes. Boxplots show median (thick horizontal lines) and outliers (black points). Significant differences between lake types within each season are indicated by asterisks. Significance codes: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ .

3.0% (Supporting Information Fig. S5). In contrast, control lake indicators were dominated by diatoms (17%), green algae (16%), golden algae (8%), and chytrids (6%) (Supporting Information Fig. S5).

## Discussion

Plankton are crucial to freshwater ecosystem functioning, and their responses to warming and nutrient enrichment are complex. We studied 10 lakes—5 of which have received warm water discharge from power plants for approximately 60 yr—offering a natural experiment to examine long-term environmental change. The observed approximately 2.0°C temperature increase reflects climate change projections, and elevated phosphorus levels in heated lakes allowed us to assess interactions between warming and nutrients. Both factors, alone and in combination, drove pronounced and seasonally variable shifts in plankton diversity and community composition.

### Shifts in community composition

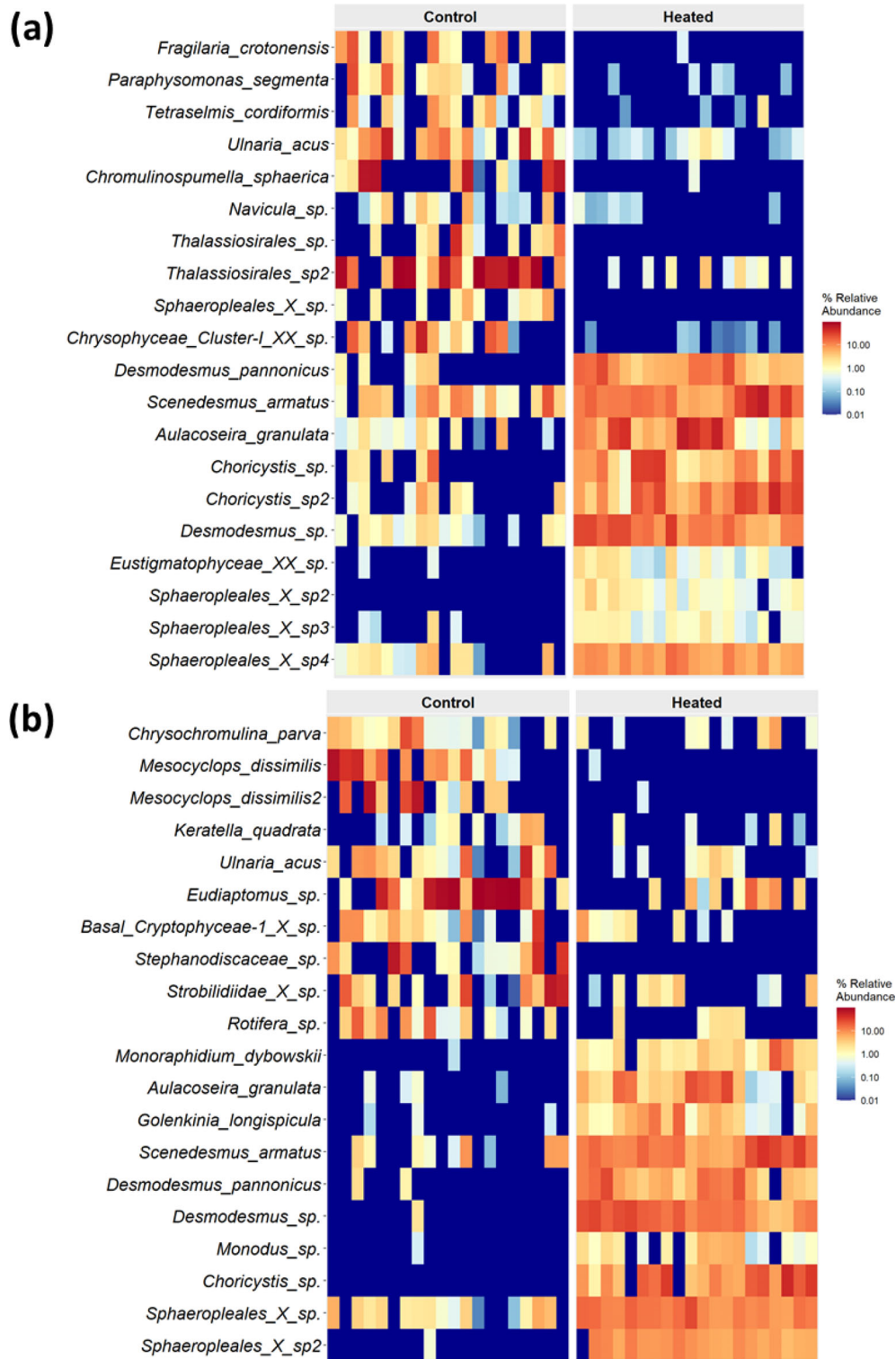
The consistently higher relative abundance of green algae in heated lakes aligns with other warming studies (Rasconi et al. 2017; Yu et al. 2018; H. Zhang, Zhang, et al. 2021) and earlier research in the same lakes (Napiórkowska-Krzebietke 2009). In contrast, golden algae—typically associated with

colder waters (Kristiansen and Škaloud 2016)—declined in abundance during summer. Diatom abundances increased in heated lakes during summer and autumn, consistent with microscopy-based records from this system (Napiórkowska-Krzebietke 2009). These seasonal dynamics were effectively captured using the eDNA approach.

Diversity was generally higher in heated lakes for several groups, including diatoms, green and golden algae, cercozoans, club fungi, and chytrids. In contrast, rotifer diversity declined in autumn, and crustacean diversity showed no consistent difference between lakes (Fig. 4), indicating taxon-specific responses to warming.

### Energy flow and role of non-native species

Mesocosm studies have shown that warming can reduce energy transfer from phytoplankton to zooplankton, diverting it toward detrital and parasitic pathways (e.g., Barneche et al. 2021; Moresco et al. 2024). In line with this, we observed lower phytoplankton resource use efficiency (Chl *a*/TP) in heated lakes in all seasons except summer (Supporting Information Fig. S1). Elevated chytrid abundance in heated lakes, especially in autumn, further supports previous findings that fungal parasitism peaks at intermediate temperatures (Rohrlack et al. 2015; Agha et al. 2018), consistent with a shift in energy flow.



**Fig. 5.** Relative read abundance of indicator species in control and heated lakes based on the DIV4 (a) and EUK15 (b) datasets. For each lake type, the 10 indicator species with the highest statistical association (stat value) are shown. CHY dataset results are not included due to low taxonomic resolution.

Higher plankton diversity in heated lakes may also reflect increased seasonal environmental variability, which creates more ecological niches. Heated lakes supported more unique

genera (22 fungal and 9 phytoplankton) than control lakes (4 and 9, respectively). These likely include functionally distinct taxa with divergent environmental preferences

(Klais et al. 2016; Pálffy et al. 2021), suggesting that thermal inputs enhance temporal niche partitioning, reduce competitive exclusion, and facilitate coexistence (Shurin et al. 2010; Lear et al. 2021).

Non-native species also contributed to elevated diversity in heated lakes. Previous studies have reported six rotifer species new to the Polish fauna in these lakes, likely introduced via the invasive macrophyte *Vallisneria spiralis* L., which has spread throughout the warmed system (Ejsmont-Karabin 2011; Ejsmont-Karabin and Hutorowicz 2011). Although we detected *Vallisneria natans* in three heated lakes using eDNA, the ASV likely represents *V. spiralis*, which lacks 18S rRNA records in GenBank.

Other non-native indicators included the Asian clam *Corbicula fluminea* O.F. Müller and a parasitic fungus tentatively identified as *Ustilago trichophora*, both detected exclusively in heated lakes. The clam was previously reported in 2003 at the Dolna Odra power station's outflow (Domagała et al. 2004). *Ustilago trichophora*, not previously recorded in freshwater, matched our ASV with 99.4% similarity and may have been introduced via vegetation or occurred as a parasite on macrophytes. Babko et al. (2010) showed that invasive macrophytes in heated lakes can support similar or greater ciliate diversity compared to native vegetation—consistent with our observation of elevated ciliate diversity in winter.

Community composition differed significantly between lake types in 11 of 12 taxonomic groups and exhibited strong seasonal dynamics. These patterns suggest altered seasonal succession in heated lakes, potentially driven by the decline of cold-adapted species (Ejsmont-Karabin et al. 2020; Ejsmont-Karabin and Weglenska 1988) and increased presence of warm-adapted taxa. Such changes likely reflect species-specific thermal tolerances in conjunction with dispersal from the regional species pool (Suzuki et al., 2025).

### Interactive effects of warming and nutrients

Warming and nutrients had complex, context-dependent effects on diversity, consistent with previously proposed additive, antagonistic, or synergistic responses (Jackson et al. 2016; Birk et al. 2020). Both warming and SRP enhanced diatom diversity, likely through distinct mechanisms: SRP relieved nutrient limitations, providing essential resources for diatom growth, while warming boosted metabolic rates, particularly benefiting thermophilic diatom species. These findings align with Dong et al. (2012), who found that both factors can promote diatom diversity, with SRP exerting a more dominant role in nutrient-limited systems and warming exerting stronger effects as nutrient availability increases. Similarly, green algal diversity increased with warming and TP, reflecting thermotolerance and high nutrient demand (Oleksy et al. 2021; Watson et al. 1997).

However, warming combined with high TN reversed these positive trends for several groups, including diatoms, green algae, and chytrids—suggesting that nutrient oversupply can

limit diversity by favoring fewer taxa—an outcome also seen in mesocosms (Verbeek et al. 2018). Comparable antagonistic patterns were observed for rotifers, whose diversity increased with warming at low SRP but declined under high SRP. These antagonistic interactions highlight how excessive nutrients can offset warming benefits.

While our analysis treated lakes as discrete units, we acknowledge the potential influence of hydrological connectivity, especially among heated lakes (Heino et al. 2021). Downstream nutrient accumulation could contribute to elevated TP and SRP, but excessive recirculation among heated lakes complicates interpretation. Although we lacked water residence time data, inflow from control to heated lakes is unlikely to explain the observed diversity patterns, as such inflow would likely dilute, not amplify, the warming and nutrient signals. Future work should incorporate water residence time and hydrological flow data to better assess spatial effects.

### Indicator species of heated and control lakes

Indicator species analyses revealed taxonomic signatures of heated vs. control lakes, suggesting clear ecological preferences related to temperature and nutrient regimes. Heated lakes were characterized by green algae such as *Scenedesmus armatus*, *Desmodesmus pannonicus*, *Choricystis* sp., and *Pseudopediastrum boryanum* as well as the diatom *Aulacoseira granulata*. These species are typically linked to nutrient-rich and pollution-tolerant environments. For instance, species of *Scenedesmus* and *Desmodesmus* are often used in wastewater treatment for their ability to assimilate ammonia, nitrates, and phosphates (Yirgu et al. 2020; Sarfraz et al. 2021). Conversely, the alga *Paraphysomonas* sp., known to prefer cold conditions (Choi and Peters 1992), served as an indicator of control lakes, reinforcing temperature as a key determinant of distribution.

### Conclusion

Our study provides new insights into how long-term warming and nutrient enrichment affect freshwater plankton communities. By analyzing a wide range of plankton groups in lakes subjected to ~60 yr of warming, we documented changes in diversity, composition, and indicator species. Warming, particularly in combination with nitrogen and phosphorus enrichment, reduced diversity in several groups, underscoring the ecological risks posed by warming–eutrophication interactions. Previous studies have shown that warming can exacerbate eutrophication by accelerating nutrient cycling, depleting oxygen levels, and enhancing primary production (Yu et al. 2018; Zingel et al. 2018; M. Zhang et al. 2021). These processes may trigger biodiversity loss, alter trophic interactions, and increase the frequency of harmful algal blooms (Moss et al. 2003; Feuchtmayr et al., 2009; Rosset et al. 2014). Our findings emphasize the need to consider

multiple, interacting stressors when predicting freshwater ecosystem responses to climate change.

### Author Contributions

Conceptualization: Justyna Wolinska, Slawek Cerbin, Michael T. Monaghan. Data collection: Justyna Wolinska, Slawek Cerbin. Data analysis: Kingsly C. Beng. Funding acquisition: Justyna Wolinska, Slawek Cerbin. Writing – original draft: Kingsly C. Beng. Writing – review and editing: Kingsly C. Beng, Slawek Cerbin, Michael T. Monaghan, Justyna Wolinska.

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### Data Availability Statement

Genetic data: Raw sequence reads are deposited in the European Nucleotide Archive at EMBL-EBI under accession number PRJEB54709 (<https://www.ebi.ac.uk/ena/browser/view/PRJEB54709>).

Sample metadata: Metadata are also stored in the European Nucleotide Archive (accession number PRJEB54709) using the data brokerage service of the German Federation for Biological Data, in compliance with the Minimal Information about any (X) Sequence standard.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article.

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