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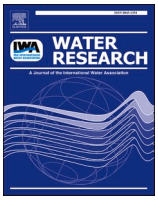

Skyglow increases cyanobacteria abundance and organic matter cycling in lakes

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ABSTRACT

Artificial light propagating towards the night sky can be scattered back to Earth and reach ecosystems tens of kilometres away from the original light source. This phenomenon is known as artificial skyglow. Its consequences on freshwaters are largely unknown. In a large-scale lake enclosure experiment, we found that skyglow at levels of 0.06 and 6 lux increased the abundance of anoxygenic aerobic phototrophs and cyanobacteria by 32 (±22) times. An ecosystem metabolome analysis revealed that skyglow increased the production of algal-derived metabolites, which appeared to stimulate heterotrophic activities as well. Furthermore, we found evidence that skyglow decreased the number of bacteria-bacteria interactions. Effects of skyglow were more pronounced at night, suggesting that responses to skyglow can occur on short time scales. Overall, our results call for considering skyglow as a reality of increasing importance for microbial communities and carbon cycling in lake ecosystems.

1. Introduction

Light is an important factor shaping the structure and productivity of aquatic ecosystems (Karlsson et al., 2009). Light controls photosynthesis and thus the production of organic matter available to heterotrophic microbes and higher trophic levels (Azam et al., 1983; Pomeroy, 1974). Moreover, light governs diel cycles such as the vertical migration of zooplankton (Ludvigsen et al., 2018; Moore et al., 2000) and fish (Mehner, 2012), thereby indirectly shaping food-web structure by influencing trophic interactions. However, since the widespread use of electric light, the night-time irradiance has rapidly increased (Falchi et al., 2016; Kyba et al., 2023, 2015). In addition to direct irradiation, artificial light propagating into the night sky can be scattered back to Earth by clouds and aerosols to reach remote areas far away from the

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original light source, which previously were thought to be unaffected by light pollution (Kyba and Hölker, 2013). This physical phenomenon, called artificial skyglow, spreads light over tens of kilometres from its sources (Falchi et al., 2016; Kyba et al., 2015). Although light intensities of skyglow are low, typically well below the level of moonlight, the highest levels measured can directly affect cyanobacteria (Poulin et al., 2014) and potentially entire ecosystems.

Bacteria are central to the functioning of ecosystems. They process large amounts of carbon globally, although their contributions vary among ecosystems depending on environmental characteristics and bacterial community structure (Drake et al., 2018; Thompson et al., 2017). The latter depends on the life strategy and capacity of bacteria to exploit resources in the environment. Cyanobacteria and aerobic anoxygenic phototrophic bacteria use light as a source of energy (Piwosz et al., 2020), whereas most heterotrophic microbes rely on organic carbon, some of which is released by phytoplankton during photosynthesis and thus directly depends on light availability as well (García et al., 2018). Heterotrophic bacteria either live freely in the water column or they are attached to particles, such as algal aggregates or zooplankton, releasing enzymes to degrade large molecules and assimilating small dissolved compounds (Grossart et al., 2010; Simon et al., 2002). Thus, artificial skyglow could act as a new selection pressure that can alter bacterial resources and communities, how and when bacteria transform organic matter, and thus ecosystem functioning. However, such hypothetical consequences of skyglow on bacteria remain untested.

Here, we performed the largest study to date evaluating the consequences of skyglow on aquatic ecosystems. We used large-scale enclosures to expose natural lake water and its plankton community to two levels of skyglow and one control with no additional light for one month. We investigated the consequences of skyglow on the community composition and activity of free-living and particle-attached bacteria by targeting both 16S rRNA genes (DNA based) and 16S rRNA transcripts (RNA based). We assessed whether any effects of skyglow occur solely at night by periodically sampling the bacterial communities both at night and during the day. Then we investigated whether any effects of skyglow on bacteria have repercussions for organic matter transformations by examining changes in the ecosystem metabolome, which we define as the pool of dissolved organic matter (DOM) resolved at the level of molecular formula (Danczak et al., 2020; Fonvielle et al., 2021). Overall, our results revealed that skyglow alters the structure and function of bacterial communities as indicated by changes in the ecosystem metabolome.

2. Materials and methods

2.1. Experimental design

The experiment was performed from the 25th of August to the 21st of September 2016 in a large enclosure facility (www.lake-lab.de) deployed in Lake Stechlin. The lake is located in a forested area approx. 80 km north of Berlin (Germany) and experiences a near-naturally dark sky (6 mlx) (Jechow et al., 2016) almost free of artificial skyglow. To simulate skyglow experimentally, we used a double-ring system with LEDs (VarioLED Flex NIKE LD4 827 SV, LEDlinear GmbH, Neukirchen-Vluyn, Germany) embedded in a silicone matrix that was specifically designed to produce diffuse lighting at low levels. The LEDs produced warm-white spectra similar to those used for street lighting at a correlated colour temperature of 2700K. Full details about the light source, including the horizontal and vertical distribution of illuminance inside the enclosures, are presented in Jechow et al. (2021). We applied three light levels: low skyglow (0.06 lx artificial illuminance), which was selected based on current light pollution levels (Falchi et al., 2016), high skyglow (6 lx) reflecting peak skyglow illuminance in the vicinity of megacities (Pun et al., 2014), and control conditions (no increase in illuminance). Illuminance levels higher than 1 lx have been measured in Berlin (Jechow et al., 2020) and 6 lx correspond to the highest skyglow reported to date, in Hong Kong (Pun et al., 2014), both during overcast conditions. Thus, although the high skyglow level represents current extreme values, high skyglow is likely to be encountered more frequently as light pollution keeps rising (Kyba et al., 2023). Since organisms sense light on a logarithmic scale (Hölker et al., 2023), the low skyglow level of 0.06 lx sits halfway between the 6 mlx of starlight in the control and the 6 lx of the high skyglow treatment. We installed the same double-ring structure atop all enclosures, including controls, to prevent shadowing or other effects induced by the structure from masking or enhancing any potential skyglow effects (Jechow et al., 2021).

Prior to the experiment, we prepared five large-scale enclosures per experimental condition as previously described (Fonvielle et al., 2021). The enclosures, 15 in total, were 9 m in diameter and had an average depth of 18.4 m (SD = 1.4 m). The epilimnion of the enclosures was sampled at midday (D) and at the end of the night (N) after the first, third and fifth week after setting up the experiment. During the first week of the experiment, no additional lighting was provided on any enclosure. Lights were switched on during the second week, three nights before sampling started. At each sampling occasion, we took integrated water samples of the whole mixed layer comprising the top 7–8 m of the water column, removed large organisms by passing the water through a 280 μm mesh screen in a funnel filter and collected the water in acid-washed 5 L glass bottles. Bottles were protected from direct sunlight during the day and brought to the laboratory within less than an hour for further sample processing and analyses.

2.2. Microbial community composition

One litre of sampled water was filtered onto 5 μm pore size polycarbonate filters (Whatman Nuclepore, Cityva, Marlborough, MA, USA) and the remaining filtrate was passed through 0.2 μm filter units (Sterivex, Merck Millipore, Burlington, MA, USA). Bacteria retained on 5 μm filters were considered to be particle-associated while bacteria retained on the 0.2 μm filters were considered to be free-living. Filters were flash-frozen in liquid nitrogen and stored at -80 °C prior to DNA and RNA extraction. The particle-associated fraction sampled at night at the last sampling date was accidentally lost. DNA and RNA from both size fractions were extracted following a modified version of an established protocol (Nercessian et al., 2005). Briefly, filters were disrupted using a FastPrep-24 5G Bead Beater (MP Biomedicals, Irvine, CA, USA) with zirconium (0.1 and 0.7 mm diameter) and glass (3 mm diameter) beads after the addition of 0.6 mL of 10% (w/v) CTAB (cetyltrimethylammonium bromide) buffer, 60 μL of 10% (w/v) SDS (sodium dodecyl sulphate), 60 μL of 10% (w/v) N-lauroylsarcosin and 0.6 mL of phenol-chloroform-isoamyl alcohol (25:24:1, v:v:v). Samples were further washed with one volume of chloroform-isoamyl alcohol (24:1, v:v) and nucleic acids were precipitated overnight at 4 °C following the addition of two volumes of 1.6 M NaCl in 30% (w:v) polyethylene-glycol. Pellets were washed with ice-cold 70% ethanol. The ethanol was removed by drying and the dried nucleic acids were dissolved in 50 μL of ultrapure water. A 25 μL aliquot was taken from each sample and stored at -80 °C for later DNA sequencing.

The remaining volume was used to obtain RNA by removing DNA with Turbo DNase (Ambion, Austin, TX, USA), following the manufacturer's specifications. We checked the DNA removal on a 1% polyacrylamide gel loaded with the products of polymerase chain reaction (PCR; 30 cycles, using the same primers described below). When DNA removal was not successful, we performed another digestion cycle with the Turbo DNase. DNA-free samples were stored at -80 °C for up to one month prior to conversion into cDNA with the SuperScript IV kit (Invitrogen, Waltham, MA, USA) following the manufacturer's instructions. Amplicons containing 5′ adapters, suitable for subsequent barcoding, were prepared in-house from cDNA and DNA samples using the primers: 5′-TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGCCTACGGGNGGC WGCAG and 5′-GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGGA CTACHVGGGTATCTAATCC. PCR products were purified using the

GeneRead Size Selection Kit (Qiagen, Hilden, Germany) and quantified by fluorometry (Quantus, Promega, Fitchburg, WI, USA). Barcoding of amplicons, Illumina Miseq sequencing and V3 chemistry were performed at G2L (Göttingen, Germany) and resulted in a total of approx. 20 million reads. All adaptors were removed after sequencing by using cutadapt (Martin, 2011) and amplicon sequence variants (ASV) were retrieved using the DADA2 pipeline (Callahan et al., 2016). Error rates within the DADA2 pipelines were learned from a subset of 1 million reads. A total of 17,387 chimeras were removed from the dataset. We obtained a total of 9186 ASVs to which we assigned taxa using a naïve Bayesian classifier and a training set from the SILVA database (Quast et al., 2013). We removed all ASVs that did not belong to the bacteria domain, which reduced the total number of ASVs to 8857. The final dataset resulted in an average total read count per sample of 11,621 (SD=6701; Fig S2). Two samples with less than 1000 reads were not included in further analyses. Sequences are available from the EBI/ENA database (https://www.ebi.ac.uk/services/dna-rna) under accession number PRJEB79348.

We computed the beta nearest taxon index (βNTI) to test whether skyglow influences microbial communities (Dini-Andreote et al., 2015; Stegen et al., 2012). We aligned sequences using the profile-to-profile approach implemented in the DECIPHER package (Wright, 2015) with a guide tree inferred from distances between shared k-mers. We computed an unrooted phylogenetic tree using the Randomized Accelerated Maximum Likelihood algorithm (Stamatakis, 2014). We retrieved the patristic distances (i.e., the distance between two ASVs in a phylogenetic tree) from the generated phylogenetic tree and computed the mean nearest taxon distance (MNTD) and the nearest taxon index (NTI) as described in Webb et al. (2002). The MNTD is a taxonomy-based metric indicative of how closely species are related within one sample. The NTI is computed using a randomly generated MNTD and the observed MNTD from one sample (Fine and Kembel, 2011). Furthermore, we computed the between-samples equivalent of MNTD and NTI (i.e., βMNTD and βNTI) to infer whether skyglow structured microbial communities in a stochastic or deterministic way (Dini-Andreote et al., 2015; Stegen et al., 2012). βNTI was retrieved by comparing the structure of the communities at the first sampling occasion before the light was switched on to those at all later sampling days. We used Wilcoxon's test to evaluate whether skyglow affected βNTI at a given sampling occasion and a linear model with skyglow as a factor with three levels to test whether skyglow affected βNTI over time.

2.3. Microbial cell counts

We fixed 10 mL of water with 25% glutaraldehyde (1% final concentration) within 1 hour of sampling, let the fixative act for 30 min at 4 °C, and then flash-froze the sample in liquid nitrogen before storing it at -80 °C. Within six weeks, we thawed the samples and used 1-mL aliquots to stain bacteria with SYBR Green I (Invitrogen, Waltham, MA, USA) at a 10,000 times dilution from the stock solution. The samples were stained for 15 min in the dark and immediately processed on a flow cytometer (Accuri™ C6; BD, Franklin Lakes, NJ, USA). Bacterial cells were counted at a flow rate of 35 μL min^{-1} until 50 μL had passed through the flow cytometer. When too many particles were detected by the flow cytometer, we prepared a new aliquot diluted with filtered (0.2 μm) mineral water to obtain a maximal concentration of 2×10^5 cells mL^{-1} before reanalysing the sample. All samples were analysed in triplicate, with a blank consisting of filtered (0.2 μm pore size membrane) mineral water processed after every fifth sample. Because all samples were from the same lake, we used the blank samples to design one gate that we applied to all samples. We calculated net growth rates as differences between cell abundances divided by elapsed time.

2.4. Ecosystem metabolome

One litre of water was passed through a pre-combusted (4 h at 450 °C) glass fibre filter (GF75, Advantec, Tokyo, Japan). We collected the filtrate in pre-combusted glass bottles, acidified the sample to a pH of 2 using 37% HCl, and within two days, we concentrated organic matter using solid phase extraction (SPE; Dittmar et al., 2008) on an Autotrace 280 (Dionex, Sunnyvale, CA, USA) automated SPE system. The resulting methanol extracts were stored at -20 °C for five months before being processed on a 15T SolariX XR FT-ICR-MS (Bruker, Ettlingen, Germany) using the same settings as previously described (Fonvielle et al., 2021). Briefly, samples were injected at a dissolved organic carbon concentration of 2.5 mg L^{-1} in 50:50 methanol:water solution. We collected 250 scans per measurement. Each sample was analysed twice on the FT-ICR-MS, and the performance of the mass spectrometer was assessed daily using an in-house deep-sea reference sample. We assigned molecular formulae using the online tool ICBM-OCEAN (Merder et al., 2020). Briefly, we used a method detection limit of 2.5, recalibrated the spectra using generalised additive models, and allowed all combinations within $C_{1–100}H_{2–200}O_{0–70}N_{0–4}S_{0–2}P_{0–1}$ with the NSP rule before exporting the molecular formulae corresponding to the likeliest match. Then, we further filtered the data and removed 1) formulae for which the absolute difference between the number of double-bound equivalents and oxygen atoms was lower than 10 (Herzsprung et al., 2014); 2) formulae that had less than one oxygen atom; and 3) formulae that contained either a nitrogen, phosphorus, or sulphur atom without CH_2 homologous series confirmation (Koch et al., 2007). To test if skyglow increased or reduced differences in the metabolome, we computed Bray-Curtis dissimilarities between each metabolome and all control metabolomes sampled on the same date and time (5 comparisons per enclosure). We averaged the Bray-Curtis dissimilarities to obtain one value representing the average dissimilarity between one enclosure and all five control enclosures. We compared each control to the four other control enclosures sampled on the same date and time.

2.5. Statistical analyses

We performed PERMAOVAs using the function *adonis2* of the *vegan* package in *R* with 1000 permutations and Bray-Curtis dissimilarities to assess skyglow effects on overall microbial community composition. We performed a total of eight PERMANOVAs, one each for the DNA and RNA data for both the free-living and particle-attached fraction collected both during daytime and at night. All PERMANOVA models included skyglow and sampling week as well as the interaction between skyglow and sampling week. We performed the PERMANOVAs on both centre-log-ratio-transformed data (obtained using the *clr* function from the *compositions* package in *R* (van den Boogaart and Tolosana-Delgado, 2008)) and on relative abundance data (obtained using the *decostand* function of the *vegan* package). The data transformations did not affect the outcome of the significance tests for skyglow. To visualise differences among samples, we also performed a principal coordinate analysis (PCoA) using the *prcomp* function of *R* on centre-log-ratio-transformed data (Gloor et al., 2017). We performed the same number of PCoAs as for the PERMANOVAs.

We fitted negative binomial generalised linear models to read counts using the *DESeq2* package (Love et al., 2014) to identify bacteria that were either promoted or suppressed by skyglow. Briefly, we first removed all ASVs that had less than 100 reads across the entire dataset to avoid model overfitting and to reduce the risk of identifying false positives. Then, the remaining read counts were normalised using the median of the ratio, which accounts for differences in sequencing depth (Anders and Huber, 2010), as implemented in the *DESeq2* pipeline. The *DESeq2* model contained only skyglow as explanatory variable, set as a factor with three levels. We considered the abundance of an ASV to be significantly affected by skyglow if the Benjamini-Hochberg corrected p-value (Benjamini and Hochberg, 1995) was lower than 0.01, thereby reducing the risk of false positives. We then used ternary plots to visualise the distribution of bacterial families between the three experimental conditions using the *ternary* package in *R* (Smith, 2017). For

graphical purposes only, we summed all read numbers within each skyglow treatment across all five replicate enclosures sampled during the day and at night and across the two sampling occasions when skyglow was applied. Next, we computed the average relative abundance of each family to show them on the ternary plots.

Similar to the analysis of the genomic data, we tested for effects of skyglow on the ecosystem metabolome using the *adonis2* function and Bray-Curtis dissimilarities, with the permutations constrained by the processing day on the FT-ICR-MS. We performed one PERMANOVA for data collected during the day and one for data collected at night. All PERMANOVA models included skyglow and sampling week as well as the interaction between skyglow and sampling week. Next, we identified compounds affected by skyglow using linear mixed effect models (Pinheiro et al., 2017). Specifically, we modelled the FT-ICR-MS signal intensities (normalised to total signal intensity per sample) of each molecular formula as a function of skyglow and Day/Night (ignoring the sampling point before exposing enclosures to skyglow) and with processing day on the FT-ICR-MS as a random effect. Including processing day in the PERMANOVAs and linear mixed effects models only accounts for shifts in total ion current over the time period required to process all samples on the FT-ICR-MS (i.e. 7 days).

We investigated whether skyglow altered bacteria-bacteria interactions using network analysis. First, we computed co-occurrence networks using the SPIEC-EASI pipeline (Kurtz et al., 2015). We centre-log-ratio-transformed raw reads from the skyglow and control enclosures to account for the compositional nature of the data. Unlike other network approaches, SPIEC-EASI uses conditional independence rather than correlation coefficients, which results in sparse networks, greatly reduces the risk of considering false bacteria-bacteria interactions, and improves robustness to variation in sample size (Kurtz et al., 2015). We used the neighbourhood selection algorithm to infer conditional independence and validated the structure of the network using the stability approach for regularisation selection (Liu et al., 2010). Based on 16S rRNA transcripts, we computed a total of five networks, one each for day and night and the three levels of skyglow used in this study. To reduce the risk of including interactions between bacteria occurring in only a few enclosures, we computed networks containing only ASVs with read counts greater than 100 across the entire dataset. We visualised the networks in Cytoscape (Shannon et al., 2003) and subsequently retrieved the closeness centrality (number of interactions) of each ASV (Doncheva et al., 2012).

All statistical analyses were performed in *R* (R Core Team, 2018). We used the functions *lm* for all linear models and always used skyglow as a factor with three levels. We used the function *wilcox.test* for all Wilcoxon tests for pairwise comparisons and the function *cor.test* to calculate all Spearman correlations. We used the *R* package *vegan* (Oksanen et al., 2013b) to compute all Shannon diversity indexes, *DESeq2* (Love et al., 2014) to perform DESeq2 analyses, and *igraph* (Csardi and Nepusz, 2006) to compute networks.

3. Results and discussion

3.1. Skyglow effects on bacterial community composition

Skyglow resulted in bacterial communities enriched with free-living cyanobacteria and aerobic anoxygenic phototrophs, thus significantly affecting the community composition of free-living bacteria at the RNA and, to a lesser extent, at the DNA level (PERMANOVA, $p<0.05$; Figs. S1, S2). Experimental skyglow significantly (DESeq2, $p<0.01$) affected 65 and 50 amplicon sequence variants (ASV) of free-living bacteria at the DNA and RNA level, respectively. The effect size ranged from an average (SD) of 0.06 (0.03) to 32 (22) and 0.04 (0.02) to 5.4 (2.4) times more reads in skyglow conditions at the DNA and RNA level, respectively (Fig. 1). Although DESeq2 normalises the data before evaluating differences among skyglow conditions, the reported log2-fold change (Fig. 1) refers to the original read counts, which do not necessarily reflect absolute bacterial numbers because of biases with amplicon sequencing (Props et al., 2017). ASVs of free-living bacteria affected by skyglow represented 4.4% and 2.9% of the respective reads obtained at the DNA and RNA level. Free-living bacteria that became more abundant were cyanobacteria (*Synechococcus* sp., *Dolichospermum* sp., *Gleocapsa* sp.), Acidobacteria (*Blastocatella* sp.), aerobic anoxygenic phototrophic

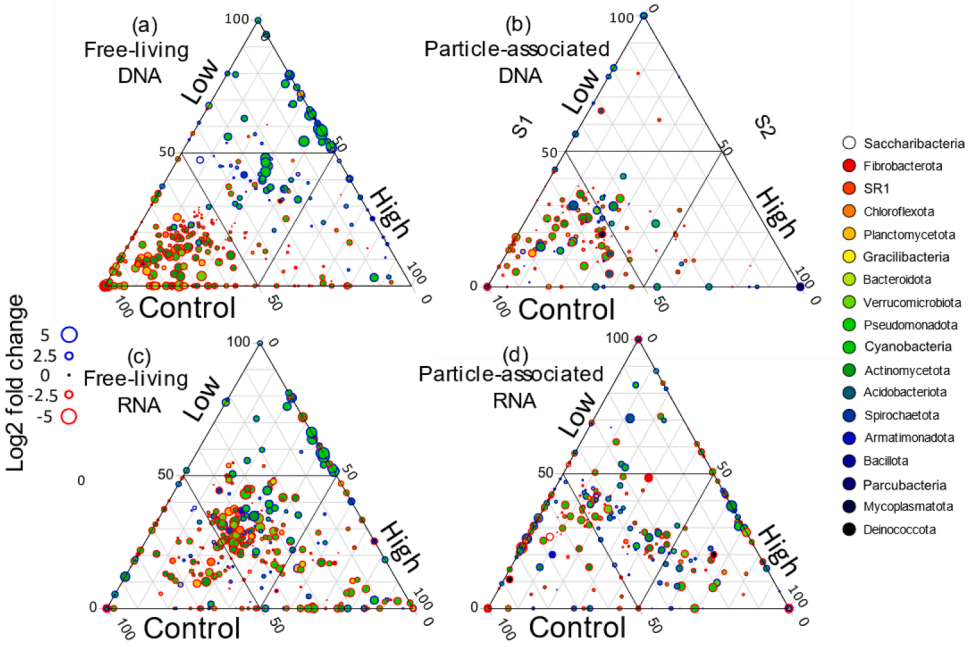

Fig. 1. Effects of skyglow on the abundance of free-living (a,c) and particle-associated (b,d) bacteria.
Ternary plots showing changes in read counts of free-living (a, c) and particle-associated (b, d) bacteria evaluated at the DNA (a, b) and RNA (c, d) level. Each dot represents one amplicon sequence variant (ASV) and its position represents its relative abundance within the three skyglow levels. Colour code for phyla (symbol filling) and log2-fold change (symbol border) denotes control and high skyglow conditions. The colour gradient for phyla reflects the phylogenetic distance between phyla with greater contrasts indicating phylogenetically more distant phyla. Control = no illumination; low = 0.06 lx; high = 6 lx.

Pseudomonata (*Sphingorhabdus* sp., *Sphingomonas* sp.) and other Pseudomonadota (*Methylobacterium* sp., *Bdellovibrio* sp., *Caulobacter* sp., *Reyranella* sp., *Afipia* sp.). The same taxa were affected by skyglow in the DNA and in the RNA fraction.

Flow cytometry showed that skyglow increased the quantity of free-living bacteria, especially during the day (Fig. S4). Skyglow significantly increased the growth rates of free-living bacteria during the day by up to an average (SD) of 1.90 (0.02) and 2.99 (0.06) times compared to the control for the low and high skyglow conditions, respectively (Fig. S4). These results indicate that the higher abundance of free-living cyanobacteria and anaerobic anoxygenic phototrophs observed at the DNA and RNA level was associated with a higher bacterial abundance in general. The community composition of particle-associated bacteria was not significantly affected by skyglow (PERMANOVA, $p>0.05$, Fig. S1, S2). However, the abundance of 58 (DNA level) and 47 (RNA level) ASVs significantly (DESeq2, $p<0.001$) differed under skyglow (Fig. 1). The effect size ranged from an average (SD) of 0.12 (0.02) to 7.0 (4.8) and 0.05 (0.03) to 21.9 (7.2) times more reads in skyglow conditions at the DNA and RNA level, respectively. Particle-associated ASVs affected by skyglow belonged primarily to Cyanobacteria and Pseudomonadota. ASVs affected by skyglow represented 27.6% and 5.2% of all particle-associated reads obtained at the DNA and RNA level, respectively. Overall, our results revealed a strong effect of experimental skyglow on free-living bacteria, even at low irradiances, but much less so on particle-associated bacterial communities.

The higher abundance of cyanobacteria and aerobic anoxygenic phototrophs in the presence of skyglow appears to be related to their capacity to harvest light energy. Both are capable of growing under low light conditions, facilitated by their ability to absorb light in the far-red wavelength range (Gisriel et al., 2020; Nowack et al., 2015). The stimulation of these phototrophs in our experiment is consistent with increases observed in the relative abundance of phototrophs following exposure to artificial light at night reported, for example, for cyanobacteria in sediments of a ditch exposed to ~8 lx of experimental light pollution (Hölker et al., 2015). Most studies assessing effects of light pollution, however, addressed effects at relatively high light levels (Gaston et al., 2014; Sanders et al., 2021). The lowest level of skyglow previously tested in studies on phototrophs was ~4 lx (Segrestin et al., 2021), contrasting with the lower level of 0.06 lx in our experiment. It is notable that such a low illuminance still triggered significant changes in microbial communities (Fig. 1), although even the highest level of light pollution tested in our study (6 lx) has been found insufficient to stimulate photosynthesis (Poulin et al., 2014).

3.2. Skyglow effects on the ecosystem metabolome

To assess how skyglow affected microbial activities, we characterised the ecosystem metabolome comprising all extracellular metabolites and their abiotic transformation products (Danczak et al., 2020; Fonvielle et al., 2021; Tanentzap and Fonvielle, 2024).

However, like for amplicon sequences, the abundance of each metabolite is not necessarily related to its absolute quantity (Zark and Dittmar, 2018). Ultra-high-resolution mass spectrometry identified a total of 2077 unique molecular formulae, each of which represents at least one metabolite (Zark and Dittmar, 2018). Skyglow altered the composition of the ecosystem metabolome (PERMANOVA, Fig. S5), especially at night (Fig. S5). Overall, skyglow increased differences between metabolomes (Fig. 2a, b) and affected the abundance of 13% of the 2077 identified metabolites (Fig. 2c, d), with effects differing depending on the sampling date (Fig. 2).

Subsequent linear mixed effect models to follow the dynamics of each metabolite (at the level of molecular formulae) identified

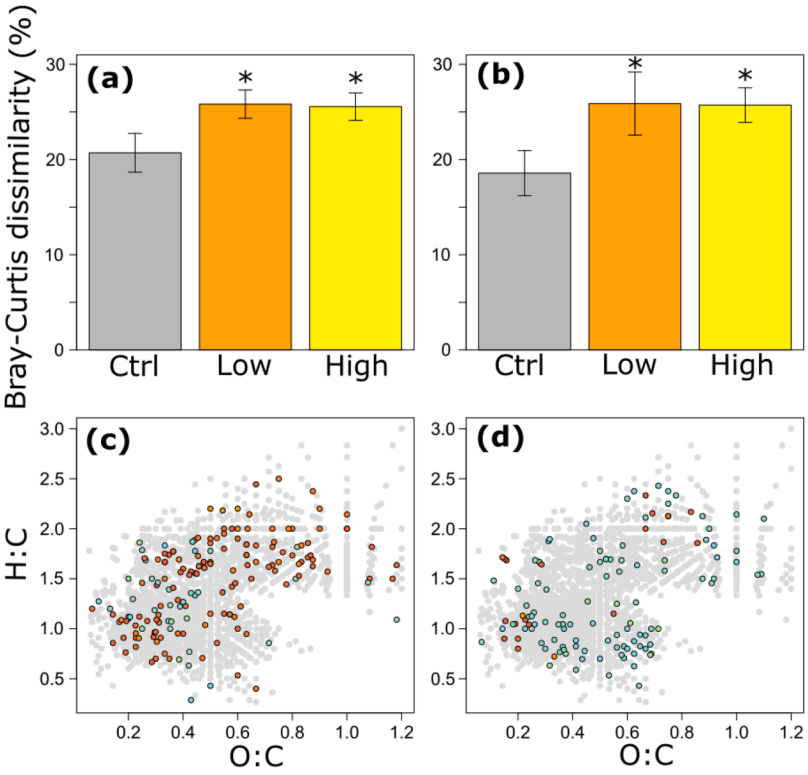

Fig. 2. Skyglow effects on the ecosystem metabolome of Lake Stechlin.
Average pairwise Bray-Curtis dissimilarities among ecosystem metabolomes of control (ctrl) enclosures and enclosures exposed to either 0.06 lux (low level) or 6 (high level) of artificial skyglow for **(a)** two or **(b)** four weeks. All metabolomes were compared to all control metabolomes obtained at the same sampling date. Errors bars are standard errors (N = 5). Asterisks indicate significant differences (general linear model, $p<0.05$) between the control and either level of skyglow. Van Krevelen plots showing significantly affected metabolites after **(c)** two and **(d)** four weeks of skyglow exposure. Red and blue dots indicate metabolites that significantly (linear mixed effects model, $p<0.05$) increased or decreased in abundance under skyglow, respectively. Grey dots indicate unaffected metabolites.

compounds affected by skyglow. Two weeks of exposure to experimental skyglow significantly increased the abundance of 136 metabolites and decreased the abundance of 41 metabolites compared to the control enclosures (Fig. 2c; linear mixed effect model, $p<0.05$). After four weeks, skyglow had significantly increased the abundance of 22 metabolites and decreased the abundance of 102 metabolites (Fig. 2d; linear mixed effect model, $p<0.05$). The molecular formulae of the 22 metabolites that increased in abundance differed from those of the 136 metabolites that had increased in abundance already after two weeks. Most metabolites increasing in abundance after two or four weeks of exposure to skyglow (89 of 158) had a H/C ratio greater than 1.5 (Fig. 2c, d) and were hence classified as bioavailable (D'Andrilli et al., 2015). These metabolites also had a molecular signature akin to that of algal-derived metabolites (Fonvielle et al., 2021; Zhang et al., 2014), indicating that skyglow affected primary producers.

Several compounds with an H:C ratio greater than 2 contained nitrogen as a heteroatom and were probably aliphatic amino sugars, which have previously been found to be common in Lake Stechlin (Fonvielle et al., 2021). The remaining 69 metabolites increasing in abundance with skyglow generally had an O:C ratio lower than 0.5 and often (23 of 69) contained nitrogen atoms as well (Fig. 2). Those metabolites are usually associated with by-products of microbial metabolism (Kim et al., 2006; Mostovaya et al., 2017) or the degradation of large polymers by fungi (Echavarri-Bravo et al., 2019), indicating that skyglow also impacted heterotrophic activities. Notably, most metabolites decreasing in abundance after four weeks of exposure to skyglow (61 of 102) corresponded to metabolites produced within the first two weeks of the experiment (Fig. 2). Other metabolites decreasing in abundance with skyglow represent plant-derived metabolites that show a high reactivity in aquatic environments (Mostovaya et al., 2017). Overall, our ecosystem metabolome analysis supports the conclusion that skyglow increases activities of primary producers with potential repercussions on heterotrophic microbes.

The dynamics of the ecosystem metabolome we observed in response to skyglow exposure suggests different effects at the end of the experiment in early autumn when solar radiation and chlorophyll-*a* concentrations had declined (ρ=-0.25, p=0.030 and, ρ=-0.31, p=0.007, respectively). Chlorophyll-*a* concentrations were higher two weeks after the start of the experiment (Fig. S6), when the abundance of both algal-derived metabolites (Fig. 2) and anoxygenic aerobic and cyanobacteria had been most increased by skyglow (Fig. S8). These results indicate that skyglow acted on a smaller number of phototrophs towards the end of the experiment, which could partly explain the observed temporal variation in skyglow effects.

Our ecosystem metabolome data also show that skyglow failed to stimulate photosynthesis. Otherwise, the proportion of algal-derived metabolites in the presence of skyglow should have been higher at the end of the experiment, when nights and hence skyglow exposure were longer than in the dark control enclosures. An alternative mechanism by which skyglow could have affected primary producers is through effects on their circadian rhythm (Noordally and Millar, 2015). Although information on genes responsible for diel changes in algal and bacterial physiology are sparse (Noordally and Millar, 2015; Ottesen et al., 2014), our ecosystem metabolome analyses of samples taken during the day and at night can track diel patterns. Accordingly, skyglow significantly reduced the number of metabolites affected by diel variation, by 65% and 53%, respectively, for the low and high skyglow treatment (Fig. S9; linear mixed effect models, $p<0.05$). Compounds showing different diel patterns in the presence of skyglow were associated with algal metabolites (Zhang et al., 2014) (Fig. S9), suggesting that skyglow interfered with the circadian rhythm of primary producers. Cyanobacteria regulate gene expression with a circadian cycle that is finely tuned to fit day-length duration (Golden and Canales, 2003; Ottesen et al., 2014). Although the circadian cycle of cyanobacteria is primarily regulated by ATP production (Rust et al., 2011) and, therefore, driven by photosynthesis, other regulatory pathways not linked to photosynthesis also exist (Ivleva et al., 2005; Katayama et al., 2003). The latter are particularly important at low irradiance levels (Katayama et al., 2003), suggesting that these pathways are particularly susceptible to mediating skyglow effects on lake primary producers. Further studies explicitly focussing on biochemical and physiological processes affected by skyglow are needed to explore this hypothesis.

We also found evidence that skyglow effects on primary producers has repercussions on heterotrophs. Although it is challenging to track the production and use of bioavailable metabolites in situ because these compounds tend to be rapidly consumed (Patriarca et al., 2021), we could identify metabolites that were produced or consumed under skyglow (Fig. 2). This suggest that skyglow-induced increases in the abundance and activity of primary producers can indirectly affect heterotrophic microbial communities and organic matter transformations as well (Sanders et al., 2021). This conclusion is further supported by our observation that the potential activity of leucine-aminopeptidase, which can break down peptides typically produced by algae, peaked two weeks after the start of our experiment (Fig. S7). However, the leucine aminopeptidase assay we performed failed to detect differences among treatments (linear model, p=0.73), nor were significant changes in the concentration of dissolved organic carbon (DOC) under skyglow (Fig. S10), suggesting that any produced carbon was quickly turned over by the microbial community. Therefore, the quantification of specific algal or bacterial metabolites is unlikely to detect skyglow-induced changes in situ. However, incubations involving stable isotope labelling or other tagging approaches (e.g Couradeau et al., 2019) could provide deeper insights into the biochemical processes affected by skyglow. Taken together, our data provide empirical evidence that low-level light pollution affecting the activity of phototrophic bacteria can have knock-on effects on heterotrophic bacterial communities and resource use in lake ecosystems (Sanders et al., 2021).

3.3. Skyglow effects on microbial interactions

Our network analysis of 16S rRNA transcripts data using the SPIEC-EASI pipeline (Kurtz et al., 2015; Fig. S3) indicated that skyglow significantly reduced the degree of bacteria-bacteria interactions (measured as closeness centrality) in enclosures affected by skyglow (Fig. 3), for both free-living (linear model, t=-15.7, $p<0.001$ and t=-32.4, $p<0.001$ for low and high skyglow, respectively) and particle-associated (linear model, t=-34.5, $p<0.001$ and t=-37, $p<0.001$, respectively) communities. It must be borne in mind, however, that the results of our network analysis reflect co-occurrences rather than effective interactions, which precludes investigating links between two particular species. Bacteria-bacteria interactions can drive population dynamics (Gralka et al., 2020) and can be either positive, for instance by complementary enzymatic activities facilitating resource access (Ebrahimi et al., 2019), or negative as in the case of resource competition (Michalska-Smith et al., 2022). Here, we found that the percentage of negative edges in the networks established for free-living bacteria was 26, 25 and 17% for control, low skyglow, and high skyglow conditions, respectively. In the networks for particle-associated bacteria, the respective values were 18, 8 and 7%. These declines with increasing skyglow exposure could indicate that skyglow reduces competition between bacteria, which often happens when resource limitation is reduced (Ackermann and Doebeli, 2004). The higher proportion of bioavailable metabolites observed in the presence of skyglow (Fig. 2) corroborates this idea and suggests that community changes in response to skyglow (Fig. 1, S2) could reflect changes in resource availability.

According to ecological theory, temporal and spatial variation in resource supply promotes plankton diversity by enabling the coexistence of species competing for the same resources (Hutchinson, 1961; Miyazaki et al., 2006). Therefore, bacteria capable of using labile compounds are expected to assume dominance when such organic compounds are consistently abundant (Girvan et al., 2005). Support for this hypothesis comes from our observation that the Shannon diversity of the 16s rRNA

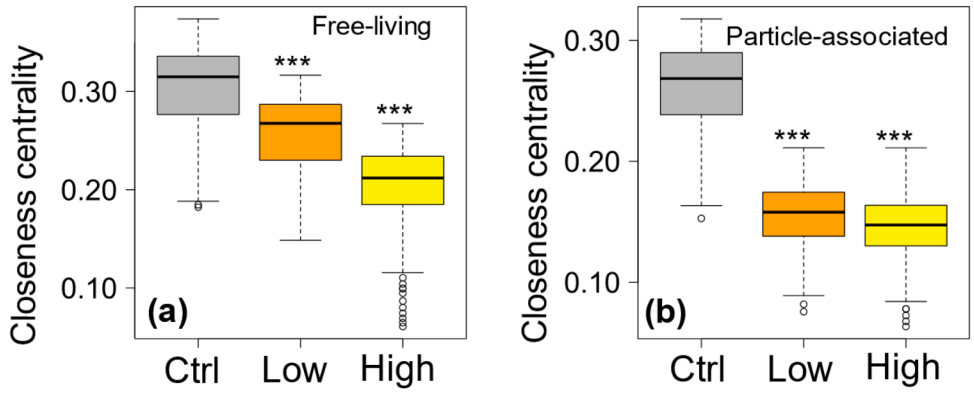

Fig. 3. Effects of skyglow on bacteria-bacteria interactions indicated by network analysis.
Boxplots representing the distribution of closeness centrality in networks based on read counts of 16S RNA transcripts of free-living **(a)** and particle-associated **(b)** bacteria. Median values (thick bars) are presented along with the 1st and 3rd quartiles (lower and upper box margins). Whiskers represent either 1.5 times the interquartile range or the maximal/minimal values if the latter is lower/higher than 1.5 times the interquartile range. Dots indicate values that are lower than 1.5 times the interquartile range. Stars indicate that skyglow significantly (linear model, $p<0.001$) affected closeness centrality. Only ASVs with more than 100 read counts of free-living (n=498) and particle-associated (n=281) bacteria were included in the analysis. Ctrl = control; low = 0.06 lx; high = 6 lx.

transcripts of free-living bacteria sampled at night was significantly affected by skyglow exposure for both the low (linear model, t=2.3, $p<0.05$) and high (t=2.9, $p<0.01$) skyglow level. A similar effect was not observed in samples collected during the day (linear model, t=-1, p=0.26 and t=-0.4, p=0.68, for low and high skyglow, respectively). Therefore, the increase in resource availability we observed and the reduction of bacterial diversity under skyglow points to the selection of a community capable of exploiting a few abundant labile organic compounds.

3.4. *Effect of skyglow on phylogenetic distance in bacterial communities*

Our comparisons of bacterial communities at the diel and biweekly time scale (Fig. 4) corroborates the notion that skyglow homogenises bacterial communities. Specifically, the between-sample nearest taxon index (βNTI) (Webb et al., 2002) we computed based on phylogenetic distances between ASVs indicates a weak homogenising effect (i.e. bacteria in the community were phylogenetically closer than expected according to the null hypothesis, βNTI<0) before exposure to skyglow (T0; Fig. 4). The latter revealed microbes in enclosures later exposed to skyglow were phylogenetically more similar to the control than expected by chance. Phylogenetic differences between free-living bacteria in skyglow and control enclosures at T0 differed between day and night, with the average βNTI being 2.1 (Wilcoxon test, W=110, p=0.001) and 3.5 (W=75, $p<0.001$) times higher at night than during the day for the low and high skyglow level, respectively (Fig. 4). The average βNTI for the particle-associated bacteria at T0 was 1.5 (W=173, p=0.002) and 0.9 (W=331, p=0.4) times higher during the night (Fig. 4). Exposure of the communities to experimental skyglow generally increased βNTI for both the free-living (linear model, t=3.0, p=0.004 and t=3.8, $p<0.001$ for low and high skyglow, respectively) and particle-associated (t=3.4, $p<0.001$ and t=4.6, $p<0.001$, respectively) bacteria sampled during the night. In samples collected during the day, βNTI for the particle-associated bacteria only increased at the high skyglow level (linear model, t=6.8, $p<0.001$; t=0.4, p=0.70 for low skyglow). Furthermore, βNTI tended to increase between the first (before skyglow exposure) and second sampling occasion (linear model, t=-2.4, p=0.02 and t=-2.7, p=0.009 for free-living bacteria exposed to low and high skyglow, respectively, and sampled during the day; otherwise non-significant), and then tended to decline or remain at a similar level (Fig. 4). Overall, our comparison of βNTI values thus indicates that skyglow effects were stronger during the night and for free-living bacteria.

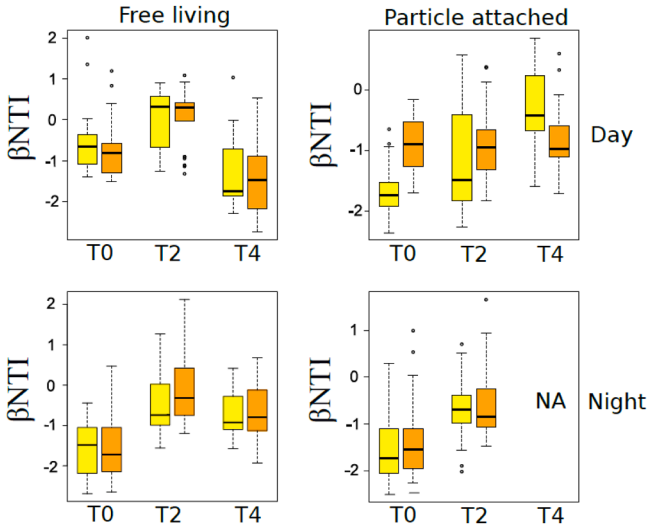

Fig. 4. Effects of skyglow on bacterial phylogenetic distance.
Boxplots showing the range of βNTI before (T0) and after two (T2) and four (T4) weeks of exposure to experimental skyglow. Median values (thick horizontal lines) are presented along with the 1st and 3rd quartiles (lower and upper box margins). Whiskers represent either 1.5 times the interquartile range or the maximal/minimal values if the latter was lower/higher than 1.5 times the interquartile range. Dots indicate values beyond 1.5 times the interquartile range. Orange and yellow boxes depict low (0.06 lx) and high (6 lx) experimental skyglow levels, respectively.

Changes in phylogenetic distance triggered by skyglow were relatively large considering the low light levels to which the communities experiencing skyglow were exposed in our experiment. For instance, the changes in βNTI we observed in response to skyglow (Fig. 4) were similar to changes in βNTI between successional stages of soil microbial communities over several decades (Tripathi et al., 2018) or almost one pH unit (Tripathi et al., 2018). The magnitude of the skyglow effect on phylogenetic community composition was similar for the two levels of skyglow tested. This outcome underlines that skyglow can affect bacterial communities at even extremely low light levels, even though effects on diel variation in microbial activity (Fig. 2) and bacteria-bacteria interactions (Fig. 3) were greater at the high skyglow level (6 lx) in our experiment.

3.5. Caveats

Several caveats need to be addressed to put the results of our experiment in perspective. The large enclosures and low levels of light pollution we used ensured a high degree of realism of the experimental conditions. However, since the duration of our experiment was limited to a period of four weeks in late summer, caution is needed when extrapolating results to other times of the year, other years or other lakes when and where plankton communities and environmental conditions differ from those encountered during the experiment. Not only do plankton communities vary among lakes, they also undergo pronounced, well-characterised seasonal successions (Sommer et al., 2012). Furthermore, in temperate and northern latitudes, where most of the world's lakes are located (Messager et al., 2016), nights are considerably shorter in late spring and early summer, when phytoplankton development is particularly dynamic. This implies that skyglow effects could be weakened during those times of the year. Such seasonal variation is further superimposed by varying weather conditions, including cloud cover, and lunar cycles, which both have strong repercussions on skyglow intensities (Hölker et al. 2023). Given the resultant uncertainties, the insights from our short-term experiment are also insufficient to infer long-term consequences of skyglow on lakes. A combination of comparative field investigations, long-term monitoring, repeated large-scale field experiments, and mechanistic studies in controlled environments will have to show whether skyglow effects grow over time or are reversible, and to what extent our observations can be generalised to other times and locations.

4. Conclusion

The experimental results presented here provide evidence that skyglow can affect the structure of lake microbial communities and ecosystem metabolomes. The observed effects are remarkable in view of the low levels of skyglow we applied to mimic realistic conditions for and beyond metropolitan areas (Falchi et al., 2016; Pun et al., 2014). Our result suggesting that increasing levels of light pollution by skyglow may increase the abundance of cyanobacteria and anoxygenic aerobic phototrophs could have significant consequences for lake ecosystems, even though extrapolation of our results is not straightforward. Light pollution has increased by as much as 10% per year over the last decade (Kyba et al., 2023). In this light, our results imply that a growing number of lakes may experience increases in cyanobacteria abundance as a consequence of skyglow alone, potentially aggravating risks of harmful algal blooms.

Similarly, in instances where lake phytoplankton, particularly cyanobacteria, have been found to increase in abundance for no obvious reason (Paltsev and Creed, 2022), artificial skyglow must be considered as one potential cause, since light is such an important factor shaping plankton communities (Karlsson et al., 2009; Litchman and Klausmeier, 2001). Given that light pollution can be tracked by remote sensing (Linares Arroyo et al., 2024), coverage of large spatial scales could be achieved with reasonable effort in monitoring programmes focussing on light pollution and its effects on lakes. The data collected in such programmes could prove beneficial beyond the early detection of harmful algal blooms, as suggested by evidence from our experiment that heterotrophic bacterial communities and ecosystem metabolomes, along with cyanobacteria and anoxygenic aerobic phototrophs, are indirectly affected by skyglow as well. Further indirect effects on plankton communities and ecosystem functioning are conceivable. Notwithstanding many remaining uncertainties, this calls for implementing simple and cost-efficient measures to reduce light pollution (Hartley and Liebel, 2020; Hölker et al., 2023) and thus lower the risk of cyanobacteria blooms and other unwanted consequences to protect lake water quality.

Data availability

The DNA sequences can be downloaded from the EBI database (https://www.ebi.ac.uk/services/dna-rna) under accession number PRJEB79348. The remaining data will be available on Figshare.

CRediT authorship contribution statement

Jeremy Fonvielle: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Lukas Thuile Bistarelli:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Yile Tao:** Writing – review & editing, Methodology, Investigation, Data curation. **Jason N. Woodhouse:** Writing – review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Tom Shatwell:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Luis A. Villalba:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Stella A. Berger:** Writing – review & editing, Conceptualization. **Christopher C.M. Kyba:** Writing – review & editing, Methodology, Conceptualization. **Jens C. Nejstgaard:** Writing – review & editing, Conceptualization. **Andreas Jechow:** Writing – review & editing, Methodology, Conceptualization. **Franziska Kupprat:** Writing – review & editing, Conceptualization. **Susanne Stephan:** Writing – review & editing, Conceptualization. **Tim J.W. Walles:** Conceptualization. **Sabine Wollrab:** Writing – review & editing, Conceptualization. **Franz Hölker:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Thorsten Dittmar:** Writing – review & editing, Validation, Resources, Methodology. **Mark O. Gessner:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Gabriel A. Singer:** Writing – review & editing, Validation, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Hans-Peter Grossart:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization.

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2025.123315.

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