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Light-dominated selection shaping filamentous cyanobacterial assemblages drives odor problem in a drinking water reservoir

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Filamentous cyanobacteria have substantial niche overlap, and the causal mechanism behind their succession remains unclear. This has practical significance since several filamentous genera are the main producers of the musty odorant 2-methylisoborneol (MIB), which lead to odor problems in drinking water. This study investigates the relationships between two filamentous cyanobacteria, the MIB-producing genus *Planktothrix* and the non-MIB-producing genus *Pseudanabaena*, in a drinking water reservoir. We firstly identified their niche characteristics based on a monitoring dataset, combined this information with culture experiments and developed a niche-based model to clarify these processes. The results reveal that the optimal light requirements of *Pseudanabaena* (1.56 mol m^{-2} d^{-1}) are lower than those of *Planktothrix* (3.67 mol m^{-2} d^{-1}); their light niche differentiation led to a fundamental replacement of *Planktothrix* (2013) by *Pseudanabaena* (2015) along with MIB decreases in this reservoir during 2013 and 2015. This study suggests that light is a major driving force responsible for the succession between filamentous cyanobacteria, and that subtle niche differentiation may play an important role in shaping the filamentous cyanobacterial assemblages that drives the MIB odor problems in drinking water reservoirs.

INTRODUCTION

Odor problems in source water caused by 2-methylisoborneol (MIB), a secondary metabolite of filamentous cyanobacteria in many reservoirs and lakes[1], have been a common issue in the Northern Hemisphere, and have now been moving southward[2–7]. The major MIB producers include *Oscillatoria*[8–10], *Planktothrix*[11], *Phormidium*[10], *Pseudanabaena*[12], *Lyngbya*[13] and *Planktothricoides*[14]. It should be noted that MIB yield varies among different strains[11,15–17], and some strains of the known MIB-producing species are in some cases not even able to produce MIB[8,13,18]. Nonetheless, MIB occurrences and concentrations are mainly determined by the presence and abundance of MIB-producing filamentous cyanobacteria in the aquatic environment.

Nutrients, water temperature and light are essential factors governing the growth and competition of phytoplankton. Recent studies have emphasized the importance of underwater light condition on their seasonal successions in both field investigations[19,20] and numeric models[21–23]. The cellular projected area (CPA, the two-dimensional area measurement by projecting cell shape on to a plane, as defined in[22]) has been proposed as a key indicator of cellular light harvesting potential, and the specific CPA (CPA/V, normalized CPA by cell volume) could be used to indicate the optimum light requirements for various species with different cell shapes[22,24]. For example, the bloom-forming cyanobacteria *Microcystis* with a low specific CPA requires high light intensity and hence is usually observed in surface water, particularly in the summer period, while filamentous cyanobacteria having a higher specific CPA tend to live in subsurface layers, where light intensity is usually low, but nutrient availability is high[25]. The low-irradiance-tolerating characteristics of filamentous

cyanobacteria have been verified by laboratory culture experiments[26] and field investigation[27]. The light niche differentiation between filamentous cyanobacteria and other phytoplankton enables us to model their succession based on ecological niche modeling[25,28–30]. However, little is known about the competition between different filamentous cyanobacterial genera, since they are likely to have substantial niche overlap. Therefore, it is desirable to know whether the changes in composition of filamentous cyanobacterial assemblages are deterministic (governed by niche differentiation) or stochastic (dominated by neutral theory).

QCS Reservoir is a newly constructed estuary reservoir used as the major drinking water resource for Shanghai, China. It directly imports highly turbid water from the Yangtze River, leading to underwater light conditions that favors filamentous cyanobacteria rather than *Microcystis*[7], and therefore has suffered from MIB odor problems since it was put into use in 2011. The filamentous cyanobacterium *Planktothrix* was the main MIB producer according to our previous study[7]. From 2011 to 2015, MIB concentrations showed a decreasing pattern along with the decrease of *Planktothrix* cell densities and the increase of another filamentous cyanobacterium, *Pseudanabaena*. We therefore hypothesize that their competition and succession might have great impact on MIB occurrence in this reservoir. The aim of this study is to identify the driving forces responsible for the filamentous cyanobacterial assemblages, so that it can provide scientific basis to solve the practical MIB problem in drinking water reservoirs. Accordingly, we identified their niche characteristics based on a monitoring dataset together with culture experiments, and developed a niche-based model to clarify these ecological processes.

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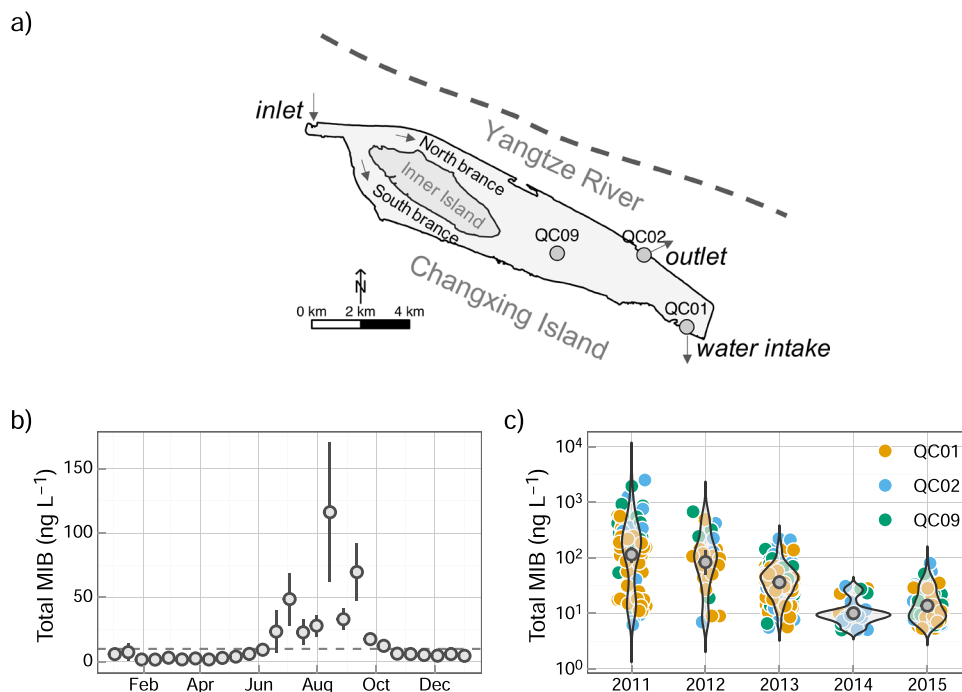
Fig. 1 Description of study sites and MIB dynamics. a Sampling sites in QCS Reservoir. **b** Seasonal dynamics of MIB concentration from 2011 to 2015. **c** Annual dynamics of MIB concentration in July to September from 2011 to 2015.

RESULTS

MIB dynamics in QCS Reservoir

MIB concentration of the river water (inlet) was rather low during the investigation (Supplementary Fig. 1). Significant seasonal variation of MIB was observed in QCS Reservoir (Fig. 1b); higher MIB concentrations (mean: 49.2 ng L^{-1}, range: 0.5–97.8 ng L^{-1}) were mainly observed during the period June to September (mean: 7.5 ng L^{-1}, range: 0.5–12.3 ng L^{-1}). The long-term development of MIB in June to September between 2011 and 2015 exhibited a significant decrease (Fig. 1c). The mean concentrations in the first year were 101.0 ng L^{-1} (range: 0.5–257.0 ng L^{-1}), equivalent to 6 times its human olfactory threshold (15 ng L^{-1},[11]), and thus aroused great attention. However, in the following 2 years the mean MIB concentrations decreased to 34.2 ng L^{-1} (range: 0.5–107.0 ng L^{-1}) and 29.4 ng L^{-1} (range: 0.5–66.4 ng L^{-1}), respectively. In 2014 and 2015, the concentrations further decreased to 6.2 ng L^{-1} (range: 0.5–15.6 ng L^{-1}).

Time series analysis of filamentous cyanobacteria

Four main filamentous cyanobacteria were recorded during the investigation in QCS Reservoir (Supplementary Fig. 2); *Planktothrix* (30.2%) and *Pseudanabaena* (30.5%) exhibited higher occurrence frequencies than *Phormidium* (14.9%) and *Lyngbya* (2.5%). *Lyngbya* was only observed for eight samples, so it was not possible to identify the seasonality. *Planktothrix* ($n = 175$), *Pseudanabaena* ($n = 168$) and *Phormidium* ($n = 88$) were mainly observed during May to October (Supplementary Fig. 3). *Planktothrix* was identified as the MIB producer in QCS Reservoir according to our previous study[7]. *Microcystis* dominated during August and September, which could affect the growth of filamentous cyanobacteria (Supplementary Fig. 3). Therefore, *Pseudanabaena* was considered as the most important competitor to *Planktothrix* based on their seasonal distribution patterns (Supplementary Fig. 3) and their habitats.

20.5% of the variances of *Planktothrix* cell density could be explained by seasonal and long-term trend terms using the GAM model (Eq. (4), Supplementary Table 7, Supplementary Fig. 5). The model suggested that the variance of *Planktothrix* was dominated by strong seasonality ($p < 0.0001$, Fig. 2a). During the investigation, no *Planktothrix* were detected in February, March and April; the earliest record of *Planktothrix* was in May, with the mean density of 6.79×10^4 cell L^{-1} (0–2.04×10^5 cell L^{-1}, 10–90% quantile, same hereinafter); the density increased in the following 3 months until late August, with a maximum of 1.01×10^6 cell L^{-1} (0–3.45×10^6 cell L^{-1}); and subsequently decreased to 8.33×10^4 cell L^{-1} (0–1.35×10^5 cell L^{-1}) in December and 2.78×10^4 cell L^{-1} (0–3.89×10^4 cell L^{-1}) in January. Besides, *Planktothrix* also showed a long-term trend with a declining pattern ($p = 0.0915$, Fig. 2b). The mean density during July to September decreased by 93% from 1.95–2.42×10^6 cell L^{-1} in 2011 and 2012 to 1.40×10^5 cell L^{-1} in 2015.

47.7% of the variance of *Pseudanabaena* could be explained by seasonal and long-term trend terms (Supplementary Table 8, Supplementary Fig. 6), and a similar seasonal pattern ($p < 0.0001$) of peak concentration (3.36×10^6 cell L^{-1}, 0–1.306×10^7 cell L^{-1}) in early September (Fig. 2c). The long-term changes of *Pseudanabaena* showed an opposite pattern ($p < 0.0001$) to *Planktothrix*; this genus became more abundant after 2014 and has kept increasing since then (Fig. 2d). Noted that, there was an early peak of *Pseudanabaena* during April and June (Fig. 2c).

Limnological and meteorological characteristics

Figure 3 shows the temporal distribution pattern of nutrients and meteorological parameters in QCS Reservoir. Nutrients including total nitrogen (TN), nitrate, ammonia and total phosphorus (TP) showed similar seasonality (Supplementary Tables 1–4), with the lowest concentrations observed in August and September owing to sedimentation losses in the summer period. Regarding the inter-annual dynamics, the TN and nitrate concentrations in 2014 were much higher than those in 2013 and 2015, ammonia showed a declining trend, while TP stayed almost unchanged between years. Precipitation was mainly observed between May to September, highly correlated with air temperature and solar radiation (Supplementary Tables 5 and 6). It should be noted that the solar radiation showed a declining trend from 2013 to 2015,
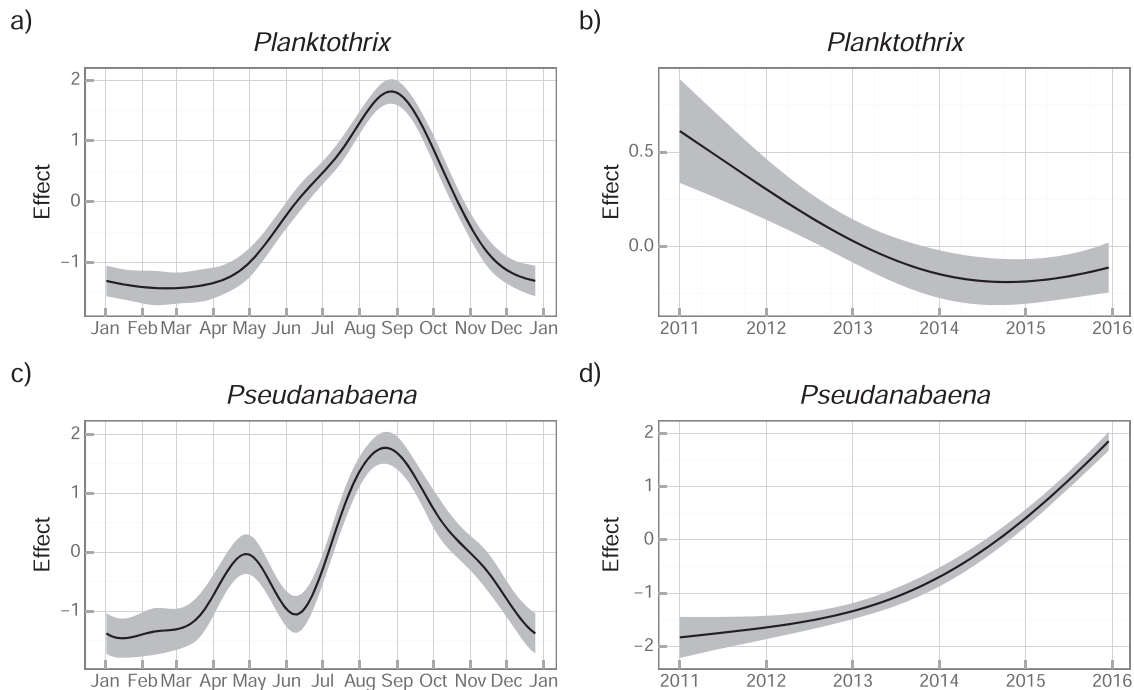
a)

Planktothrix

b)

Planktothrix

c)

Pseudanabaena

d)

Pseudanabaena

Fig. 2 Temporal distribution of two filamentous cyanobacteria ($\log_{10}(1 + N)$, unit: cells L^{-1}) from 2011 to 2015 separated into seasonal and long-term trends by generalized additive models. a Seasonal variation of *Planktothrix*. **b** Inter-annual dynamics of *Planktothrix* from 2011 to 2015. **c** Seasonal variations of *Pseudanabaena*. **d** Inter-annual dynamics of *Pseudanabaena* from 2011 to 2015. Shaded areas represent 95% confidence intervals.

possibly owing to the higher precipitation in the later years. Wind speed and relative humidity showed different seasonal patterns from 2013 to 2015.

Ecological Niche modeling of *Planktothrix* and *Pseudanabaena*

According to several published research[31–33] and our previous culture experiments[15,34] and field studies[7,11,35], we firstly selected water temperature, light availability, nutrients (including total nitrogen, nitrate, ammonia, total phosphorus), wind speed, and daily maximum air temperature as the potential predictors of cyanobacterial abundance Six predictors were selected including water temperature, light availability, total N, total P, ammonia and wind speed, according to linear models (LM1 and LM2) between these predictors (X) and *Planktothrix* ($Y_1 = \log_{10}(N_1 + 1)$, Supplementary Table 9) and *Pseudanabaena* ($Y_2 = \log_{10}(N_2 + 1)$, Supplementary Table 10) associated with backward stepwise selection (Supplementary Tables 11 and 12) and variance inflation factor (VIF, Supplementary Table 13). These predictors were subsequently classified into 4 groups based on the correlation analysis between each two predictors (Supplementary Fig. 7), which are (i) water temperature and light availability (T&I); (ii) Total N and ammonia (TN&NH4); (iii) Total P (TP) and (iv) wind speed (WS). The interactions between the predictors within each group were considered by modeling the interaction between T and I by bivariate tensor-product smoothers. GAM models for abundances of *Planktothrix* (GAM1, Supplementary Table 14) and *Pseudanabaena* (GAM2, Supplementary Table 15) were fitted with these predictors. The results suggested T&I and TN&NH4 were significantly correlated with the abundance of *Planktothrix*, while T&I, TP and WS were significant correlated with that of *Pseudanabaena*.

Based on the results above, the niche models of *Planktothrix* (GAM3, Supplementary Table 16) and *Pseudanabaena* (GAM4, Supplementary Table 17) were determined using their corresponding key explaining variables. In the temperature and light availability plane, both *Planktothrix* and *Pseudanabaena* exhibited greater abundance in high-temperature conditions (>20 °C).

Pseudanabaena could sustain higher abundance under lower light conditions (0.7–1.5 mol m^{-2} d^{-1}, $p < 0.001$) compared to *Planktothrix* (1.4~2.3 mol m^{-2} d^{-1}, $p < 0.001$), as illustrated in Fig. 4a and c. *Planktothrix* was less abundant in high total N and ammonia conditions ($p = 0.007$, Fig. 4b). While *Pseudanabaena* was slightly more abundant in moderate total P ($p = 0.064$) and moderate wind speed ($p = 0.004$) conditions.

Growth characteristics of *Planktothrix* and *Pseudanabaena* under different light doses

Since *Planktothrix* and *Pseudanabaena* exhibited different growth potentials under different light conditions, a culture experiment was performed to investigate the effect of light levels on their growth yield (Fig. 5a). The results suggested that light dose has a large impact: the cell density of *Planktothrix* in stationary phases (day 15–35) increased along with the light dose when it was <3.67 mol m^{-2} d^{-1}, while the growth was inhibited under higher light dose. The optimum light dose for *Pseudanabaena* is 1.56 mol m^{-2} d^{-1}, which was lower than that of *Planktothrix*. This suggested that photoinhibition exists for *Pseudanabaena* when the light dose was >3.67 mol m^{-2} d^{-1}.

Relationship between niche space and temporal trajectories of environmental factors in QCS Reservoir

The focal niche spaces of *Planktothrix* and *Pseudanabaena* were determined with the boundary defined by the 90% quantile of predicted abundances. The seasonal trajectories of environmental factors (water temperature & PAR) in QCS Reservoir are illustrated in Fig. 5b. In 2013, the trajectory went through the focal niche space of *Planktothrix* in July and August, indicating that *Planktothrix* had an advantage over *Pseudanabaena* in this year. In the following 2 years, especially for July and August, the trajectories followed different paths due to the lowered solar radiation and went through the niche space of *Pseudanabaena* instead. This probably enhanced the competitive ability of *Pseudanabaena*.
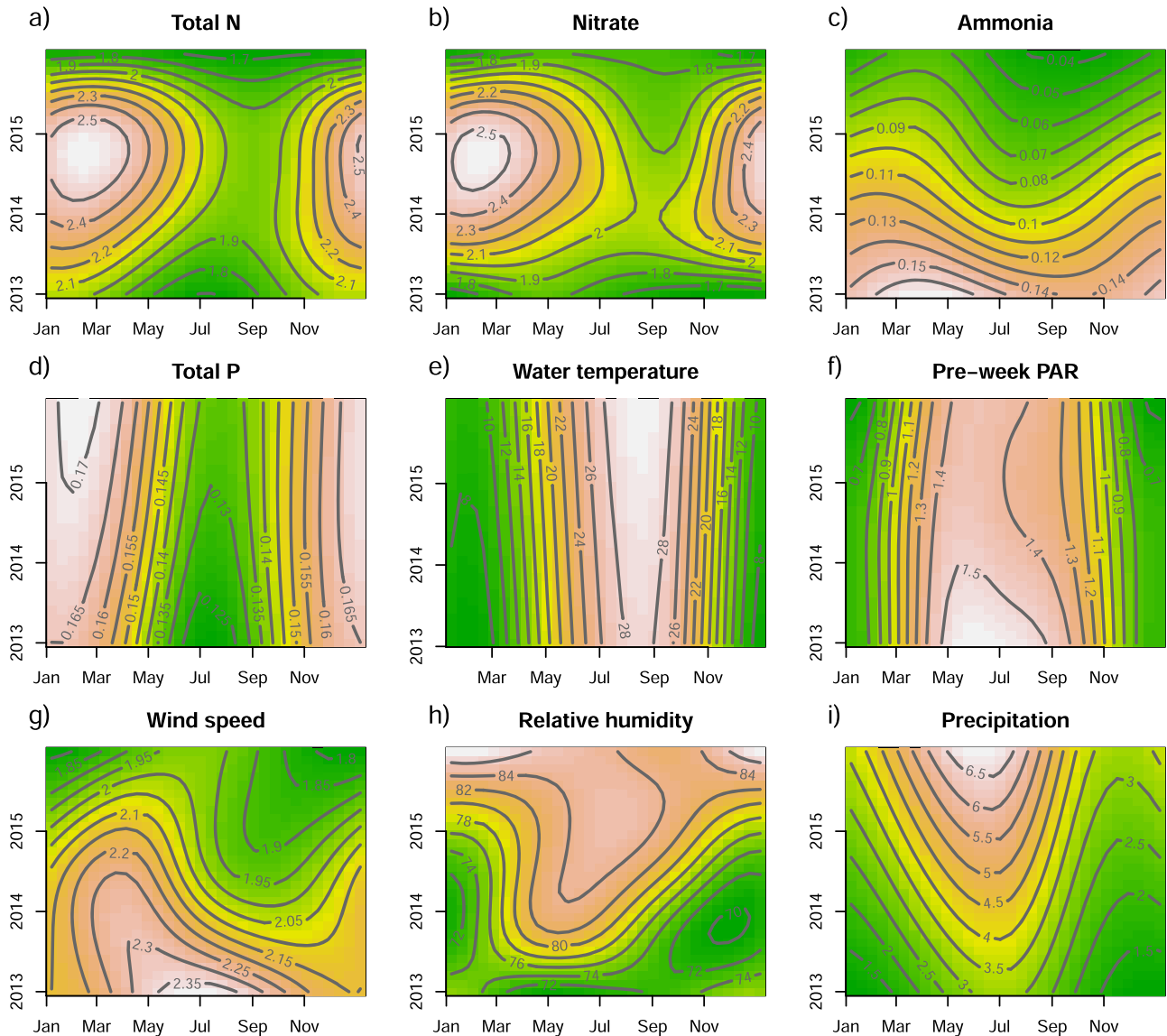
Fig. 3 The seasonal and inter-annual dynamics of environmental factors in QCS Reservoir from 2013 to 2015 according to generalized additive time series models. The shapes of the fitted surfaces are indicated by color (white: high; green: low) as well as the numbers along the contour lines. **a** Total nitrogen (mg L^{-1}). **b** Nitrate (mg L^{-1}). **c** Ammonia (mg L^{-1}). **d** Total phosphorus (mg L^{-1}). **e** Water temperature (°C). **f** The mean PAR of 1 week before investigation (mol m^{-2} d^{-1}). **g** Wind speed (m s^{-1}). **h** Relative humidity (%). **i** Precipitation (mm d^{-1}).

DISCUSSION

Planktothrix was the main MIB producer in QCS Reservoir during 2011 and 2015, as identified in our previous study[7], and the synchronous declines of this genus and MIB (Figs. 1 and 2) supported this interpretation. The driving forces responsible for the *Planktothrix* decline are therefore important for understanding the odor problems of QCS Reservoir.

Another filamentous cyanobacterium, isolated and identified as non-MIB-producing *Pseudanabaena*, showed an increasing trend during the study period. Both *Planktothrix* and *Pseudanabaena* showed the same seasonal patterns in this reservoir; in particular, *Planktothrix* was more abundant in the first 2 years while *Pseudanabaena* was more abundant afterwards (Fig. 2). Filamentous cyanobacteria tolerate low light[36], and many studies have shown that they tend to grow in spring and/or autumn seasons[8,11,37]. In this study, *Planktothrix* and *Pseudanabaena* were mainly observed during the summer period (July to September) and did not follow the typical seasonality of filamentous cyanobacteria. We speculate that the unusually low water

transparency in the reservoir (~40–60 NTU in turbidity, QC01) creates a habitat with low subsurface water light intensity, which favors filamentous cyanobacteria but is inhospitable to heliophilic *Microcystis*. In addition, the absence of surface *Microcystis* will also provide a more favorable underwater light environment for filamentous cyanobacteria[25].

Light niche differentiation between filamentous cyanobacteria and *Microcystis* can explain the competition between them, as reported in a study of Miyun Reservoir[25]. However, the situation in QCS Reservoir is different, since the MIB-producing *Planktothrix* has no competition from surface-blooming *Microcystis* but rather from the ecologically similar *Pseudanabaena*, during 2013 to 2015. The succession and/or competition between them are difficult to determine due to their niche overlap.

The temporal dynamics of limnological conditions in QCS Reservoir suggests different seasonal and inter-annual patterns (Fig. 3). The presence of nutrients in appropriate concentrations is one fundamental requirement for net primary production and accumulation of phytoplankton biomass, while nutrients have
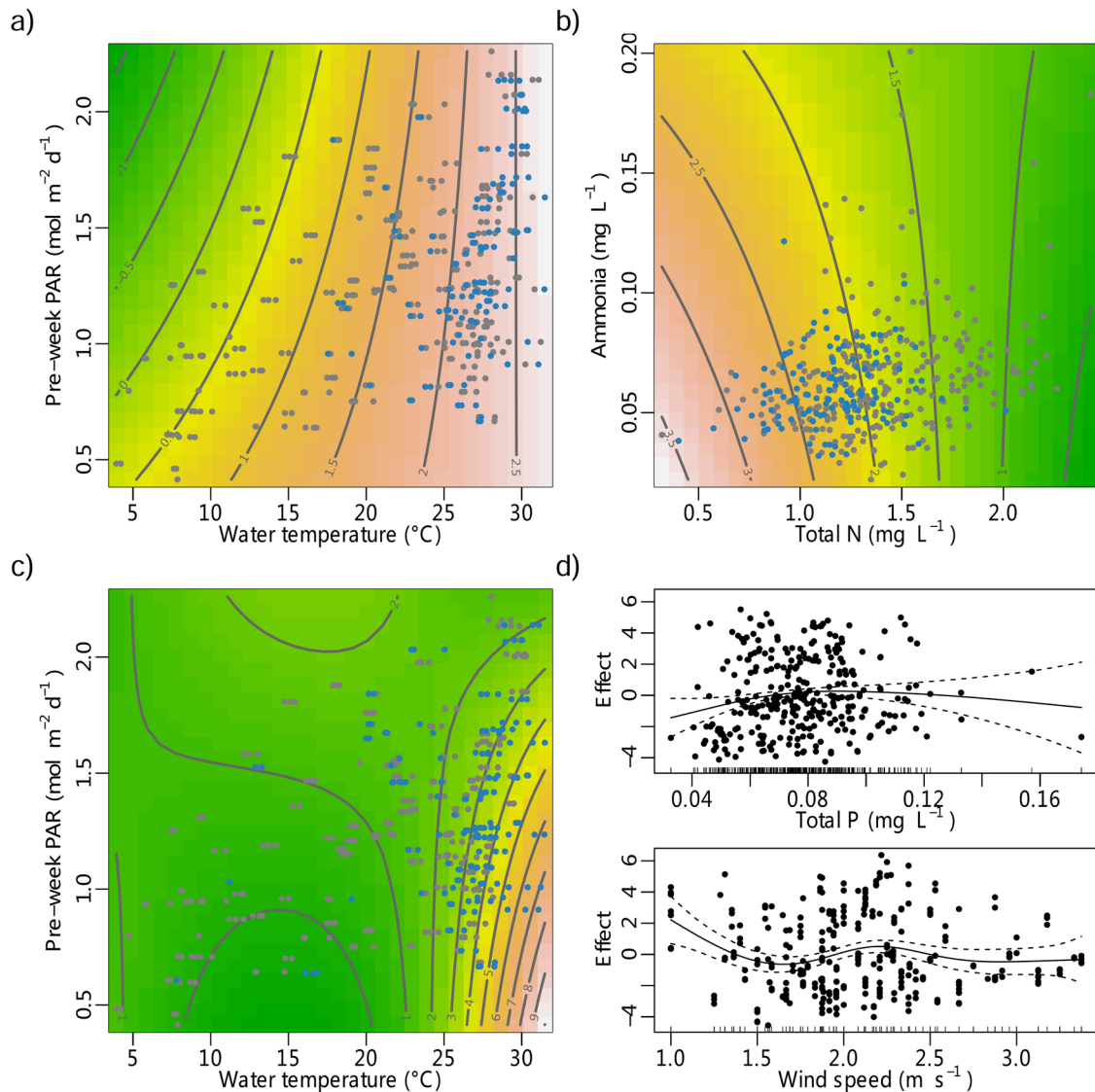
Fig. 4 Illustration of niche models (GAM3 and GAM4) of two filamentous cyanobacteria. a Effects surface for water temperature and pre-week PAR on growth of *Planktothrix*. **b** Summed effects surface for total N and ammonia on growth of *Planktothrix*. **c** Summed effects surface for water temperature and pre-week PAR on growth of *Pseudanabaena*. **d** Partial effects of total P and wind speed on growth of *Pseudanabaena*. In in **a**, **b**, and **c**, the contour colors and lines indicate the predicted logarithms of cell densities ($\log_{10}(1 + N)$, cells L^{-1}) in the two genera (from low to high represented by green to bright orange); gray dots represent the absences of the corresponding genus and purple dots represent the presences. In **d** lines are smoothed effect of total P (top) and wind speed (down) on growth of *Pseudanabaena*, dots are partial residuals of model GAM4.

been recently considered to be of limited value and to even be useless to shape the phytoplankton dynamics if we focus on the genus level[38]. Culture studies have also observed the insignificant effect of nutrient concentrations on the growth of several filamentous cyanobacteria strains including *Planktothrix agardhii*[39] and *Phormidium* sp.[40]. Although the nutrients (except TP) exhibited inter-annual changes in QCS Reservoir, the concentrations are generally sufficient to support the observed biomasses of filamentous cyanobacteria. The 15th Workshop of the International Association for Phytoplankton Taxonomy and Ecology summarized a series of research works, suggesting that the physical environment should be regarded as an important structuring tool for phytoplankton assemblages[38]; in particular, the light availability has gathered increasing attention[38].

Filamentous cyanobacteria seem to have lower optimum temperatures compared to other cyanobacteria, e.g., *Planktothrix agardhii* can grow better at 18–25 °C[39,41–44], while the preferred temperature

range of *Microcystis* is higher (*Microcystis aeruginosa*: 24–34 °C[45–47]; *Microcystis wesenbergii*: 25–35 °C[47]; *Microcystis ichthyoblabe*: 30–36 °C[48]), as summarized by[49]. Culture studies have shown that temperature is an important factor governing the growth of filamentous cyanobacteria when temperature varies greatly (e.g. >5 °C, Supplementary Table 1). For example, the red-pigmented *Planktothrix rubescens* has more competitive success at 15 °C, while the green-pigmented *Planktothrix agardhii* is more competitive at 25 °C[42]. No significant difference of water temperature was observed during July to September from 2013 to 2015 in QCS Reservoir, except the temperature of August in 2015 higher than in 2013 and 2014 (Fig. 5b), suggesting temperature may not the major contributor regarding the replacement of *Pseudanabaena* from *Planktothrix*. Nevertheless, the role of temperature regarding the succession and/ or competition still requires more specific study, since it usually correlated with light intensity so that it is hard to distinguish its contribution.
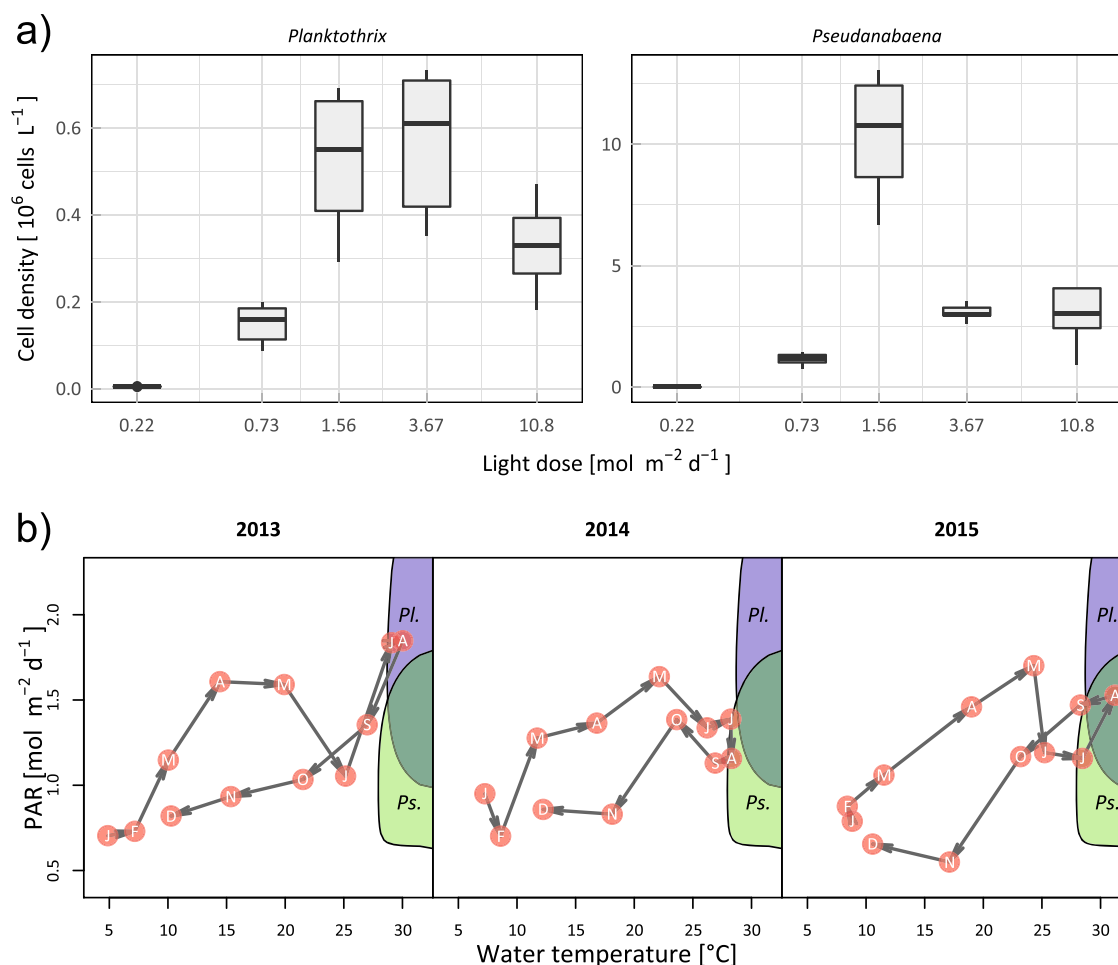
a)

b)

Fig. 5 Growth of *Planktothrix* and *Pseudanabaena* under culture conditions including 5 levels of light doses. a and field environment of QCS Reservoir from 2013 to 2015. **b** Growth yield of *Planktothrix* and *Pseudanabaena* within stationary phase (day 15–35) was used. Source data of *Planktothrix* growth is from[34]. Boxplot is Tukey style, where the bottom and top of the boxes denote the 25% and 75% quantiles, the ends of whiskers represent minimum and maximum cell densities with outliers removed, and the bands in the boxes denote the median cell densities. The zones colored purple and green denote the 90% quantile niche spaces (water temperature & pre-week PAR) of *Planktothrix* and *Pseudanabaena*, respectively. The red circles with a letter inside (J–D = January–December) denote the environmental conditions (represented by mean water temperature and mean pre-week PAR) in the corresponding month.

In general, a "light niche" specified by light intensity and spectral composition can promote phytoplankton species replacement. Growth rate responses to these different light levels are among major traits that determine the ecological success of phytoplankton species[50,51]. In this study, our results as demonstrated in Fig. 4 indicated that these two genera still have slight light niche differentiation, which probably is responsible for the replacement of *Planktothrix* by *Pseudanabaena* in later years. The light niche differentiation was also verified by the culture experiment (Fig. 5a[34]), showing that the optimum light dose of *Planktothrix* is lower than for *Pseudanabaena*, although these two genera were both recognized as low-irradiance specialists[26,27]. Furthermore, we summarized the light preferences of 10 *Planktothrix* strains and 2 *Pseudanabaena* strains (Table 1), showing a consistent conclusion with this study that the optimum light intensities of all *Pseudanabaena* strains are lower than those of *Planktothrix*. Nevertheless, a more targeted comparison is needed to verify the difference of light optimum between the two genera. The competitive advantage of *Planktothrix* at high solar radiation conditions was weakened in 2014 and 2015 owing to the lowered solar radiation (July–August: 1.27 ± 0.37 mol m^{-2} d^{-1} and 1.34 ± 0.41 mol m^{-2} d^{-1}) compared that in 2013 (1.84 ± 0.33 mol m^{-2} d^{-1}). On the other hand, *Pseudanabaena* was promoted in lower light conditions and hence outcompeted

Planktothrix in QCS Reservoir. Therefore, the subtle light niche differentiation of these two filamentous genera probably is the driving factor responsible for the succession and/or competition between *Planktothrix* and *Pseudanabaena*.

Other factors may also play important roles on their succession, e.g., *Planktothrix* posses gas vesicles, while *Pseudanabaena* not. The reservoir is well mixed during the whole year, and the depth of euphotic layer is relatively low due to high turbidity loading from Yangtze River. The gas vesicles of *Planktothrix* can provide buoyancy that enable the cells to perform vertical migrations or to maintain themselves in the euphotic zone[52].

Vellend's new conceptual synthesis in community ecology[53] has identified four distinct processes including selection, drift, speciation and dispersal. Under this framework, the succession of *Planktothrix* and *Pseudanabaena* in QCS Reservoir may dominate by the selection process, on the premise of the dispersal process that imported new *Pseudanabaena* from the Yangtze River, although the supporting evidence for this is limited. Owing to the decrease of irradiance of July and August in 2014 and 2015, we speculate that *Pseudanabaena* had higher fitness than *Planktothrix* and that this promoted the replacement.

Solar radiation seems an essential factor governing the competition between the filamentous cyanobacteria *Planktothrix* and *Pseudanabaena* in the present study, hence adjusting the

Table 1. Effects of environmental factors on filamentous cyanobacterial growth.

No.	Strain	Light (μE m^{-2} s^{-1})	Temperature (°C)	Ref.
1	*Oscillatoria redekei*	50–180 > 40 > 20 > 10	23 > 17 > 11 > 5	[41]
2	*Oscillatoria agardhii*	50 > 24 ≈ 95 > 12	25 > 20 ≈ 15 > 30	[39]
3	*Oscillatoria agardhii*	50 ≈ 24 ≈ 12 > 95	25 ≈ 30 ≈ 20 > 15	[39]
4	*Planktothrix agardhii*	180 > 100 > 50 > 40 > 20 > 10	23 > 17 > 11 > 5	[41]
5	*Planktothrix agardhii*	45–80 > 110 > 40 > 20–25 > 8		[73]
6	*Planktothrix agardhii*	60 > 80 > 20 ≈ 125 > 10 > 5 > 2	25 > 15	[42]
7	*Planktothrix agardhii*	60 > 100 ≈ 40 > 10 > 500		[74]
8	*Planktothrix agardhii*		18 > 30	[43]
9	*Planktothrix rubescens*	300 > 200 > 80 > 60 > 2–40	25 > 15	[42]
10	*Planktothrix rubescens*	60–120 > 35 > 25 > 10–15 > 5	20 > 10	[44]
11	*Planktothrix* sp.	85 > 36 > 250 ≈ 17 > 5		[34]
12	*Phormidium tenue*		27 > 30 ≈ 21 > 24 > 18	[75]
13	*Pseudanabaena* sp.	36 > 85 ≈ 250 > 17 > 5		-
14	*Pseudanabaena* sp.		10 > 25 > 35	[26]
15	*Pseudanabaena galeata*	30 ≈ 50 > 100 > 300 ≈ 10 > 600		[76]
16	*Lyngbya kuetzingii*	20 > 75 ≈ 10 > 0	25 > 35 > 10	[77]

Oscillatoria agardhii was renamed to *Planktothrix agardhii*[78].
≈ denotes approximate growth under the two comparing conditions.

underwater light climate could be a possible measure to regulate the filamentous cyanobacteria composition. Besides, since MIB is mainly produced by filamentous cyanobacteria, it is therefore possible to inhibit MIB-producing strains but enhance the non MIB-producing strains by adjusting the light climate. For instance, the non MIB-producing *Pseudanabaena* is a benign replacement for MIB-producing *Planktothrix*, by reducing the underwater light intensity by adjusting the water level[54] or increasing the turbidity via flow management. The strategy to control odor problems in QCS Reservoir is beyond of this study and will be discussed further in a subsequent publication.

METHODS

Study area and laboratory analysis

This is a follow-up study for[7]. QCS Reservoir (32°27'N, 121°38'E), located in Changxing Island in the Yangtze estuary, is a newly built reservoir used as the drinking water resource for Shanghai. The bathymetry map shows that the water depth in the reservoir varies from 2.7 m in the upstream area to 12.1 m in the downstream area, and an island in the upper section splits the water flow into two branches (Fig. 1a). The hydraulic retention time is in the range of 21.3 ± 2.2 d (April) and 124.1 ± 8.9 (December), the mean water turbidity is in the range of 22.7 ± 23.8 NTU (March) and 40 ± 44.5 NTU (December), and the mean water transparency is in the range of 55 ± 16 cm (September) and 80.35 ± 36.71 cm (March). The reservoir imports the water from Yangtze River via inlet gate. Since the abundance of phytoplankton and the concentrations of odor compounds of the river water are very low, three routine sampling sites including QC01 (water intake), QC02 and QC09 (reservoir center) located in the lower section of the reservoir were selected, as illustrated in Fig. 1a. Since the whole reservoir is well-mixed[7] throughout the year, 2 L surface water samples (0.5 m) at each site were collected using a Kemmerer water sampler for other water quality.

Phytoplankton analysis was performed weekly from 2011 to 2015; odorant identification and quantification were performed every day from 2011 to 2015; nutrients and other water quality were recorded every day since 2013. Physicochemical variables such as water temperature, pH, dissolved oxygen (DO), turbidity, and conductivity were measured in-situ with a multi-parameter probe (YSI EXO2, Yellow Springs, Ohio, USA).

Subsamples for MIB and geosmin detection were added 10 mg L^{-1} HgCl$_2$ to prevent biodegradation and stored in light-blocking bottles, and analyzed within 72 h using the solid phase micro-extraction (SPME) method coupled with gas chromatography-mass spectrometry (GC-MS)

(Agilent 6890/5975, Agilent Tech., USA)[11]. SPME was performed using an automated device (Combi PAL GC MultiFunction Autosampler, CTC Analytics, Switzerland) as follows: samples were shaken at 65 °C for 20 min, then the SPME fiber was exposed in the head-space of the vial for 10 min in order to absorb the odor compounds. The fiber was transferred to the injection port of the gas chromatograph and desorbed in the splitless mode at 250 °C for 3 min. Calibration standards for MIB (Supelco Inc.) were used. 2-isopropyl-3-methoxypyrazine (Supelco Inc.) was added to each sample as internal standard. This method has a detection limit of 1 ng L^{-1} for both compounds.

Subsamples (1000 mL) for cell enumeration were preserved with 5% Lugol's iodine[55] and left to settle for 48 h, then pre-concentrated 20× and kept in the dark until cell counting. The identification of cyanobacterial species was carried out following[56] and revised according to ref. [57]. The phytoplankton were identified and enumerated using an upright microscope (Olympus BX53, Japan) following the protocol established by[58]. The filamentous cyanobacteria abundances were quantified based on the length of each filament and the mean cell length of each strain. The number of cells in colony species such as *Microcystis* sp. was estimated based on colony volume and mean cell number per volume. The mean cell morphological characteristics including cell length, cell volume etc. were determined according to >50 filaments/colonies of each strain using a in-house developed cell counting tool (CCT v1.4, https://drwater.rcees.ac.cn, in Chinese).

The total global radiation (I_g, MJ m^{-2} d^{-1}) of Chongming Island (<20 km) was extracted from China Meteorological Data Service Center (CMDC)[59]. Photosynthetically Active Radiation (PAR_E, 400–700 nm, MJ m^{-2} d^{-1}) values were determined by a simplified model (Eq. (1)), according to 30 years of estimations of total global radiation and photosynthetically active radiation (PAR) in central China[60].

$$PAR_E = \frac{1666.4}{3983.9} \times I_g = 0.4183 I_g \qquad (1)$$

The PAR quantum (PAR_Q, mol m^{-2}·d^{-1}) was estimated according to Eq. (2), where the coefficient 4.57 (μmol m^{-2}·s^{-1} per W·m^{-2}) is adopted for the PAR of sky sunlight[61].

$$PAR_Q = \frac{PAR_E \times 10^6}{24 \times 60 \times 60} \times \frac{1}{4.57} \times \frac{24 \times 60 \times 60}{10^6} = \frac{0.4183 I_g}{4.57} = 0.09153 I_g \qquad (2)$$

Culture experiments of filamentous cyanobacteria under different light intensities

Two filamentous cyanobacteria, *Planktothrix* sp. (FACHB-1375) and *Pseudanabaena* sp. (FACHB-1277), were obtained from the Freshwater

Algae Culture Collection at the Institute of Hydrobiology, FACHB, China. Culture experiments were performed by growing the two genera in BG11 medium[62] at 25 °C and 5 different light intensities (5, 17, 36, 85, 250 μmol m^{-2} s^{-1}, 12:12 h light:dark cycle) in accordance with measured light intensities at different depths in the field. The triplicate samples were destructively collected from each set every 4 days over a 35 days' culture period. Data for *Planktothrix* has been published in[34]. The light doses (I_{dose}, mol m^{-2} d^{-1}) were calculated from the instantaneous light intensities (I, μmol m^{-2} s^{-1}) and daily radiation time (12 h) according to Eq. (3).

$$I_{dose} = \frac{12 \times 60 \times 60}{10^6}I = 0.0432I \quad (3)$$

The growth yield of *Planktothrix* and *Pseudanabaena* were determined according to the quantiles (25%, 50%, 75%) of cell densities observed within stationary phase (day 15–35).

Time series analysis

Generalized additive models (GAMs)[63] were used to model the seasonal and long-term patterns of environmental factors and filamentous cyanobacteria cell densities, as shown in Eq. (4). Thin plate spline (TS-spline)[64] were used to represent the long-term trend terms; while cyclic cubic splines, which have an additional constraint ensuring continuity between the beginning and the end of a year[65], were used for the seasonal terms.

$$y = \beta_0 + f_{seasonal}(x_1) + f_{trend}(x_2) + \varepsilon, \quad \varepsilon \sim N(0, \sigma^2) \quad (4)$$

where $f_{seasonal}$ and f_{trend} are smooth functions for the seasonal and interannual trend of environmental factors and cell densities; x_1 denotes the sampling week number and x_2 denotes the sampling date in units of decimal years. To make it clear, R Language demonstration code is given in the supplementary material.

To avoid autocorrelation from observations of successive time series, which might result in negatively biased estimation of regression coefficients and residuals, a first-order autoregressive model (AR(1), Eq. (5)) was employed for the error term.

$$\varepsilon_i = \phi \varepsilon_{i-1} + v_i \quad (5)$$

Different model structures were compared with likelihood ratio tests and the Akaike Information Criterion (AIC).

Ecological niche modeling

Ecological niche modeling (ENM), also known as species distribution modeling (SDM) uses computer algorithms to predict the distribution of a species across geographic space and time using environmental data. Water temperature (T), pre-week PAR (I, the mean PAR of the week before the sampling date) and nutrients (ammonia nitrogen, total nitrate, total phosphate) were used as predictors (x_i) of filamentous cyanobacterial abundances (y).

Here, we use the Generalized Additive Model (GAM) to model the abundances of the two filamentous cyanobacteria, as shown in Eq. (6). We use cell density to utilize more of the available information while many other studies use binary absent/present data to represent the biotic response to environmental conditions.

$$\log_{10}(1 + (E(y_j))) = \beta_0 + \sum_{j=1}^{J}\sum_{k=1}^{K}\delta_{jk}b_{1j}(x_1)b_{2k}(x_2) + \varepsilon_j \quad (6)$$

where b_1 and b_2 are basis functions, J and K are corresponding basis dimensions and δ is a matrix of unknown coefficients. Interactions among the indicators were evaluated by the tensor product ($f_1(x_1) \otimes f_2(x_2)$[66]).

ENM were performed following several steps as describe below:

1. Correlation analysis between filamentous cyanobacteria abundances (including *Planktothrix* and *Pseudanabaena*) and environmental factors as the potential predictors according to the two linear models (name as LM1 and LM2) as summarized in Supplementary Tables 9 and 10;
2. Backward Stepwise model simplification of LM1 and LM2 were performed to further sort out the possible predictors for both genus (Supplementary Tables 11 and 12);
3. Variance inflation factors (VIF) were computed for the predictors given by step 2 (Supplementary Table 13);
4. Correlation coefficients among the predictors were calculated using Pearson method to evaluate the potential interacting effects among predictors (Supplementary Fig. 6);

5. Based on the results of step 4, the predictors were assembled accordingly with appropriate smooth functions of GAM models for *Planktothrix* (named as GAM1, Supplementary Table 14) and *Pseudanabaena* (named as GAM2, Supplementary Table 15);
6. ENMs (named as GAM3 and GAM4) were optimized according to the importance of predictors in GAM1 and GAM2 (Supplementary Tables 16 and 17).

Estimated abundances of targeted species versus environmental factors were illustrated with contour maps. Quantile niche space was identified by the boundary defined by the 90% quantile of estimated abundances for each genus.

Statistical analysis and illustration

All data analysis and illustration were performed using R 4.0[67]. Data pretreatment and summary were performed using the **dplyr**[68] package in R, regression analysis including linear and generalized linear models were performed using the **stats** package[67], generalized additive modeling was performed using the **mgcv** package[69,70] quantile regression analysis was performed using the **quantreg** package[71]; contour figures were created by the **graphics** package[67], other figures were prepared using the **ggplot2** package[72].

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COMPETING INTERESTS

The authors declare no competing interests.

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