



# Seasonal and long-term trends in the spatial heterogeneity of lake phytoplankton communities over two decades of restoration and climate change

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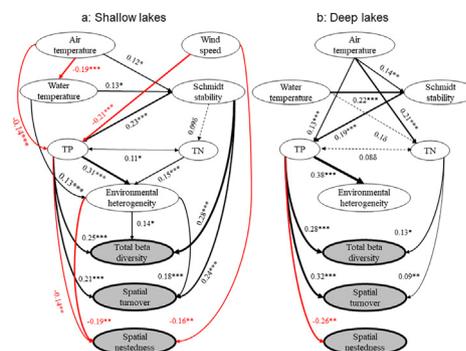
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## HIGHLIGHTS

- Temporal trends in spatial phytoplankton heterogeneity across lakes are quantified.
- Heterogeneity of environments and phytoplankton shows clear seasonality.
- The seasonality tends to be less marked in deep than in shallow lakes.
- Restoration measures cause homogenisation of environments and phytoplankton.
- Climates have weak cascading effects on phytoplankton heterogeneity.

## GRAPHICAL ABSTRACT



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## ABSTRACT

World-wide, reducing the external nutrient loading to lakes has been the primary priority of lake management in the restoration of eutrophic lakes over the past decades, and as expected this has resulted in an increase in the local environmental heterogeneity, and thus biotic heterogeneity, within lakes. However, little is known about how the regional spatial heterogeneity of lake biotic communities changes with restoration across a landscape. Using a long-term monitoring dataset from 20 Danish lakes, we elucidated the seasonal and long-term trends in the spatial heterogeneity of climate, local abiotic variables and phytoplankton communities over two decades of restoration and climate change at landscape level. We found significant seasonality in the spatial heterogeneity of most climatic and local drivers as well as in the total beta diversity (Sørensen coefficient) and its turnover components (Simpson coefficient) of phytoplankton communities among the lakes. The seasonality tended to be less marked in deep than in shallow lakes. We found significant spatial homogenisation of most local drivers (except for alkalinity) and phytoplankton communities after two decades of restoration and that turnover dominated the temporal responses of the total beta diversity of phytoplankton communities. Path analyses showed that the homogenisation of phytoplankton communities was mainly due to a decrease in spatial heterogeneity of total phosphorus and Schmidt stability in shallow lakes and to a decrease in spatial total phosphorus and total nitrogen heterogeneity in deep lakes. However, albeit weakly, the spatial heterogeneity of the phytoplankton

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communities was affected indirectly by climatic warming in both shallow and deep lakes and directly by wind speed in shallow lakes. We conclude that restoration of eutrophic lakes may lead to an increase in the local heterogeneity of phytoplankton communities at lake scale and an increase in homogeneity at landscape scale.

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## 1. Introduction

Understanding how community composition varies over space and time (i.e., beta diversity) is a central goal in community ecology (Whittaker, 1972; Anderson et al., 2011). In freshwater lakes, eutrophication is a key driver of the community dynamics of phytoplankton (Reynolds, 1984; Harper, 2012). Usually it leads to a marked reduction of environmental heterogeneity and thereby filtering out of species that are sensitive to the characteristics of eutrophic conditions such as shading, hypoxia, high ammonia levels and reduced grazing by zooplankton (Reynolds, 1984). This could greatly diminish community dissimilarity among sites and thus lead to biotic homogenisation, at least at local scale (Rahel, 2002; Menezes et al., 2015; Cook et al., 2018; Monchamp et al., 2018; Salgado et al., 2018; Wengrat et al., 2018), which may result in degradation of biological diversity and freshwater ecosystem functions (Rahel, 2002; Salgado et al., 2018). To improve the ecological quality of lakes, major efforts have been made in many countries to reduce the external nutrient loading in order to promote restoration (Coveney et al., 2005; Jeppesen et al., 2005; Jeppesen et al., 2007b; Pomati et al., 2012). An increase in habitat heterogeneity (due to, e.g., macrophyte recovery and high water transparency creating higher benthic production) and thereby biotic heterogeneity would be expected during restoration (Jeppesen et al., 2002; Lauridsen et al., 2003; Jeppesen et al., 2007a; Hilt et al., 2013; Özkan et al., 2016; Lefcheck et al., 2018; Murphy et al., 2018). However, the effects of external nutrient loading reduction and internal nutrient loading may vary over time from lake to lake, largely depending on the specific measures introduced, and with different effects on the local abiotic and biotic community composition (Jeppesen et al., 2002; Lauridsen et al., 2003; Søndergaard et al., 2003; Anneville et al., 2005; Jeppesen et al., 2005; Pomati et al., 2012). Furthermore, changes in biotic community dynamics may vary significantly among the lakes in a given region depending on changes in trophic state or large-scale forcing (e.g., climate warming) (Anneville et al., 2005; Jeppesen et al., 2005). Therefore, the temporal abiotic and biotic responses will eventually differ among lakes at the regional scale, and little is known about how spatial abiotic and biotic heterogeneity varies with restoration between lakes across a large landscape.

During the last 1 to 5 decades, external nutrient loading reduction following eutrophication has been applied to many lakes worldwide, and in some lakes this has coincided with a weak increase in summer air and surface water temperatures (Coveney et al., 2005; Jeppesen et al., 2005; Jeppesen et al., 2007b; Pomati et al., 2012). Previous studies have described the effects of restoration on the physico-chemical conditions and limnology of lakes, showing decreases in-lake total phosphorus/nitrogen (TP/TN) and chlorophyll *a* (chl *a*) concentrations and increases in Secchi depth (Köhler et al., 2005; Søndergaard et al., 2005; Dove and Chapra, 2015). As for phytoplankton communities, restoration may be accompanied by a local (within-lake) increase in richness and compositional changes (Anneville et al., 2005; Jeppesen et al., 2005; Özkan et al., 2016). Moreover, on a short time scale, studies have shown significant seasonal responses by local abiotic variables and biotic communities (Søndergaard et al., 2005; Thackeray et al., 2008; Zhang et al., 2011), as well as plastic changes in the seasonal succession and phenology of phytoplankton communities during restoration (Winder and Cloern, 2010; Weithoff et al., 2015; Anneville et al., 2018; Pálffy and Vörös, 2019). Remarkably, both local abiotic variables and biotic communities exhibit highly different responses between

shallow and deep lakes, largely reflecting the much stronger benthic pelagic coupling and the lack of stratification in shallow lakes (Jeppesen et al., 2005; Søndergaard et al., 2005; Salmaso, 2010; Menezes et al., 2015; Dolman et al., 2016). Although many studies have indicated that global warming could potentially interact with restoration in influencing local phytoplankton communities (Anneville et al., 2005; Thackeray et al., 2008; Pomati et al., 2012; Özkan et al., 2016; Verbeek et al., 2018), the role of spatial climatic heterogeneity in determining the spatial heterogeneity of local abiotic variables and biotic community dynamics has yet to be fully explored.

Using an extensive dataset (1989–2008) from 20 Danish lakes (Özkan et al., 2014; Özkan et al., 2016), we assessed the seasonal and long-term trends in the spatial heterogeneity of phytoplankton community composition (i.e., spatial beta diversity) across lakes (regional scale) and related these to climatic (e.g., air temperature, precipitation, solar irradiance, wind speed, etc.) and local abiotic drivers (e.g., water environments, considering factors such as nutrients, chlorophyll *a*, pH, water temperature, suspended solids, Secchi depth, etc.). Our study addressed the following questions: 1) how does the spatial heterogeneity of climatic and local abiotic drivers across lakes vary at seasonal scale (within year) and long time scale (among years)? We hypothesised that the spatial heterogeneity of local abiotic variables across lakes would decrease (i.e., the lakes would become more similar) because most highly loaded lakes have undergone a strong decrease in external loading (Søndergaard et al., 2005); 2) how does the spatial beta diversity of phytoplankton communities vary at seasonal and long time scale, and how are these patterns controlled by climatic and local abiotic drivers? We hypothesised that local abiotic variables, especially of water nutrients (e.g., TP and TN), would be the most important drivers. Specifically, we further elucidated how temporal trends in spatial abiotic and biotic heterogeneity differ between shallow and deep lakes and how the relative importance of climatic and local abiotic drivers varies in determining the spatial patterns of phytoplankton communities between shallow and deep lakes, expecting depth-depending responses of environments and phytoplankton to nutrient loading (Jeppesen et al., 2005; Søndergaard et al., 2005; Dolman et al., 2016).

## 2. Materials and methods

### 2.1. Data collection

Twenty lakes were monitored between 1989 and 2008 as part of the Danish monitoring programme on the aquatic environment (Fig. S1). Winter samples (December–February) were excluded due to varying sampling intervals between lakes and years, with some lakes not being sampled during winter in some years because they were frozen. The average sampling interval of the lakes was 14 days from May to October and 30 days in the other months included. The total sampling frequency was 360 for each lake across the study period (1989–2008). Phytoplankton samples were taken mid-lake at depth-integrated locations covering the photic zone (i.e., 2\*times the Secchi depth). Details on plankton sampling, identification, counting and measurements of abiotic variables for 17 of the 20 lakes can be found in Özkan et al. (2014). For the remaining 3 lakes (Furesøen Storesø, Engelsholm, Kvie Sø), the sampling methods and frequency were the same as described in Özkan et al. (2014) and followed the same sampling protocol. All taxa were aggregated to genus level due to variation in the degree of species level identification between the different plankton groups and

time and for the purpose of avoiding the risk of effects of variation in the identification skills of the taxonomists. The phytoplankton data were screened for potential inconsistencies and corrections were made using an inclusive approach according to Özkan et al. (2014), involving, for example, recalculation of the missing information (e.g., biomass being registered without counting) using original information or a representative average for the taxon in question.

We collected samples for the analysis of lake water chemistry simultaneously with the phytoplankton samples from the photic zone. The local abiotic variables considered included lake water temperature (WT), Schmidt stability index (an index of water column stratification calculated from temperature profiles) (Idso, 1973), total phosphorus (TP), total nitrogen (TN), chlorophyll-a (Chl-a), silicate (SiO<sub>2</sub>), suspended solids (SS), Secchi depth (SD), pH and total alkalinity (TA). We measured WT at one-metre intervals at the deepest point of the lake and calculated the Schmidt stability index according to Matlab codes from Lake Analyser software (Read et al., 2011) when WT was recorded at least to the mid-depth of the lake. Climatic variables included mean air temperature, wind speed, solar irradiance (from daily averages interpolated to 20 km grids) and precipitation (from daily averages interpolated to 10 km grids and corrected for wind and altitude depending on the month of the year, Danish Meteorological Institute) (Özkan et al., 2014).

## 2.2. Spatial heterogeneity of environmental variables and phytoplankton communities

Spatial heterogeneity was defined as the spatial variability or dissimilarity among lakes at each sampling campaign, yielding  $n = 360$  observations for each index of spatial heterogeneity for each variable. Univariate (for each variable) and multivariate (all variables handled in two sets: climatic and local abiotic variables) spatial heterogeneity was estimated separately for climatic and local abiotic drivers.

The spatial heterogeneity for each climatic and local abiotic driver was calculated as the coefficient of variation (CV: standard deviation divided by the mean of the data) for all lakes at each sampling event.

Multivariate spatial heterogeneity for climate drivers was calculated as the Euclidean dissimilarity coefficient (i.e., the shortest distance between two sampling points in an Euclidean space where each environmental variable constitutes an axis) of mean air temperature, wind speed, solar irradiance and precipitation among lakes for each time point of the time series (Gower and Legendre, 1986).

Multivariate spatial heterogeneity for local abiotic drivers was calculated as the Euclidean dissimilarity coefficients of Chl-a, pH, Secchi depth, SiO<sub>2</sub>, SS and alkalinity among lakes for each time point in the time series. TP and TN were not included in these metrics because they were also considered as important dependent variables in the models (e.g., generalized multilevel path models).

Spatial heterogeneity of phytoplankton communities was calculated as the Sørensen dissimilarity coefficient among lakes, which can be considered as the overall total beta diversity at regional scale (Baselga, 2010). The Sørensen dissimilarity coefficient of phytoplankton communities was separated into the Simpson dissimilarity coefficient (a measure of turnover without influence of richness differences) and the nestedness dissimilarity coefficient (a measure of nestedness resulting from richness differences) of phytoplankton communities (Baselga, 2010; Legendre, 2014).

The spatial heterogeneity analysis of variables was conducted separately for shallow lakes ( $N = 12$ , mean depth < 3 m) and deep lakes ( $N = 8$ , mean depth > 3 m) for each time point of sampling (Table S1).

## 2.3. Statistical analysis

The time series of the spatial heterogeneity of all abiotic and biotic variables were separated into seasonal trends, long-term trends and residual variability with generalized additive models (GAM) using the

“gam” function and cubic regression spline from the R-package “mgcv” (Wood, 2017). GAM can identify a nonlinear relationship between variables with different smoothing methods and in this way reveal nonlinearities and abrupt changes hidden in the time series. We specified a Gaussian normal distribution as *family* for the predictors in the GAM models.

We estimated the significance ( $P < .05$ ) of each variable in the seasonal trends from the GAM results, a significant trend indicating occurrence of seasonality. We calculated Pearson correlation coefficients to compare the correlation among the seasonal trends in spatial heterogeneity of all the tested variables.

Moreover, we assessed the significance of long-term trends for the spatial heterogeneity of each tested variable by regressing de-seasonalised residuals versus year using generalized linear models. The de-seasonalised residuals were derived from GAM models extracting seasonal trends for each variable and were constantly around the mean and variance of months.

We assessed how the spatial heterogeneity of climatic and local abiotic variables governed the spatial heterogeneity (beta diversity) of phytoplankton communities using two complementary approaches. Firstly, we modelled the beta diversity metrics of phytoplankton (total beta diversity, spatial turnover, nestedness) as a function of the heterogeneity of climatic and local abiotic variables using ordinary least squares regressions. All model variables were de-seasonalised residuals. We checked if temporal dependence was a problem for our models and included temporal structure in the models using the *corArma* function (Zuur et al., 2009). We applied model selection using second-order Akaike's information criterion (AIC) to select the best models with the most important explanatory variables for the beta diversity coefficients. We only selected models with delta AIC < 2 relative to the best model as suggested by Burnham and Anderson (2002). We calculated the sum of Akaike weights including all models to evaluate the relative importance of explanatory variables. We performed model selection and model averaging using functions of the “MuMIn” package (Barton, 2014).

Secondly, we applied generalized multilevel path models (GMPM) to test multivariate relationships among the spatial beta diversity of phytoplankton communities and the spatial heterogeneity of TP, TN, water temperature and Schmidt stability as well as the multivariate spatial heterogeneity of the remaining climatic and lake water variables (Shipley, 2009). GMPMs were fitted using a d-sep approach as proposed by Shipley (2009), which is based on an acyclic graph that describes the hypothetical multi-variate relationships and independence claims between variables. This approach was preferred instead of the standard SEM (with latent variables) because it can include the non-normal data, temporal and spatial dependence error structures between variables and small sample sizes that occur widely in ecological datasets (Shipley, 2009). We performed the GMPMs and generated the causal network with all component models using the “piecewiseSEM” package in R (Lefcheck, 2016). Our models included several key paths: 1) climatic variables influencing water temperature and Schmidt stability; 2) TP, TN, water temperature and Schmidt stability affecting environmental heterogeneity and phytoplankton beta diversity; 3) environmental heterogeneity affecting phytoplankton beta diversity. In addition, we included the potential paths by which climate, water temperature and Schmidt stability affect TP and TN although changes in TP and TN mostly reflected the reduced external nutrient loading. As the directions of the TP and TN paths were not hypothesised, we included an additional correlation between TP and TN in the GMPMs and a significant correlation was observed between TP and TN in both shallow and deep lakes. Before we conducted the GMPMs, we applied generalized linear models with temporal autoregressive error structures (i.e., *corArma* function) to examine separately each hypothesised path. We used Shipley's test of directional separation to estimate the goodness of fit for each path model (Shipley, 2009), a chi-squared test of Fisher's *C* statistic to test the significance ( $P > 0.05$ ) of the path models (Shipley, 2013) and the AICc procedure to select the best model (Shipley, 2013). Notably, the

interaction terms were excluded according to the AICc procedure. We determined the coefficient of determination ( $R^2$ ) for each component model, which can be used to assess the variance explained across the set of models in the GMPMs. We used standardised path coefficients to present the direct, indirect and total effects of the predictors (Grace and Bollen, 2005). The strength of direct effects were defined as the standardised path coefficient, which is a unitless measure of association and thus can be compared for the same relationship in different models and for different relationships within and among models. Standardised coefficients are also useful for computing indirect effects. The strength of indirect effects can be calculated by multiplying the standardised path coefficients along the path. For example, we computed the indirect pathway from TP to environmental heterogeneity to spatial turnover of phytoplankton by multiplying the path coefficients. The strength of total effects was calculated as the sum of direct and indirect effects.

All statistical tests were conducted separately for shallow and deep lakes, respectively, and were performed using R version 3.51 software (R Core, 2013).

### 3. Results

#### 3.1. Seasonal trends in spatial abiotic and biotic heterogeneity

In the time series (1989–2008), solar irradiance (SI), wind speed (WI) and pH showed much lower spatial heterogeneity (mean CV < 0.6, Table 1) than all the other local abiotic variables (Table 1). Among all the climatic and local abiotic variables, spatial heterogeneity tended to be higher for shallow lakes than for deep lakes, except for SS (Table 1). The total beta diversity of phytoplankton (the Sørensen coefficient) was typically higher in deep than in shallow lakes, which could mainly be attributed to higher spatial turnover (i.e., Simpson coefficient) rather than to changes in spatial nestedness (Table 1).

The spatial heterogeneity of climatic variables, local abiotic variables and the phytoplankton community composition exhibited significant seasonal trends (Table 1, Figs. 1, S2 & S3), except for air temperature (AT) and precipitation in both shallow and deep lakes, the Schmidt stability index and TA in shallow lakes and the spatial nestedness of

phytoplankton in deep lakes. Seasonality explained between 5.3% (Chl-a) and 43.1% (water temperature) of the variability in the data (Table 1). For shallow lakes, the heterogeneity of water temperature was well explained by seasonality (Table 1), with lower heterogeneity during summer and higher heterogeneity in early spring and autumn (Fig. 1). Climatic heterogeneity as well as the spatial nestedness of phytoplankton displayed similar seasonal trends, with the lowest heterogeneity during early summer between day 150 and 200 and higher heterogeneity in spring and autumn (Fig. 1). The spatial heterogeneity of lake nutrient concentrations showed remarkable opposite patterns for TP and TN (Fig. 1). Total beta diversity and spatial turnover showed consistent seasonal trends, with more dissimilar phytoplankton communities in lakes during summer than in the other seasons. For the deep lakes, seasonal trends in the climate heterogeneity of water temperature, total beta diversity and the spatial turnover of phytoplankton demonstrated similar patterns as for the shallow lakes (Fig. 1). However, the seasonal trends were less pronounced for the CV of TP and TN and the environmental heterogeneity and spatial nestedness of phytoplankton in the deep vs. the shallow lakes (Table 1), which showed a more similar seasonal distribution pattern (Fig. 1).

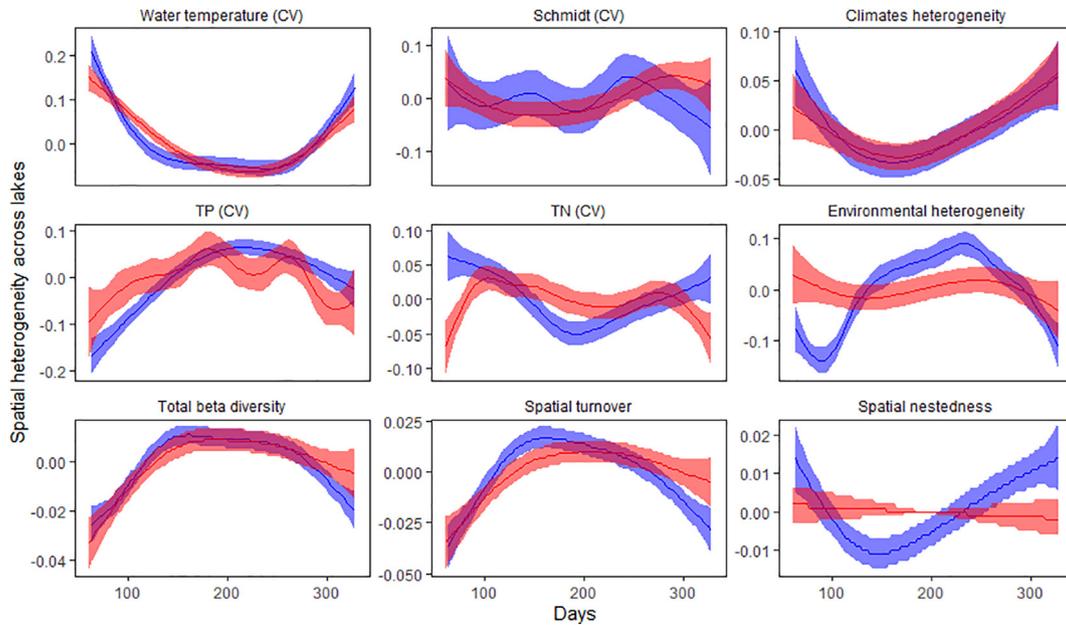
In the shallow lakes, the seasonal trends in total beta diversity as well as spatial turnover were strongly negatively associated with the CV of air temperature, solar irradiance, water temperature, TN, total alkalinity and climatic heterogeneity and positively with the CV of precipitation, TP, pH, silicate, Secchi depth, suspended solids and environmental heterogeneity (Table S2). Spatial nestedness was strongly positively associated with the CV of solar irradiance and climatic heterogeneity and negatively associated with the CV of precipitation and silicate (Table S2). In deep lakes, the seasonal trends in total beta diversity as well as spatial turnover were strongly negatively associated with the CV of air temperature and water temperature and positively associated with the CV of TP (Table S2).

#### 3.2. Long-term trends in spatial abiotic and biotic heterogeneity

For shallow lakes, we found significant temporal increases in climate heterogeneity and the CV of wind speed and decreases in total beta

**Table 1**  
Mean and range values of the coefficient of variations of climate variables and local abiotic variables, multivariate climate heterogeneity (Euclidean dissimilarity coefficients of climate variables), environmental heterogeneity (Euclidean dissimilarity coefficients of chlorophyll-a, pH, silicate, Secchi depth, suspended solids and alkalinity) and three beta diversity measures of phytoplankton: Sørensen coefficient (i.e. total beta diversity), Simpson coefficient (beta diversity due to spatial turnover) and nestedness coefficient (beta diversity due to spatial nestedness—resultant richness differences) across two decades of monitoring. Explained variance (*Var.exp.*) and significance (*P*-value) of seasonal trends (1989–2008) are also given, with significant values in bold. All values are reported separately for shallow and deep lakes.

Variables	Shallow lakes				Deep lakes			
	Mean	Range	<i>Var.exp.</i>	<i>P</i> -value	Mean	Range	<i>Var.exp.</i>	<i>P</i> -value
Climate variables								
Air temperature	0.08	0.08–4.43	0.012	0.359	0.08	0.08–5.12	0.028	0.342
Solar irradiance	0.1	0.01–0.51	<b>0.131</b>	<0.001	0.1	0.01–0.6	<b>0.195</b>	<0.001
Precipitation	0.52	0.09–3.09	0.024	0.058	0.54	0.06–2.52	0.025	0.061
Wind speed	0.16	0.03–0.43	<b>0.192</b>	<0.001	0.2	0.03–0.61	<b>0.123</b>	<0.001
Climatic heterogeneity	0.48	0.13–1.14	<b>0.085</b>	<0.001	0.49	0.14–1.06	<b>0.069</b>	<0.001
Local abiotic variables								
Water temperature	0.16	0.02–0.84	<b>0.431</b>	<0.001	0.13	0.02–1.33	<b>0.348</b>	<0.001
Schmidt stability	2.04	0.61–3.46	0	0.802	1.65	0.49–2.8	<b>0.061</b>	0.001
Total phosphorus	0.93	0.21–1.9	<b>0.159</b>	<0.001	0.97	0.02–1.76	<b>0.073</b>	0.002
Total nitrogen	0.74	0.28–1.31	<b>0.14</b>	<0.001	0.6	0.04–1.01	<b>0.076</b>	0.002
Chlorophyll-a	1.06	0.35–2.1	<b>0.055</b>	0.037	1.32	0.22–2.48	<b>0.053</b>	0.018
pH	0.15	0.01–0.25	<b>0.116</b>	<0.001	0.05	0–0.1	<b>0.123</b>	<0.001
Silicate	1.05	0.06–2.36	<b>0.3</b>	<0.001	1.02	0–2.16	<b>0.177</b>	<0.001
Secchi depth	0.73	0.11–1.27	<b>0.151</b>	<0.001	0.55	0.05–0.99	<b>0.06</b>	0.003
Suspended solids	0.78	0.28–1.6	<b>0.063</b>	0.001	1.21	0.11–2.27	<b>0.314</b>	<0.001
Alkalinity	0.84	0.24–1.69	0.015	0.194	0.28	0.05–0.72	<b>0.108</b>	<0.001
Environmental heterogeneity	2.44	0.97–3.18	<b>0.421</b>	<0.001	1.99	0.81–3.92	0.018	0.333
Spatial beta diversity and its component								
Total beta diversity	0.88	0.64–0.94	<b>0.23</b>	<0.001	0.82	0.33–1	<b>0.101</b>	<0.001
Spatial turnover	0.82	0.56–0.91	<b>0.214</b>	<0.001	0.76	0.33–1	<b>0.076</b>	<0.001
Spatial nestedness	0.06	0.01–0.2	<b>0.116</b>	<0.001	0.06	0–0.2	0.001	0.479



**Fig. 1.** Seasonal trends (1989–2008) in the coefficient variations (CV) of water temperature, Schmidt stability, total phosphorus (TP), total nitrogen (TN), climatic heterogeneity (Euclidean dissimilarity coefficients of climatic variables), environmental heterogeneity (Euclidean dissimilarity coefficients of chlorophyll-a, pH, silicate, Secchi depth, suspended solids and alkalinity) and the three multiple-site beta diversity measures: Sørensen dissimilarity (i.e. total beta diversity), Simpson dissimilarity (beta diversity due to spatial turnover) and nestedness dissimilarity (beta diversity due to spatial nestedness–resultant richness differences) between shallow (blue) and deep (red) lakes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

diversity, spatial turnover, environmental heterogeneity, the CV of water temperature, Schmidt stability, TP, Chl-a, pH, Secchi depth, SI and SS (Table 2, Figs. 2, S4 & S5).

For deep lakes, we found significant temporal increases in climatic heterogeneity, spatial nestedness and the CV of wind speed and decreases in total beta diversity, spatial turnover, environmental heterogeneity, the CV of water temperature, TP, TN, Chl-a, pH, Secchi depth and SS (Table 2, Figs. 3, S4 & S5).

Among all the tested climatic and local abiotic variables (Table 3), total beta diversity of phytoplankton was mainly determined by the CV of water temperature, Schmidt stability, TP, pH and TA (negative) across shallow lakes and by the CV of TP, TN, Chl-a and SI across deep lakes. Spatial turnover was mostly determined by the CV of Schmidt stability, TP and pH across shallow lakes and by the CV of TP, TN, SI and Secchi depth across deep lakes. Spatial nestedness was mainly determined by the CV of wind speed (negative), TP (negative), Chl-a, pH (negative) and TA (negative) across shallow lakes and by the CV of air temperature, wind speed, TP (negative) and Secchi depth across deep lakes.

For both shallow and deep lakes, total beta diversity as well as its turnover component was positively associated with the CV of TP, TN, Schmidt stability and environmental heterogeneity, while spatial nestedness was negatively associated with the CV of TP and environmental heterogeneity (Figs. S6, S7). Spatial nestedness was negatively related to the CV of wind speed for shallow lakes and positively related to the CV of air temperature and wind speed, but no clear relations with climatic heterogeneity appeared (Fig. S8).

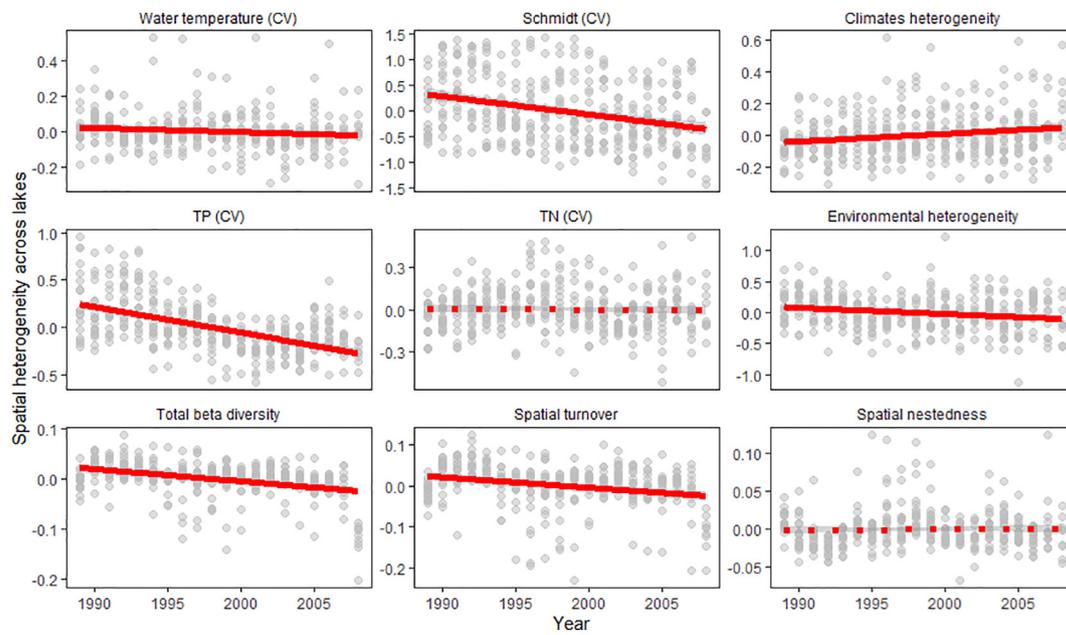
### 3.3. Multivariate relationships between spatial heterogeneity of climates, local abiotic variables and phytoplankton communities

To explore the multivariate cascading relationships between the CV of four climatic variables (i.e., AT, SI, WS, precipitation), environmental heterogeneity, the CV of water temperature, Schmidt stability, TP, TN and phytoplankton beta diversity (total beta diversity, spatial turnover, spatial nestedness), the stepwise AICc model selection process yielded final path models for each of the three dissimilarity coefficients (Fig. 4). For shallow lakes, the accepted models explained 25% of the

**Table 2**

Linear fit slopes of the linear models for the relationship between the investigated variables and time. Significant slopes are highlighted in bold. Variables are de-seasonalised residuals of the coefficient of variations of climatic and local abiotic variables, climate heterogeneity (Euclidean dissimilarity coefficients of climatic variables), environmental heterogeneity (Euclidean dissimilarity coefficients of chlorophyll-a, pH, silicate, Secchi depth, suspended solids and alkalinity) and the three multiple-site beta diversity measures: Sørensen coefficient (i.e. total beta diversity), Simpson coefficient (beta diversity due to spatial turnover) and nestedness coefficient (beta diversity due to spatial nestedness–resultant richness differences) between shallow and deep lakes.

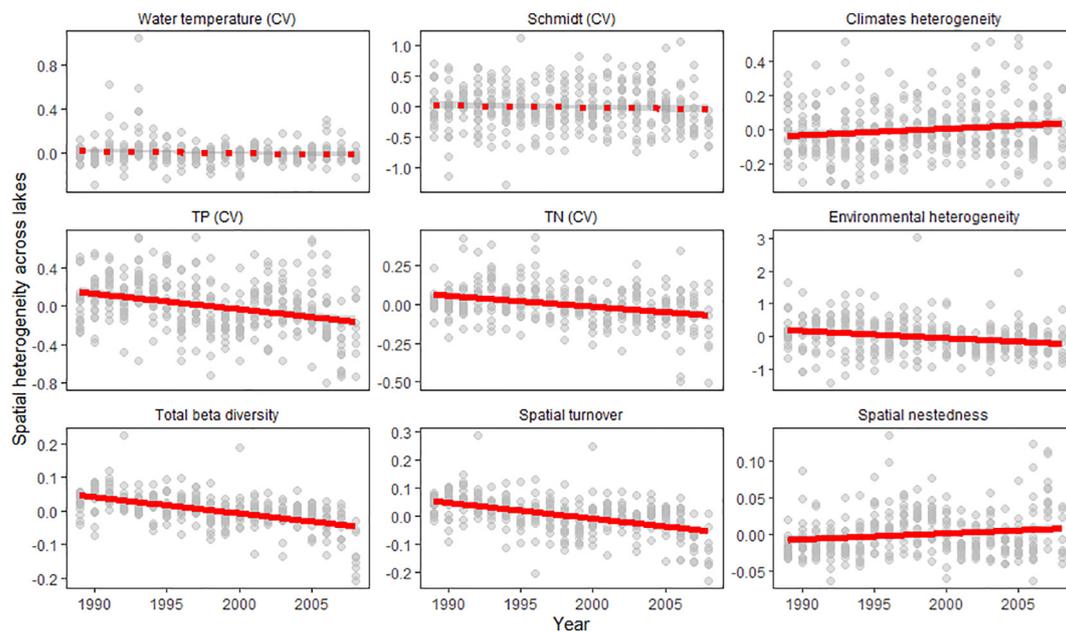
Parameters	Shallow lakes			Deep lakes		
	Slope	P-value	R <sup>2</sup> .adjusted	Slope	P-value	R <sup>2</sup> .adjusted
<b>Climatic variables</b>						
Air temperature	−0.003	0.321	0.000	−0.004	0.140	0.003
Solar irradiance	0.001	0.158	0.003	0.000	0.651	−0.002
Precipitation	−0.003	0.267	0.001	−0.003	0.416	−0.001
Wind speed	<b>0.004</b>	<0.001	0.186	<b>0.003</b>	<0.001	0.038
Climatic heterogeneity	<b>0.005</b>	0.001	0.030	<b>0.004</b>	0.010	0.016
<b>Local abiotic variables</b>						
<b>Water</b>						
temperature	<b>−0.002</b>	0.021	0.012	−0.002	0.065	0.007
Schmidt stability	<b>−0.035</b>	<0.001	0.088	−0.003	0.316	0.000
Total phosphorus	<b>−0.027</b>	<0.001	0.299	<b>−0.016</b>	<0.001	0.101
Total nitrogen	−0.001	0.681	−0.002	<b>−0.007</b>	<0.001	0.108
Chlorophyll-a	<b>−0.012</b>	<0.001	0.061	<b>−0.029</b>	<0.001	0.109
pH	<b>−0.003</b>	<0.001	0.101	<b>−0.002</b>	<0.001	0.242
Silicate	<b>−0.013</b>	<0.001	0.146	<b>−0.002</b>	0.053	0.008
Secchi depth	<b>−0.003</b>	0.039	0.009	<b>−0.032</b>	<0.001	0.125
Suspended solids	<b>−0.017</b>	<0.001	0.117	<b>−0.020</b>	<0.001	0.123
Alkalinity	<b>0.003</b>	0.037	0.009	0.000	0.687	−0.002
Environmental heterogeneity	<b>−0.010</b>	<0.001	0.038	<b>−0.022</b>	<0.001	0.057
<b>Spatial beta diversity and its component</b>						
Total beta diversity	<b>−0.002</b>	<0.001	0.141	<b>−0.005</b>	<0.001	0.309
Spatial turnover	<b>−0.003</b>	<0.001	0.066	<b>−0.006</b>	<0.001	0.247
Spatial nestedness	0.000	0.665	−0.002	<b>0.001</b>	0.003	0.021



**Fig. 2.** Long-term trends (shallow lakes, 1989–2008) in de-seasonalised residuals (residuals from GAM models extracting seasonal trends for each variable) of the coefficient variations (CV) of water temperature, Schmidt stability, total phosphorus (TP), total nitrogen (TN), climatic heterogeneity (Euclidean dissimilarity coefficients of climatic variables), environmental heterogeneity (Euclidean dissimilarity coefficients of chlorophyll-a, pH, silicate, Secchi depth, suspended solids and alkalinity) and the three multiple-site beta diversity measures: Sørensen coefficient (total beta diversity), Simpson coefficient (beta diversity due to spatial turnover) and nestedness coefficient (beta diversity due to spatial nestedness-resultant richness differences). Regression lines are drawn in red. Solid line indicates significant relationships and dashed line indicates non-significant relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

variation ( $R^2$ ) of total beta diversity ( $\chi^2 = 25.2$ ,  $df = 32$ ,  $P = .8$ ,  $AIC = 93.2$ ), 22% of spatial turnover ( $\chi^2 = 23.9$ ,  $df = 30$ ,  $P = .78$ ,  $AIC = 93.9$ ) and 10% of spatial nestedness ( $\chi^2 = 25.6$ ,  $df = 32$ ,  $P = .78$ ,  $AIC = 93.6$ ). The CV of SI and precipitation were not retained in the final model for shallow lakes. The CV of AT showed negative effects on the CV of water temperature ( $R^2 = 0.04$ ) and positive effects on the CV of Schmidt stability ( $R^2 = 0.03$ ). The CV of TP ( $R^2 = 0.11$ ) was negatively affected by the CV of AT and WS and positively affected by the CV of Schmidt

stability, while the CV of TN ( $R^2 = 0.01$ ) was marginally affected by the CV of Schmidt stability. The CV of TP was significantly positively associated with the CV of TN. The CV of TP (31–32%) and Schmidt stability (34–37%) were the strongest predictors (Tables S3 and S4), promoting total beta diversity and its turnover component, either directly or indirectly via enhancing the environmental heterogeneity (15–16%) of the lakes (Tables S3 and S4). However, the CV of TP (30%) and environmental heterogeneity (28%), followed by the CV of WS (18%) and Schmidt

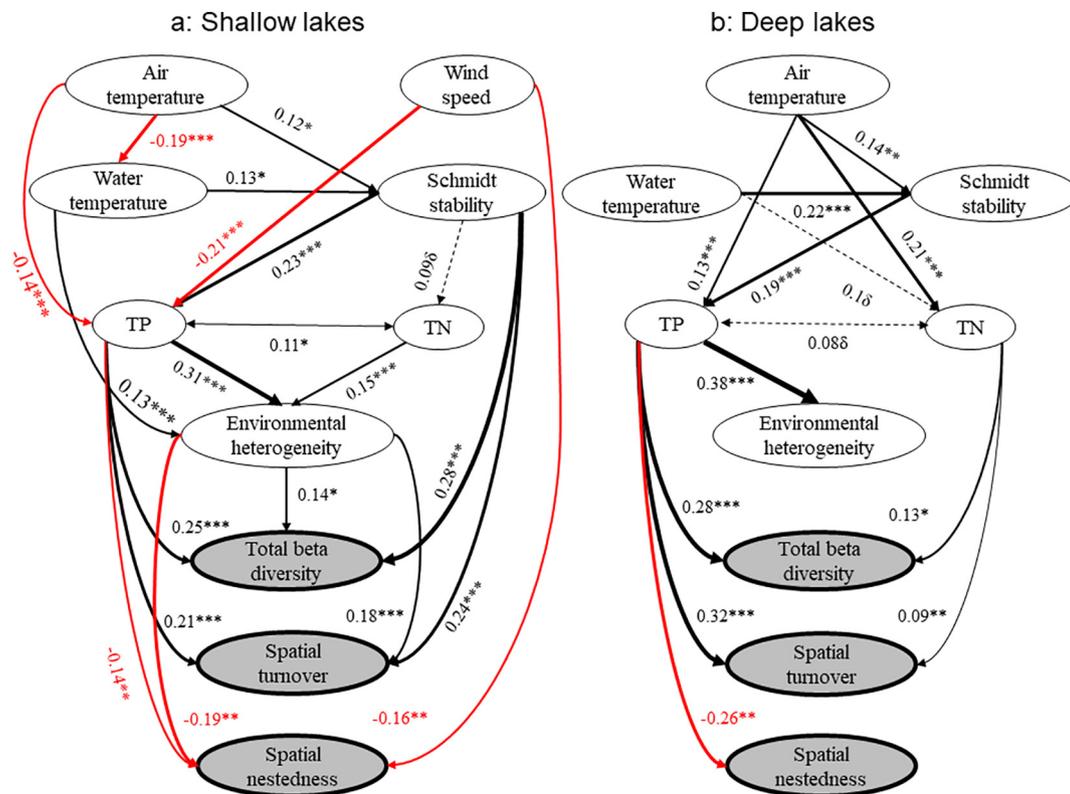


**Fig. 3.** Long-term trends (deep lakes, 1989–2008) in de-seasonalised residuals (residuals from GAM models extracting seasonal trends for each variable) of the coefficient variations (CV) of water temperature, Schmidt stability, total phosphorus (TP), total nitrogen (TN), climatic heterogeneity (Euclidean dissimilarity coefficients of climatic variables), environmental heterogeneity (Euclidean dissimilarity coefficients of chlorophyll-a, pH, silicate, Secchi depth, suspended solids and alkalinity) and the three multiple-site beta diversity measures: Sørensen coefficient (total beta diversity), Simpson coefficient (beta diversity due to spatial turnover) and nestedness coefficient (beta diversity due to spatial nestedness-resultant richness differences). Regression lines are drawn in red. Solid line indicates significant relationships and dashed line indicates non-significant relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 3**

Relative importance (*RI*) of explanatory variables for all model compilations and standardised coefficients (*beta*) obtained from model averaging over all combinations of model terms. Models were calculated for the three multiple-site beta diversity measures: Sørensen coefficient (i.e. total beta diversity), Simpson coefficient (beta diversity due to spatial turnover) and nestedness coefficient (beta diversity due to spatial nestedness-resultant richness differences), respectively. All variables are de-seasonalised residuals (residuals from GAM models extracting seasonal trends for each variable). For *RI*, 1.00 indicates that this particular variable is selected in all models, whereas 0 means that the variable is not selected in any of the models. *Beta* indicates the directions between the beta diversity coefficient and the environmental variable. If a given variable (not shown in the table) was not included in the most important beta diversity models (*AIc*c < 2.0), the direction of influence was obtained from a full model including all the variable candidates. The most important predictors of each metric are given in bold, and the marginally important predictors of each metric are shown in italics. \* *P* < .05; \*\* *P* < .01; \*\*\* *P* < .001.

Variables	Total beta diversity				Spatial turnover				Spatial nestedness			
	Shallow lakes		Deep lakes		Shallow lakes		Deep lakes		Shallow lakes		Deep lakes	
	<i>beta</i>	<i>RI</i>	<i>beta</i>	<i>RI</i>	<i>beta</i>	<i>RI</i>	<i>beta</i>	<i>RI</i>	<i>beta</i>	<i>RI</i>	<i>beta</i>	<i>RI</i>
<b>Climate variables</b>												
Air temperature	0.000	0.53	0.06	0.17	0.000	0.08			0.000	0.09	<b>0.01</b>	<b>1.00</b>
Solar irradiance	0.000	0.03	0.028	0.34	0.001	0.08	0.037	0.21	-0.004	0.20		
Precipitation	0.000	0.03					0.000	0.04	0.000	0.07	0.000	0.11
Wind speed			-0.08	0.40	0.045	0.67	-0.11	0.66	<b>-0.05</b>	<b>1.00</b>	<b>0.03</b>	<b>0.85</b>
<b>Local abiotic variables</b>												
Water temperature	<b>0.008</b>	<b>0.80</b>	-0.004		0.003	0.19			0.000	0.07	0.000	0.09
Schmidt stability	<b>0.01</b>	<b>1.00</b>		0.04	<b>0.01</b>	<b>1.00</b>			0.000	0.08	0.000	0.09
Total phosphorus	<b>0.01</b>	<b>1.00</b>	<b>0.05</b>	<b>1.00</b>	<b>0.02</b>	<b>1.00</b>	<b>0.07</b>	<b>1.00</b>	<b>-0.01</b>	<b>1.00</b>	<b>-0.03</b>	<b>1.00</b>
Total nitrogen			<b>0.04</b>	<b>1.00</b>			<b>0.04</b>	<b>0.81</b>				
Chlorophyll-a	0.001	0.09	<b>0.02</b>	<b>1.00</b>	-0.001	0.19	0.003	0.25	<b>0.01</b>	<b>1.00</b>	0.005	0.75
pH	<b>0.50</b>	<b>1.00</b>	0.221	0.70	<b>0.70</b>	<b>1.00</b>	0.259	0.70	<b>-0.20</b>	<b>1.00</b>		
Silicate	0.007	0.71	<b>0.02</b>	<b>1.00</b>	0.001	0.09	<b>0.02</b>	<b>1.00</b>	0.001	0.20	-0.034	0.10
Secchi depth	-0.002	0.33	0.011	0.21			<b>0.06</b>	<b>1.00</b>	0.000	0.09	<b>0.00</b>	<b>1.00</b>
Suspended solids	0.007	0.70					0.11		0.000	0.09	0.000	0.14
Alkalinity	<b>-0.04</b>	<b>1.00</b>	-0.002	0.05			0.07		<b>-0.04</b>	<b>1.00</b>		



**Fig. 4.** Generalized multilevel path models showing the cascading effects of climate and restoration on the coefficient of variations of water temperature and Schmidt stability, TP, TN, environmental heterogeneity (Euclidean dissimilarity coefficients of chlorophyll-a, pH, silicate, Secchi depth, suspended solids and alkalinity) and the three multiple-site beta diversity measures: Sørensen coefficient (i.e. total beta diversity), Simpson coefficient (beta diversity due to spatial turnover) and nestedness coefficient (beta diversity due to spatial nestedness-resultant richness differences) between shallow (a) and deep (b) lakes. All variables are de-seasonalised residuals of their original values. Arrows represent the flow of causality among variables. Bidirectional arrows between TP and TN were included as they are highly coupled with no hypothesised casual direction. Path coefficients (i.e., numbers associated with each arrow) are standardised partial regression coefficients. Arrow width is proportional to the standardised path coefficients and can be interpreted as the relative importance of each factor. Black arrows represent positive linear relationships, red arrows represent negative linear relationships, and dashed arrows represent marginal relationships (*P* < 0.1). The statistical significance for linear relationships was tested using likelihood-ratio tests. \*: *P* < 0.05; \*\*: *P* < 0.01; \*\*\*: *P* < 0.001; δ: *P* < 0.1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stability (12%), strongly decreased the partial nestedness of phytoplankton (Table S5).

For deep lakes, the accepted models explained 15% of the variation ( $R^2$ ) of total beta diversity ( $\chi^2 = 23.5$ ,  $d.f. = 36$ ,  $P = .95$ ,  $AIC = 87.5$ ), 15% of spatial turnover ( $\chi^2 = 20.6$ ,  $d.f. = 32$ ,  $P = .94$ ,  $AIC = 88.7$ ) and 8% of spatial nestedness ( $\chi^2 = 20.7$ ,  $d.f. = 32$ ,  $P = .94$ ,  $AIC = 88.7$ ). The CV of WS, SI and precipitation were not retained in the final model for deep lakes (Fig. 4). The CV of AT showed positive effects on the CV of Schmidt stability ( $R^2 = 0.03$ ), TP and TN. The CV of WT had positive effects on the CV of Schmidt stability, which had positive effects on the CV of TP. The CV of TP was marginally associated with the CV of TN. The CV of TP (52–72%) was the strongest predictor directly promoting total beta diversity and spatial turnover and decreasing the spatial nestedness of phytoplankton (Table S6). The CV of TN (14–24%) was the second most important driver directly promoting the total beta diversity and spatial turnover of phytoplankton (Table S6). The CV of AT (11–13%) was the third most important driver, mainly through indirect cascading effects on phytoplankton community beta diversity via the CV of TP and TN (Table S6). The CV of Schmidt stability and WT had weak positive effects on total beta diversity and spatial turnover and negative effects on the spatial nestedness of phytoplankton (Table S6).

#### 4. Discussion

We used a long-term semi-monthly dataset on environmental variables and phytoplankton community composition in 20 Danish lakes to investigate seasonal and annual trends in the spatial heterogeneity of environmental variables and phytoplankton composition. We observed 1) significant seasonality in the spatial heterogeneity of most environmental variables and in the spatial beta diversity of phytoplankton communities, 2) significant long-term temporal decreases in the spatial environmental heterogeneity as well as the spatial beta diversity of phytoplankton communities and, additionally, 3) that the spatial homogenisation of phytoplankton could largely be attributed to the spatial heterogeneity of TP and Schmidt stability in shallow lakes and the decrease in spatial TP and TN heterogeneity in deep lakes. Nonetheless, the spatial heterogeneity of the phytoplankton community was affected indirectly by climatic warming in both shallow and deep lakes and directly by wind speed in shallow lakes, albeit only weakly so.

##### 4.1. Significant seasonality in spatial abiotic and biotic heterogeneity

In both shallow and deep lakes, the lowest spatial heterogeneity was observed for climate and water temperature during summer, while higher spatial heterogeneity was observed during early spring and late autumn. This may reflect the facts that the lake water column is relatively undisturbed and water mixing is at its lowest in Danish lakes during the summer. This is due to the usually calmer winds and higher air temperatures, leading to strongly synchronous responses of surface water temperature among lakes irrespective of depth, area and water column stability (Jeppesen et al., 2013; Özkan et al., 2016).

The spatial heterogeneity of TP peaked during summer in both type of lakes, but most pronounced in shallow lakes, likely reflecting marked variations in internal phosphorus loading and consequent phosphorus release between lakes in summer (Søndergaard et al., 2003; Søndergaard et al., 2013). In contrast, the spatial heterogeneity of TN showed a decrease during summer, especially for shallow lakes, which may be due to a common decrease in N loading and an increase in the loss of nitrate by denitrification due to the higher temperatures (Dolman et al., 2016), particularly in shallow lakes with good contact between water and sediment, leading to low inorganic nitrogen concentrations in summer (Søndergaard et al., 2017). Higher summer temperatures could also promote weak stratification, which may increase denitrification and the loss of N (Dolman et al., 2016). The less pronounced patterns in the heterogeneity of TP, TN and other environmental variables in the epilimnion of the deep lakes may, in part, be due to

thermal stratification that prevents a close coupling between sediment and surface water (Søndergaard et al., 2017). Furthermore, the more pronounced environmental heterogeneity in shallow lakes than in deep lakes may also be due to a large variation in the abundance of macrophytes in summer in shallow lakes (Lauridsen et al., 2003).

The total beta diversity (i.e., Sørensen coefficient) and spatial turnover (i.e., Simpson coefficient) of phytoplankton communities in both shallow and deep lakes showed a significant peak in summer. This correlates well with the observed summer peaks in the heterogeneity of TP and other environmental variables, likely reflecting strong environmental control over the seasonal beta diversity of phytoplankton (Özkan et al., 2016). A major change in the composition of the dominant phytoplankton during summer (Reynolds et al., 2002; Jeppesen et al., 2005; Özkan et al., 2016), such as diatom and/or dinophyte dominance in mesotrophic lakes and cyanobacteria and/or chlorophyte dominance in eutrophic lakes, and a lower variability in the phytoplankton community during other seasons, such as diatom dominance in most lakes during spring, might have contributed to the greater spatial turnover during summer (Anneville et al., 2004; Litchman and Klausmeier, 2008; Schwaderer et al., 2011). Spatial nestedness, however, exhibited a reverse pattern and had the lowest values in summer for shallow lakes, while no significant pattern emerged in the deep lakes. This suggests that spatial turnover dominates the seasonal changes in spatial heterogeneity (i.e., total beta diversity) of phytoplankton communities.

##### 4.2. Relative importance of climatic and local abiotic drivers in determining long-term trends in the spatial heterogeneity of phytoplankton

We observed a significant long-term increase in the spatial heterogeneity of wind speed as well as climate heterogeneity, with potential consequences for the temporal variations of water temperature and Schmidt stability in lake waters, as shown by path models (Fig. 4). In shallow lakes, however, both the spatial heterogeneity of air temperature and wind speed had negative and indirect effects on total beta diversity and spatial turnover, mainly mediated by spatial TP heterogeneity and, next, the spatial heterogeneity of water temperature and Schmidt stability. The climatic warming associated with the North Atlantic Oscillation (NAO) has important effects on surface water temperature and mixing processes, leading to a strong temporal increase in Schmidt stability and a firmer vertical spatial structure of the lakes when NAO is high (George et al., 2004; Flaim et al., 2016). Furthermore, the increased spatial heterogeneity of wind speed in shallow lakes led to decreased spatial nestedness of the phytoplankton communities, suggesting that regional climatic heterogeneity could have direct influences on the spatial patterns of phytoplankton communities. This result is supported by previous findings that the temporal variability of wind speed had marked effects on water nutrients and thus phytoplankton communities in shallow lakes (Deng et al., 2018; Rusak et al., 2018; Zhang et al., 2018). By contrast, for deep lakes, air temperature was the only climatic driver retained in the final path model, having significant indirect effects (11–13%) on the total beta diversity, spatial turnover (positive) and spatial nestedness (negative) of the phytoplankton communities. Although the overall contribution of climatic heterogeneity to the total beta diversity and spatial turnover of phytoplankton communities was relatively lower in the shallow lakes (7–8% of air temperature and wind speed) than in the deep lakes (12–13% of air temperature), our results provide evidence that climatic drivers had cascading effects on phytoplankton community composition in both shallow and deep lakes.

The temporal trends in spatial TP and TN heterogeneity were partly explained (usually less than 11%, though) by the spatial heterogeneity of air temperature, wind speed and Schmidt stability in shallow lakes and by the spatial heterogeneity of air temperature and Schmidt stability in deep lakes. The observed potential cascading effects of climatic heterogeneity on spatial TP and TN heterogeneity should be interpreted with caution as the temporal trends in climatic variables were much

more uniform across lakes, and their effects on TP and TN remained uncertain. The high unexplained variation could reflect the different magnitude of external nutrient loading reductions, which is strongly influenced by the original nutrient concentration of the lake as well as the fact that the reduction efforts were most comprehensive for the most eutrophic lakes. The highly eutrophic lakes experienced strong decreases in TP and TN concentrations, while weak or even no changes were recorded for most moderately trophic and mesotrophic lakes (Özkan et al., 2016). This will eventually lead to decreases in the data dispersion around the mean and thus in the spatial heterogeneity of TP and TN across lakes.

According to the path analysis, the decreased spatial TP heterogeneity in both shallow and deep lakes was the most important factor causing spatial homogenisation of phytoplankton communities, either directly or indirectly through a reduction of the spatial environmental heterogeneity. In addition, decreased spatial TN heterogeneity in deep lakes remained the second most important factor resulting in spatial homogenisation of phytoplankton communities. This positive association between the spatial heterogeneity of environments and the biotic community has also been reported for other organisms in both terrestrial (Gianuca et al., 2017; Liu et al., 2018; Uriarte et al., 2018) and aquatic ecosystems (Menezes et al., 2015; Alahuhta et al., 2017; Cook et al., 2018; Salgado et al., 2018). In our study, the key environmental variables in nutrient-rich lakes tended to become more similar to those in less nutrient-rich lakes following an external nutrient loading reduction (Özkan et al., 2016). That is, the lower spatial heterogeneity of TP and the lower spatial environmental heterogeneity both had subsequent effects on phytoplankton community structure. Previous results have indicated that the phytoplankton community in most hypertrophic lakes undergoing strong decreases in external nutrient loading shows increased local heterogeneity, thereby resembling the phytoplankton communities of meso-oligotrophic lakes (Özkan et al., 2016); however, at the same time the similarity of phytoplankton communities among lakes increased and spatial heterogeneity decreased (Anneville et al., 2004; Anneville et al., 2005). This implies that the human measures introduced to reduce the external nutrient loading might markedly increase the local heterogeneity of hypertrophic but not necessarily of oligotrophic lakes, creating regional homogenisation of phytoplankton communities. Furthermore, the decrease in the spatial heterogeneity of phytoplankton communities was largely due to significant decreases in spatial turnover and increases in spatial nestedness. The markedly more narrow nutrient gradients after restoration in the lakes may have resulted in the loss of hyper-eutrophic phytoplankton communities (Anneville et al., 2005), which may explain the temporally diminished importance of the spatial turnover component observed in our study. With restoration, however, the species richness of phytoplankton increases in the most hypertrophic lakes in the direction of more mesotrophic taxa (Anneville et al., 2005; Jeppesen et al., 2005; Özkan et al., 2014), which may explain the increase in importance of spatial nestedness. Notably, the relative contribution of spatial TP heterogeneity to phytoplankton beta diversity was much lower in shallow (32–34%) than in deep lakes (72–76%). This is largely attributed to the circumstance that most variations of spatial heterogeneity of phytoplankton in shallow lakes were accounted for by the spatial heterogeneity of Schmidt stability.

Decreased spatial heterogeneity of Schmidt stability was the most important driver in decreasing the total beta diversity and its turnover components of the phytoplankton community across shallow lakes, either directly or indirectly via changes in spatial TP heterogeneity. Previous studies have indicated a temporally coincident variation between phytoplankton community dynamics and thermal stratification (Winder and Schindler, 2004) and the timing of ice break up (Weyhenmeyer et al., 1999; Adrian et al., 2006). These lake physical processes are coincident with variations in climatic indicators, such as the North Atlantic Oscillation (Weyhenmeyer et al., 1999; George et al., 2004). Furthermore, the climate changes could interact with

restoration by influencing the thermal stratification and water physical processes (Flaim et al., 2016), which have been considered as drivers of long-term changes in the abundance and composition of planktonic communities (Anneville et al., 2005; Thackeray et al., 2008). This may explain the mediating effects of Schmidt stability on phytoplankton community composition observed at regional scale. In deep lakes, however, we found no significant temporal trends in the spatial heterogeneity of Schmidt stability and only weak indirect effects on phytoplankton community composition, which further suggests that the water mixing processes and their climate-mediating effects under the environmental conditions considered here are unlikely to influence the spatial patterns of phytoplankton when water depth increases.

It has been widely recognised that temporal variations in local phytoplankton community composition are the result of both changes in nutrient loading and in climate (Anneville et al., 2004; Anneville et al., 2005; Jeppesen et al., 2005; Pomati et al., 2012; Flaim et al., 2016). Our results provide further evidence of the fact that both climatic and local abiotic drivers contributed to the spatial patterns of phytoplankton communities at landscape scale, either seasonally (not including winter) or in the long term. The potential cascading effects of climate heterogeneity (i.e., air temperature and wind speed) on the spatial heterogeneity of phytoplankton communities were, as expected, controlled by the change in water temperature and mixing patterns, albeit the magnitude and direction depended on the water depth. However, the temporal dynamics of the phytoplankton communities responded more strongly to local abiotic drivers (i.e., TP and Schmidt stability in shallow lakes, TP and TN in deep lakes). Local management measures taken to reduce external nutrient loading have led to synchronous declines in TP and TN as well as synchrony of the temporal changes in local abiotic drivers and phytoplankton communities (Anneville et al., 2004; Anneville et al., 2005; Özkan et al., 2014, 2016). Actually, these measures have only led to strong decreases in the external nutrient loading only for one third of 20 studied lakes, indicating the temporal trends in spatial heterogeneity of biotic and abiotic variables are mainly dominated by the restoration of hypereutrophic lakes (Özkan et al., 2016). This could greatly increase local biotic heterogeneity especially in hypertrophic lakes towards communities of meso-oligotrophic status and eventually decrease the biotic dissimilarity among lakes and thus biotic homogenisation at regional scale. Furthermore, the phytoplankton communities tended to be spatially homogenised across lakes towards relatively low nutrient loadings at both seasonal (i.e., spring and autumn) and long-term scale (i.e., meso-oligotrophic status after a period of restoration). We, therefore, conclude that restoration of eutrophic lakes may lead to an increase in the local heterogeneity of phytoplankton communities at lake scale and to an increase in homogeneity at landscape scale.

#### CRediT authorship contribution statement

**Hui Fu:** Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Funding acquisition. **Guixiang Yuan:** Funding acquisition, Writing - review & editing. **Korhan Özkan:** Data curation, Writing - review & editing. **Liselotte Sander Johansson:** Methodology, Investigation, Writing - review & editing. **Martin Søndergaard:** Conceptualization, Investigation, Methodology, Writing - review & editing. **Torben L. Lauridsen:** Conceptualization, Investigation, Methodology, Writing - review & editing. **Erik Jeppesen:** Conceptualization, Investigation, Methodology, Writing - review & editing, Supervision, Funding acquisition, Project administration.

#### Declaration of competing interest

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

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.141106>.

## References

- Adrian, R., Wilhelm, S., Gerten, D., 2006. Life-history traits of lake plankton species may govern their phenological response to climate warming. *Glob. Chang. Biol.* 12, 652–661.
- Alahuhta, J., Kosten, S., Akasaka, M., Auderset, D., Azzella, M.M., Bolpagni, R., Bove, C.P., Chambers, P.A., Chappuis, E., Clayton, J., 2017. Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude. *J. Biogeogr.* 44, 1758–1769.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., 2011. Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28.
- Anneville, O., Souissi, S., Gammeter, S., Straile, D., 2004. Seasonal and inter-annual scales of variability in phytoplankton assemblages: comparison of phytoplankton dynamics in three peri-alpine lakes over a period of 28 years. *Freshw. Biol.* 49, 98–115.
- Anneville, O., Gammeter, S., Straile, D., 2005. Phosphorus decrease and climate variability: mediators of synchrony in phytoplankton changes among European peri-alpine lakes. *Freshw. Biol.* 50, 1731–1746.
- Anneville, O., Dur, G., Rimet, F., Souissi, S., 2018. Plasticity in phytoplankton annual periodicity: an adaptation to long-term environmental changes. *Hydrobiologia* 824, 121–141.
- Barton, K., 2014. *MuMIn*: multi-model inference. R package version 1.12.1. Available at: <https://cran.r-project.org/web/packages/MuMIn/index.html>.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19, 134–143.
- Burnham, K., Anderson, D., 2002. *Model Selection and Multi-model Inference*. 2nd edn. Springer, New York.
- Cook, S.C., Housley, L., Back, J.A., King, R.S., 2018. Freshwater eutrophication drives sharp reductions in temporal beta diversity. *Ecology* 99, 47–56.
- Core, R.D., 2013. R: a language and environment for statistical computing team RDC Vienna, Austria 2006. ISBN 3900051-07-0, URL <http://www.R-project.org>.
- Coveney, M., Lowe, E., Battoe, L., Marzolf, E., Conrow, R., 2005. Response of a eutrophic, shallow subtropical lake to reduced nutrient loading. *Freshw. Biol.* 50, 1718–1730.
- Deng, J., Paerl, H.W., Qin, B., Zhang, Y., Zhu, G., Jeppesen, E., ... Xu, H., 2018. Climatically-modulated decline in wind speed may strongly affect eutrophication in shallow lakes. *Science of The Total Environment* 645, 1361–1370.
- Dolman, A.M., Mischke, U., Wiedner, C., 2016. Lake-type-specific seasonal patterns of nutrient limitation in German lakes, with target nitrogen and phosphorus concentrations for good ecological status. *Freshw. Biol.* 61, 444–456.
- Dove, A., Chapra, S.C., 2015. Long-term trends of nutrients and trophic response variables for the Great Lakes. *Limnol. Oceanogr.* 60, 696–721.
- Flaim, G., Eccel, E., Zeileis, A., Toller, G., Cerasino, L., Obertegger, U., 2016. Effects of re-oligotrophication and climate change on lake thermal structure. *Freshw. Biol.* 61, 1802–1814.
- George, D.G., Jarvinen, M., Arvola, L., 2004. The influence of the North Atlantic oscillation on the winter characteristics of Windermere (UK) and Paajarvi (Finland). *Boreal Environ. Res.* 9, 389–400.
- Gianuca, A.T., Declerck, S.A., Lemmens, P., De Meester, L., 2017. Effects of dispersal and environmental heterogeneity on the replacement and nestedness components of  $\beta$ -diversity. *Ecology* 98, 525–533.
- Gower, J.C., Legendre, P., 1986. Metric and Euclidean properties of dissimilarity coefficients. *J. Classif.* 3, 5–48.
- Grace, J.B., Bollen, K.A., 2005. *Interpreting the Results From Multiple Regression and Structural Equation Models*.
- Harper, D., 2012. *Eutrophication of Freshwaters: Principles, Problems and Restoration*. Springer Science & Business Media.
- Hilt, S., Köhler, J., Adrian, R., Monaghan, M.T., Sayer, C.D., 2013. Clear, crashing, turbid and back-long-term changes in macrophyte assemblages in a shallow lake. *Freshw. Biol.* 58, 2027–2036.
- Idso, S.B., 1973. On the concept of lake stability. *Limnol. Oceanogr.* 18, 681–683.
- Jeppesen, E., Jensen, J.P., Søndergaard, M., 2002. Response of phytoplankton, zooplankton, and fish to restoration: an 11 year study of 23 Danish lakes. *Aquat. Ecosyst. Health Manag.* 5, 31–43.
- Jeppesen, E., Søndergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., Coveney, M.F., Deneke, R., Dokulil, M.T., Foy, B., 2005. Lake responses to reduced nutrient loading—an analysis of contemporary long-term data from 35 case studies. *Freshw. Biol.* 50, 1747–1771.
- Jeppesen, E., Meerhoff, M., Jacobsen, B., Hansen, R., Søndergaard, M., Jensen, J., Lauridsen, T., Mazzeo, N., Branco, C., 2007a. Restoration of shallow lakes by nutrient control and biomanipulation—the successful strategy varies with lake size and climate. *Hydrobiologia* 581, 269–285.
- Jeppesen, E., Søndergaard, M., Meerhoff, M., Lauridsen, T.L., Jensen, J.P., 2007b. Shallow lake restoration by nutrient loading reduction—some recent findings and challenges ahead. *Shallow Lakes in a Changing World*. Springer, pp. 239–252.
- Jeppesen, E., Kronvang, B., Jørgensen, T.B., Larsen, S.E., Andersen, H.E., Søndergaard, M., Liboriussen, L., Bjerring, R., Johansson, L.S., Trolle, D., 2013. Recent climate-induced changes in freshwaters in Denmark. *Climatic Change and Global Warming of Inland Waters: Impacts and Mitigation for Ecosystems and Societies*, pp. 155–171.
- Köhler, J., Hilt, S., Adrian, R., Nicklisch, A., Kozerski, H., Walz, N., 2005. Long-term response of a shallow, moderately flushed lake to reduced external phosphorus and nitrogen loading. *Freshw. Biol.* 50, 1639–1650.
- Lauridsen, T.L., Jensen, J.P., Jeppesen, E., Søndergaard, M., 2003. Response of submerged macrophytes in Danish lakes to nutrient loading reductions and biomanipulation. *Hydrobiologia* 506, 641–649.
- Lefcheck, J.S., 2016. *piecewiseSEM*: piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods Ecol. Evol.* 7, 573–579.
- Lefcheck, J.S., Orth, R.J., Dennison, W.C., Wilcox, D.J., Murphy, R.R., Keisman, J., Gurbisz, C., Hannam, M., Landry, J.B., Moore, K.A., 2018. Long-term nutrient reductions lead to the unprecedented recovery of a temperate coastal region. *Proc. Natl. Acad. Sci.* 115, 3658–3662.
- Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. *Glob. Ecol. Biogeogr.* 23, 1324–1334.
- Litchman, E., Klausmeier, C.A., 2008. Trait-based community ecology of phytoplankton. *Annu. Rev. Ecol. Syst.* 39, 615–639.
- Liu, J., Vellend, M., Wang, Z., Yu, M., 2018. High beta diversity among small islands is due to environmental heterogeneity rather than ecological drift. *J. Biogeogr.* 45, 2252–2261.
- Menezes, R.F., Borchsenius, F., Svenning, J.C., Davidson, T.A., Søndergaard, M., Lauridsen, T.L., Landkildehus, F., Jeppesen, E., 2015. Homogenization of fish assemblages in different lake depth strata at local and regional scales. *Freshw. Biol.* 60, 745–757.
- Monchamp, M.-E., Spaak, P., Domaizon, I., Dubois, N., Bouffard, D., Pomati, F., 2018. Homogenization of lake cyanobacterial communities over a century of climate change and eutrophication. *Nature Ecology Evolution* 2, 317–324.
- Murphy, F., Schmieder, K., Baastrup-Spohr, L., Pedersen, O., Sand-Jensen, K., 2018. Five decades of dramatic changes in submerged vegetation in Lake Constance. *Aquat. Bot.* 144, 31–37.
- Özkan, K., Jeppesen, E., Davidson, T.A., Søndergaard, M., Lauridsen, T.L., Bjerring, R., Johansson, L.S., Svenning, J.-C., 2014. Cross-taxon congruence in lake plankton largely independent of environmental gradients. *Ecology* 95, 2778–2788.
- Özkan, K., Jeppesen, E., Davidson, T.A., Bjerring, R., Johansson, L.S., Søndergaard, M., Lauridsen, T.L., Svenning, J.-C., 2016. Long-term trends and temporal synchrony in plankton richness, diversity and biomass driven by re-oligotrophication and climate across 17 Danish lakes. *Water* 8, 427.
- Pálffy, K., Vörös, L., 2019. Phytoplankton functional composition shows higher seasonal variability in a large shallow lake after a eutrophic past. *Ecosphere* 10, e02684.
- Pomati, F., Matthews, B., Jokela, J., Schildknecht, A., Ibelings, B.W., 2012. Effects of re-oligotrophication and climate warming on plankton richness and community stability in a deep mesotrophic lake. *Oikos* 121, 1317–1327.
- Rahel, F.J., 2002. Homogenization of freshwater faunas. *Annu. Rev. Ecol. Syst.* 33, 291–315.
- Read, J.S., Hamilton, D.P., Jones, I.D., Muraoka, K., Winslow, L.A., Kroiss, R., ... Gaiser, E., 2011. Derivation of lake mixing and stratification indices from high-resolution lake buoy data. *Environmental Modelling & Software* 26 (11), 1325–1336.
- Reynolds, C.S., 1984. *The Ecology of Freshwater Phytoplankton*. Cambridge University Press.
- Reynolds, C.S., Huszar, V., Kruk, C., Naselli-Flores, L., Melo, S., 2002. Towards a functional classification of the freshwater phytoplankton. *J. Plankton Res.* 24, 417–428.
- Rusak, J.A., Tanentzap, A.J., Klug, J.L., Rose, K.C., Hendricks, S.P., Jennings, E., ... White, D.S., 2018. Wind and trophic status explain within and among-lake variability of algal biomass. *Limnology and oceanography letters* 3 (6), 409–418.
- Salgado, J., Sayer, C.D., Brooks, S.J., Davidson, T.A., Goldsmith, B., Patmore, I.R., Baker, A.G., Okamura, B., 2018. Eutrophication homogenizes shallow lake macrophyte assemblages over space and time. *Ecosphere* 9, e02406.
- Salmaso, N., 2010. Long-term phytoplankton community changes in a deep subalpine lake: responses to nutrient availability and climatic fluctuations. *Freshw. Biol.* 55, 825–846.
- Schwaderer, A.S., Yoshiyama, K., de Tezanos Pinto, P., Swenson, N.G., Klausmeier, C.A., Litchman, E., 2011. Eco-evolutionary differences in light utilization traits and distributions of freshwater phytoplankton. *Limnol. Oceanogr.* 56, 589–598.
- Shipley, B., 2009. Confirmatory path analysis in a generalized multilevel context. *Ecology* 90, 363–368.
- Shipley, B., 2013. The AIC model selection method applied to path analytic models compared using ad-separation test. *Ecology* 94, 560–564.
- Søndergaard, M., Jensen, J.P., Jeppesen, E., 2005. Seasonal response of nutrients to reduced phosphorus loading in 12 Danish lakes. *Freshw. Biol.* 50, 1605–1615.
- Søndergaard, M., Jensen, J.P., Jeppesen, E., 2003. Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia* 506, 135–145.
- Søndergaard, M., Bjerring, R., Jeppesen, E., 2013. Persistent internal phosphorus loading during summer in shallow eutrophic lakes. *Hydrobiologia* 710, 95–107.
- Søndergaard, M., Lauridsen, T.L., Johansson, L.S., Jeppesen, E., 2017. Nitrogen or phosphorus limitation in lakes and its impact on phytoplankton biomass and submerged macrophyte covers. *Hydrobiologia* 795, 35–48.

- Thackeray, S., Jones, I., Maberly, S., 2008. Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change. *J. Ecol.* 96, 523–535.
- Uriarte, M., Muscarella, R., Zimmerman, J.K., 2018. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. *Glob. Chang. Biol.* 24, e692–e704.
- Verbeek, L., Gall, A., Hillebrand, H., Striebel, M., 2018. Warming and oligotrophication cause shifts in freshwater phytoplankton communities. *Glob. Chang. Biol.* 24, 4532–4543.
- Weithoff, G., Rocha, M.R., Gaedke, U., 2015. Comparing seasonal dynamics of functional and taxonomic diversity reveals the driving forces underlying phytoplankton community structure. *Freshw. Biol.* 60, 758–767.
- Wengrat, S., Padial, A.A., Jeppesen, E., Davidson, T.A., Fontana, L., Costa-Böddeker, S., Bicudo, D.C., 2018. Paleolimnological records reveal biotic homogenization driven by eutrophication in tropical reservoirs. *J. Paleolimnol.* 60, 299–309.
- Weyhenmeyer, G.A., Blenckner, T., Pettersson, K., 1999. Changes of the plankton spring outburst related to the North Atlantic oscillation. *Limnol. Oceanogr.* 44, 1788–1792.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21, 213–251.
- Winder, M., Cloern, J.E., 2010. The annual cycles of phytoplankton biomass. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365, 3215–3226.
- Winder, M., Schindler, D.E., 2004. Climatic effects on the phenology of lake processes. *Glob. Chang. Biol.* 10, 1844–1856.
- Wood, S., 2017. R package 'mgcv': Mixed GAM Computation Vehicle With Automatic Smoothness Estimation.
- Zhang, M., Shi, X., Yang, Z., Yu, Y., Shi, L., Qin, B., 2018. Long-term dynamics and drivers of phytoplankton biomass in eutrophic Lake Taihu. *Sci. Total Environ.* 645, 876–886.
- Zhang, Y., Yin, Y., Liu, X., Shi, Z., Feng, L., Liu, M., Zhu, G., Gong, Z., Qin, B., 2011. Spatial-seasonal dynamics of chromophoric dissolved organic matter in Lake Taihu, a large eutrophic, shallow lake in China. *Org. Geochem.* 42, 510–519.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology With R*. Springer Science & Business Media.