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Riverine phytoplankton functional groups response to multiple stressors variously depending on hydrological periods

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ABSTRACT

Rivers and related freshwater ecosystems are facing increasing natural disturbance and anthropogenic stressors. Understanding the key ecological processes that govern the riverine biota in aquatic ecosystems under multiple pressures has crucial importance. However, there is still insufficient knowledge in quantifying of stressors interactions. Moreover, the understanding of the responses of riverine phytoplankton to multiple stressors is still scarce from catchment aspect. As an interdisciplinary study, the catchment hydrological processes were linked to ecological responses in this study, and we chose phytoplankton functional groups (PFGs) instead of taxonomic classifications of algae to examine their responses to land-use pattern (L), hydrological regime (H), and physicochemical condition (P) across two contrasting hydrological periods (dry, wet). The traits-based phytoplankton functional groups are highly suggested as robust bio-indicators for better understanding the current ecological status. The hydrological regime was described by a matrix indices of hydrological alteration based on the outputs of a well-established ecohydrological model (SWAT). The results from variation partitioning analysis showed that P and H dominate during the dry period and P in high flows. Structural equation models (SEM) showed that the skewness of 7 days discharge emerged as a key driver of H, and had always an indirect effect on functional group **TB** (benthic diatoms) during both hydrological periods. The functional group **M** (mainly composed by *Microcystis*) has directly related to phosphorous in both periods, while indirectly to L of urban area in high flow period, and water bodies in low flow period. This study emphasized that climate change and anthropogenic activities such as altering flow regime and land-use pattern affect directly or indirectly riverine phytoplankton via physicochemical conditions. In addition, our findings highlighted that biomonitoring activities require detailed investigation in different hydrological periods. SEM is recommended for improved understanding of phytoplankton responses to the changing environment, and for future studies to fulfill the increasing demand for sustainable watershed management regarding aquatic biota.

Keywords:

Phytoplankton functional groups,

Land-use pattern,

Hydrological regime,

Physicochemical condition,

Structural equation model

1. Introduction

Riverine phytoplankton is one of the vital primary producers in the river ecosystem, and acts as robust bio-indicator responding to multiple stressors (Hilton et al., 2006). It is widely used for bio-assessment of freshwater ecosystems in recent years (EC, 2000). Benthic diatoms are one of significant elements of riverine phytoplankton recruitment, especially in the fine substrate rivers (Bolgovics et al., 2017). Short water residence time lead to benthic diatoms dominance (Reynolds, 1994; Wang et al., 2018), while dynamic flow velocity results in shifts of the share of benthic diatoms in the phytoplankton community (Wu et al., 2007). Moreover, flow alteration influence riverine phytoplankton assemblages by altering nutrient delivery, light availability, dewatering of habitats or severe vertical mixing (Reynolds, 2006). Despite diatom dominance, several studies demonstrate that running water can also suffer the negative consequences of cyanobacterial blooms, resulting from anthropogenic eutrophication and changing environment (Bowling et al., 2016; Stanković et al., 2012). Intensive agriculture and urbanization strongly affect freshwater biodiversity through flow modification and nutrient over-enrichment by fertilizer, pesticides, and sewage fluxes (Bussi et al., 2016; Harris and Smith, 2016; Katsiapi et al., 2012). Changing climate conditions, specifically global warming and altered rainfall patterns, play additional interactive roles in modulating cyanobacterial blooms frequency, intensity and geographic distribution in a long-term aspect (Paerl, 2017; Paerl et al., 2011). Therefore, multiple stressors including natural disturbances (drought and floods) and anthropogenic stressors (human-induced water pollution, eutrophication) are affecting riverine phytoplankton directly or indirectly. Understanding the key ecological processes that govern riverine phytoplankton community in aquatic ecosystems under multiple pressures has crucial importance. It is a fundamental prerequisite for robust bio-assessment, as well as sustainable watershed management. However, investigations and analysis of stressors interactions were much insufficient. Studies about the response of riverine phytoplankton to multiple stressors from catchment scale are still scarce.

Interactions of multiple stressors determine the occurrence and survival of algae. In turn, phytoplankton response to stressors by associated functions of tolerance, preference, and sensitivities of distinct traits (Kruk et al., 2017; Litchman and Klausmeier, 2008). In this study, we chose phytoplankton functional groups (PFGs) instead of taxonomic classifications of phytoplankton dynamics to investigate their response to multiple stressors in a better way: land-use pattern (L), hydrological regime (H) and physicochemical condition (P) (see Fig. 1, a schematic diagram developing a conceptual framework). PFGs concept suggested aggregating species with similar features into a few functional groups. Each group was described according to the physiological, morphological and ecological traits, as well as common environmental sensitivities and tolerances (Borics et al., 2007; Reynolds et al., 2002). For elaboration of the phytoplankton-based quality assessment, Borics et al. (2007) replenished and evaluated PFGs in rivers, considering four parts: trophic state, turbulence character, time sufficient for development of the given assemblage and risk. Code **TB** (composed by benthic diatoms) and code **M** (mainly composed by limnophilic *Microcystis spp.*) represent two highly different functional groups of riverine phytoplankton. **TB** is assigned to mesotrophic, highly lotic preference benthic species with low risk of harm, while **M** assigned to hypertrophic nutrient status, lentic preference, climax assemblages with potential toxicity. Mischke et al. (2011) also selected the proportions of Cyanobacteria and Pennales (as typical benthic diatom) to assess the trophic status of German Rivers. They concluded an unhealthy status with a high proportion of Cyanobacteria, while they detected a healthy status with a high percentage of Pennales. We were working with a lentic-lotic continuum watershed in a rural area under natural hydrology disturbance and human-induced stressors. Based on the previous investigation of this catchment, we found nutrients, especially the nitrate loads, were highly related with agriculture activities in the Treene basin (Haas et al., 2016). **TB** were dominant in most of the study area, while their share varied in time and space(Qu et al., 2018b). The temporary intensive occurrence of *Microcystis* in dry season received high concerns from the local stakeholders (Qu et al., 2018a). Therefore, we are especially interested in these two functional groups **TB** and **M**, in addition to the phytoplankton community characteristics. We hypothesized that: 1) High flow condition promote to **TB** domination over the others; 2) High share of agriculture land-use rise ascendancy of **M** in the community. Our study aims to disentangle the causal-effects relationship of multiple stressors and riverine phytoplankton community (indicated by PFGs) from wet and dry seasons. The answers would give novel insights into the complex pathways of joint impact of natural and anthropogenic descriptors on riverine phytoplankton community in lowland rivers across contrasting hydrological periods.

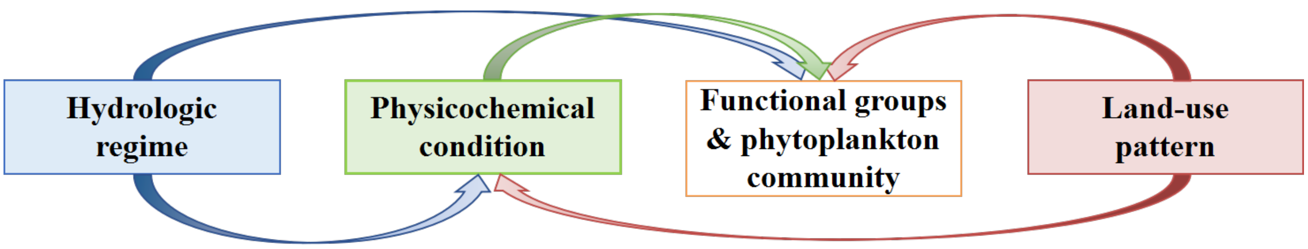


Fig. 1 Schematic diagram showing the major factors (e.g., hydrological regime, physicochemical condition, and land-use pattern), which govern the pattern of phytoplankton functional groups and community structures. Those controls include state factors, interactive controls, direct controls and indirect controls, which eventually causes the difference of phytoplankton communities.

2. Material and methods

2.1. Study area and sampling sites

This study was carried out in Treene River, a lowland watershed located in the northern Germany. As a lowland catchment, the maximum elevation of Treene basin is 76 m, with watershed area of 517 km^2. The Treene catchment is in a temperate climate zone, which is influenced by marine climate. Meanwhile it has a typical seasonal pattern of discharge, with the highest water flow in winter and the lowest in summer and autumn (Guse et al., 2015a). Field surveys were carried out in two hydrological periods (a wet period in December 2014 and a dry period in September 2015) on 59 sampling sites which covered mainstream and tributaries of the catchment. The abbreviation of the site names are according to each sub-basin where they are located in: Bo for Bollingstedter Au, Je for Jerrisbek, Ju for Juebek, Ki for Kielstau, Sa for Sankermark See, and Tr for the mainstream of Treene. The numbers count along the longitudinal axis of rivers from the outlet to upstream. The sampling points in close distance of lakes are not located in the lake, but rather are situated systematically downstream following the lakes (Fig. 2).

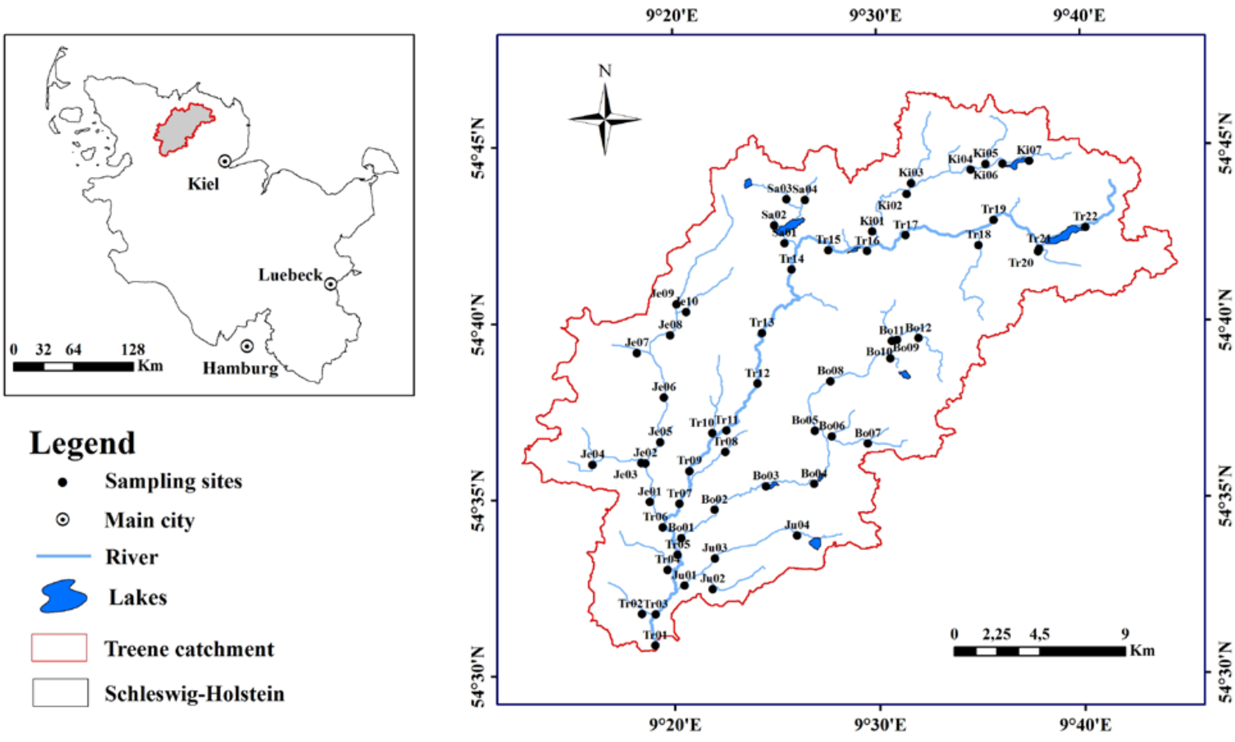


Fig. 2 The location of the Treene catchment and 59 sampling points in Schleswig-Holstein state of Germany.

2.2. Land-cover pattern analysis (L)

The catchment landscape is dominated by agricultural land-use. Around 50% of the area is covered by arable land, and around 30% by winter pasture. Soils in the north of the catchment (natural region of Angeln) are nutrient-rich and have a pH value ranging 6 to 7, while the pH of soils in the south-east of the catchment (Geest) varies from 4 to 5.5 (Tavares, 2006). Therefore, in the Angeln natural region, corresponding to Kielstau and Treene upstream catchments, agricultural fields are more common, meanwhile, in the southern Geest region (e.g., Jerrisbek and Juebek catchments) pastures constitute to a bigger part. The Treene catchment can be characterized by a slightly undulating landscape, with various depressions and lakes (Kiesel et al., 2010). Land-use data was provided by the Schleswig-Holstein State Bureau of Surveying and Geo-information (LVERMGEO-SH, 2012). The land-use analysis performed via ArcGIS software (Version 10.0, ESRI, US) processing (Fig. A. 1). Eight land-use types were classified: agricultural land-generic (AGRL), forests (FRST), rangeland (RNGE), industrial area (UIDU), urban areas (URMD), water bodies (WATR), wetland (WETL) and winter pasture (WPAS). The upstream watershed area from each sampling site was accumulated, and the land-use within this area was considered as the land-use pattern affecting the sampling site. In this case, the sites located at downstream and near to the lakes or cities presented a higher percentage of water bodies or urban area. For example, the sites located on the upstream region of a city has none percentage of urban area land-use, while the downstream sites have decreasing percentages along the river flow.

2.3. Hydrological regime analysis (H)

Except for water depth and velocity which were measured *in situ* at the sampling points (velocity – using FlowSens Single Axis Electromagnetic Flow Meter, Hydrometrie, Germany), the hydrological regime was mainly described by the indicators of hydrological alteration (IHA) (Olden and Poff, 2003). The IHA, illustrating the hydrographic signatures from the duration, frequency, timing magnitude and rate of flow events, are ecological relevant and can be calculated based on daily discharge data and are also used in hydrology (Kiesel et al., 2017; Pool et al., 2017). The daily discharge time series in this study based on the output of the ecohydrological SWAT model (Soil and Water Assessing Tool). In this model application, the model discretization for the Treene catchment resulted into 108 sub-basins. In a multi-site calibration, six hydrological stations which distributed in the catchment were used to consider the spatial heterogeneity in reproducing discharge. The modeling period subdivided into a calibration (2001 to 2005) and a validation period (2006 to 2016). To evaluate the model performance, we used three well-known performance measures: Nash-Sutcliffe Efficiency, Percent Bias and RSR (root mean square error divided by standard deviation) (see Guse et al., 2015b for details). Daily modeled discharge values were used for subbasins in which at least one sampling point located. At this moment, the sampling points were related to the model results from the closest outlet of a sub-basin outlet. We used 57 hydrological indices from IHA describing the traits of hydrological regime. The final hydrological matrix included: magnitude, frequency, rate of flow events and *in situ* measurement (Table A.1).

2.4. Physicochemical factors analysis (P)

Physicochemical factors collection included a field *in situ* measurements and laboratory measurement. Water temperature (WT), pH, electric conductivity (EC) and dissolved oxygen (DO) of the surface water were measured *in situ* using Portable Meter (WTM Multi 340i and WTW Cond 330i, Germany) at each sampling site. Simultaneously, two water samples were stored in pre-cleaned plastic bottles (500 ml each) for nutrient analysis in the laboratory. They were partially filtered through GF/F glass microfiber filter (Whatmann 1825-047) for collecting the total suspended substances. Both filtered and unfiltered samples were kept frozen at -20 ℃ until measurement. Concentrations of total phosphorus (TP), phosphate-phosphorus (PO_4^{3-}-P), ammonium-nitrogen (NH_4^+-N), nitrate-nitrogen (NO_3^--N), nitrite-nitrogen (NO_2^--N), chloride (Cl^-) and sulfate (SO_4^{2-}) were measured using the standard methods of DEV (Deutsche EinheitsverfahrenzurWasser-, Abwasser- und Schlammuntersuchung). Dissolved inorganic nitrogen (DIN) was defined as the summation of nitrite-nitrogen (NO_2^--N), nitrate-nitrogen (NO_3^--N) and ammonium-nitrogen (NH_4^+-N), and the nitrogen to phosphorus ratio (NPR) is the ratio between DIN and TP. In this study, we chose DIN:TP ratio instead of the TN:TP ratio, since DIN:TP can better discriminate the N and P limitation of phytoplankton (Bergström, 2010). Total suspended solids (TSS) were measured according to Standard Operating Procedure for Total Suspended Solid Analysis (Federation and

Association, 2005).

2.5. Phytoplankton collecting and processing

Phytoplankton samples were quantitatively analyzed with a known concentration from the subsurface (5 - 40 cm) water of the river by plankton net. Identification included two steps. First, soft algae was identified in a Fuchs-Rosenthal chamber with an optical microscope (Nikon Eclipse E200-LED, Germany) at ×400 magnification, after employing the sedimentation method for the samples (Sabater et al., 2008). Taxonomic identification was based on the references of Hu and Wei (2006) and Burchardt (2014). Second, for further determination of the diatom species in the samples, permanent slides were prepared after oxidization (using 5ml of 30% hydrogen peroxide, H_2O_2, and 0.5ml of 1mol/l hydrochloric acid, HCl), and then 0.1 ml of the diatom-ethanol mix was transferred on a 24×24 mm coverslip. Diatoms were identified with the optical microscope (Nikon Eclipse E200-LED, Germany) at ×1000 under oil immersion, based on the key books by Bey (2013), Hofmann et al. (2011) and Bak et al. (2012). Algal biomass was calculated using the approximation of cell morphology to regular geometric shapes, assuming the fresh weight unit as expressed in mass, where 1 mm^3/L = 1 mg/L (Huang, 2000; Wetzel and Likens, 2013). We then calculated the relative biomass of every species as their abundance. Based on the criteria proposed by Reynold (2002), species that contributed more than 5% of the total biomass were sorted into functional groups, and the phytoplankton functional classification was done according to Reynolds et al. (2002), Borics et al. (2007) and Padisák et al. (2009). Species not mentioned in the references were assigned to a group according to their morphological and ecological characteristics and the environmental conditions prevailing during their greatest occurrence (Devercelli, 2006). In this study, we specially focused on the functional group **M** (species mainly from genus: *Microcystis* consisted by *Microcystis* *aeruginosa*, *M. wesenbergii*, *M. viridis*) and **TB** (mainly composed of benthic Pennales, typically genus such as: *Navicula*, *Nitschia*, *Gomphonama*, *Fragilaria*). From the references, this two group of algae have different strategies, preference of living, and they present two characteristic conditions: highly lotic river sections with **TB** dominance, while **M** dominance in eutrophicated lentic habitats (Borics et al., 2007).

2.6. Statistical analysis

For achieving the best performance, the phytoplankton functional groups abundance matrix was Hellinger transformed (Legendre and Gallagher, 2001; Legendre and Legendre, 2012). Firstly, the analysis of PERMANOVA was conducted for testing the difference of PFG composition (function: *adonis* of the R-package: vegan). In the meanwhile, the three sets of abiotic variables (i.e., L, H and P) collinearity was tested when using all variables in the model of explaining variations of phytoplankton communities (function: *cor* of the R-package: stats). Afterwards, a forward selection (Blanchet et al., 2008) was carried out to choose a parsimonious subset of explanatory variables (function: *forward.sel* of the R-package: adespatial), and then the multivariate community structure was modeled under variation partitioning analysis (Borcard et al., 1992) (function: *rda*, *varpart* of the R-package: vegan). We then constructed structural equation model (SEM) (Westland, 2016) for quantitative evaluation of the relationship between human and natural stressors on PFG composition, as well as the potential effect of land-use and hydrology on in-stream nutrients. We used reduced-multidimensional data rather than original PFG matrices in the analysis since SEM can only handle one-dimensional variables. Nonmetric multidimensional scaling (NMDS) ordination was applied to produce reduced-dimensional data of PFG composition, measured as the first NMDS axis scores for each site (i.e., NMDS1) to represent the main condition of the whole phytoplankton community composition (function: *metaMDS* of the R-package: vegan). To achieve the SEM, we first proposed the conceptual model for the three bio-indicators (PFG: **TB**, **M** and NMDS1). The conceptual model included all possible pathways between the response variables and their key abiotic variables, which identified by general linear model (function: *glm* and *step* of the R-package: stats). In addition to the direct pathways, we also checked the indirect ones to see if variables exerted further effects via mediation variables. From the initial model, we then specified the pathways. All non-significant paths were eliminated stepwise until all remaining paths were significant related to the response variables. Standardized path coefficients were calculated for each pathway for a better comparable in the SEM. The overall final model fit was evaluated with root mean square error of approximation (RMSEA), and the comparative fit index (CFI). RMSEA approach to 0, and CFI close to 1.0 indicate a good fit of the model (Grace, 2006). In this study, SEM was constructed by *sem* in the R-package: lavaan.

All analyses were conducted with the R software (version 3.5.1, R Development Core Team, 2018).

3. Results

3.1. Description of watershed hydrological regime and physicochemical condition

From the model outputs, the indicators of hydrological alteration varied across the two studied periods. Water flow has a higher magnitude and fluctuation in the high flow (December) than in the low flow period (September) (e.g., at the outlet of the catchment Tr01, Fig. A. 2). Some other typical hydrological indices, for instance, H20 which represents the skewness of seven days of discharge, has an opposite spatial trend during these two periods (Fig. A. 3). The index H20 ranges from -0.775

to 2.439. Most values of H20 were positive with a range of 0.043 to 2.439. They were negative skewed only in the upstream of the main river (specifically sites: Tr16 - Tr22) in high flow period, and tributary Jerrisbek during dry season. We observed a relatively high value in the tributary Jerrisbek during the wet season (with an average value of 2.038). The key hydrological indicators were summarized after pre-selection excluding the ones with significant multi-collinearity (Table 1).

The local physicochemical variables measured *in situ* varied considerably among different hydrological periods and sub-catchments (Fig. A. 4). Firstly, the difference of water temperature (WT) in two seasons was remarkable, and mean values in December 2014 and September 2015 were 5.69 ℃ and 1424 ℃, respectively (Table 1). The value of pH followed a similar pattern in different sub-basins, while mean value in September was slightly higher than in December (8.084 > 7.487, Table 1). The concentrations of ammonium-nitrogen (NH_4^+-N) showed a higher concentration in December compared to September (average: 0.307 mg/L > 0.158 mg/L, Table 1, also see more details in Fig. A. 4). Conversely, nitrate-nitrogen (NO_3^--N) concentration showed lower in December than in September (average: 3.551 mg/L < 9.243 mg/L, Table 1, also see more details in Fig. A. 4). Dissolved inorganic nitrogen (DIN) followed a similar pattern as nitrate-nitrogen. We observed a decreasing trend of phosphate-phosphorus (PO_4^{3-}-P) concentration while an increasing trend of nitrogen to phosphorous ratio (NPR) along the mainstream of Treene (Tr) in September 2015. Except for the sub-basin Juebek, the average value and fluctuation of NPR in September was higher than in December (Fig. A. 4). The concentrations of NH_4^+-N and PO_4^{3-}-P in sub-basin Kielstau were always significantly higher than other sub-basins at both investigation periods. Generally, the nutrient contents such as NO_3^--N, DIN and NPR in wet season were lower than in dry season (Table 1).

Table 1 Summary of important hydrological (H), and physicochemical (P) variables with their codes and descriptions in this study. Variables with significant multicollinearity (spearman correlation coefficient greater or equal to 0.75) are excluded from the table.

Variables						
Code	Unit	Description	High flow		Low flow	
			Mean	SD	Mean	SD
H		**Hydrological parameter**				
H01	m^3/s	Discharge at the sample day	2.274	4.38	0.299	0.52
H20	-	Skewness of 7 days' discharge	0.955	0.686	0.814	0.696
H36	-	Skewness of 30 days' discharge	1.143	0.636	1.428	0.435
H41	days	Low flood pulse count 30 days	13.373	10.257	22.373	3.737
H42	days	High flood pulse count 3 days	1.492	1.467	0	0
H55	-	Rate of change in 7 days	-0.038	0.089	-0.017	0.032
P		**Physicochemical parameter**				
WT	℃	Water temperature	5.69	1.581	14.237	1.619
pH	-	pH	7.487	0.474	8.084	0.407
NH4	mg/L	Ammonium-nitrogen (NH_4^+-N)	0.307	0.276	0.158	0.266
NO3	mg/L	Nitrate-nitrogen (NO_3^--N)	3.551	1.772	9.243	6.784

NO2	mg/L	Nitrite-nitrogen (NO_2^--N)	0.02	0.019	0.054	0.119
TP	mg/L	Total phosphorus	0.225	0.116	0.211	0.209
PO4	mg/L	Phosphate-phosphorus (PO_4^{3-}-P)	0.077	0.058	0.072	0.109
NPR	-	Nitrogen to phosphorus ratio	21.002	14.926	79.739	67.715
SO4	mg/L	Sulfate (SO_4^{2-})	31.819	10.923	44.087	14.572

3.2. Variation of phytoplankton assemblages

We observed 396 algal taxa from the 118 samples and they were classified into 21 phytoplankton functional groups (PFGs). Among them, there were 16 groups in December 2014, while 19 groups in September 2015. The PERMANOVA analysis showed a significant dissimilarity of phytoplankton functional groups composition both temporal (high water flow period and low water flow period) and spatial (sub-basins). We also found that biomass increased significantly from high flow to low flow period in the sub-basins of Tr, Sa and Ju, while fewer changes occurred in the sub-basins of Bo, Je and Ki (Fig. 3). In both hydrological periods, functional group **TB** constituted a high portion in sub-basins: Bo (87% - Dec. 2014, 68% - Sep. 2015) and Je (98% - Dec.2014, 64% - Sep. 2015). In contrast, the functional group **M** percentage increased in the sub-basin of Tr, Ki, Sa and Ju from December to September (Table A. 2).

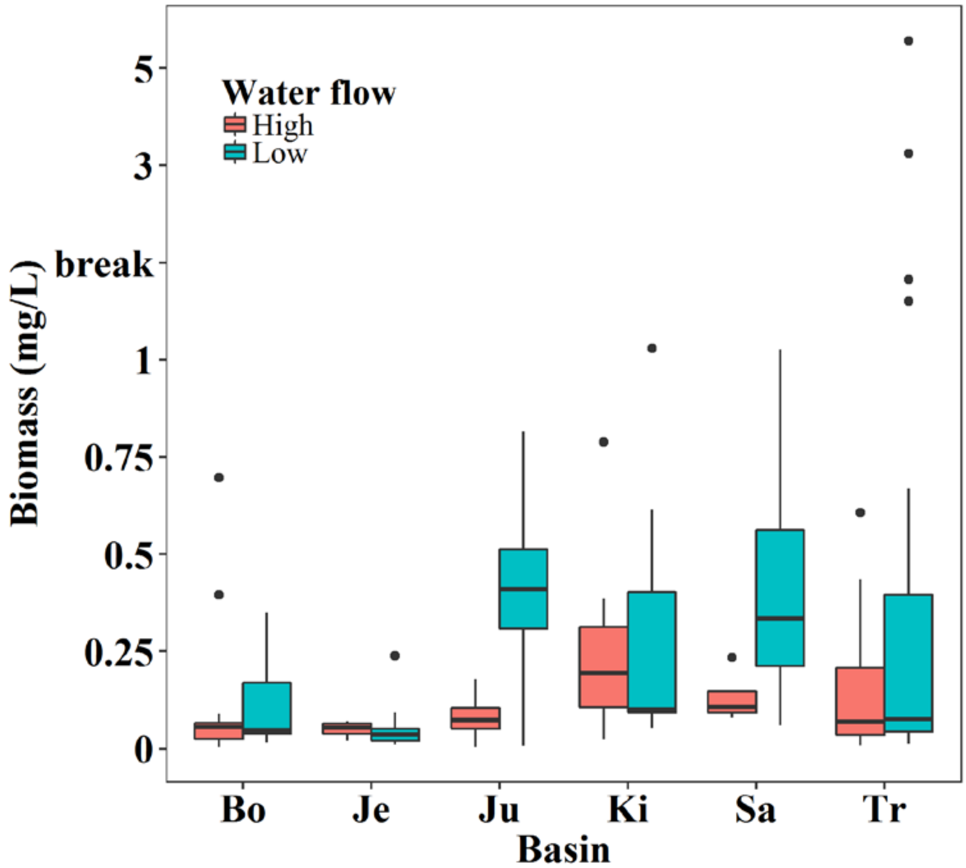


Fig. 3 Average biomass in different basins (Bo represents for sub-basin Bollingstedter Au, Je for Jerrisbek, Ju for Juebek, Ki for Kielstau, Sa for Sankermark See and Tr for mainstream of Treene)

3.3. Effect of abiotic factors on phytoplankton functional groups

3.3.1. Relationship described by variation partitioning

In wet season (Dec. 2014), there were 3 L, 5 H and 5 P variables selected by a forward selection (supporting information Table A. 3). All the groups showed significant relationships with PFGs (by *anova* function in R, $p<0.001$). According to variation partitioning analysis, the three sets could explain 44% of the variation in PFGs (Fig. 4). The variations purely explained by H, L and P were 4%, 2% and 6%, respectively, while the shared fraction of the three variables was 14%. In general, the joint contribution by H and P (H×P, 9%) was higher than those by H×L (2%) and P×L (7%). In the dry season (Sep. 2015), there were 2 L, 1 H and 6 P variables selected by a forward selection

(Table A. 3). The PFGs variation was mostly related to the effect of P (their pure effect explained 10% of the variation), whereas the pure effect of H was the least (only accounted for 0.4%). The variation partitioning also showed that both wet and dry periods had similar explanation fraction of land cover (Dec. 2014: 2%; Sep. 2015: 2%).

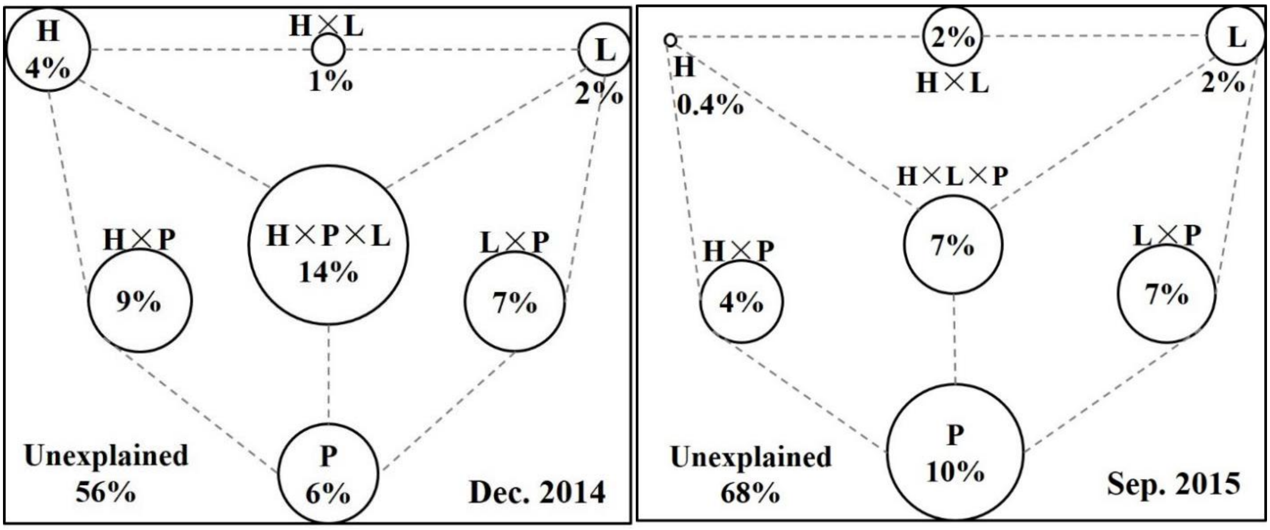


Fig. 4 Contributions of the hydrological (H), land-cover (L) and physicochemical (P) variables to the variances in phytoplankton functional groups (PFGs). Each diagram represents a given biological variation partitioned into the pure effects of H, L and P (i.e. when removing the variations caused by other two factors), interaction between any two variables (H×L, L×P, H×P), interaction of all three factors (H×L×P) and unexplained variation (total variation = 100). The analysis includes two scenarios: left: illustrate the situation in December of 2014 (n=59), right: show the results in September of 2015 (n=59).

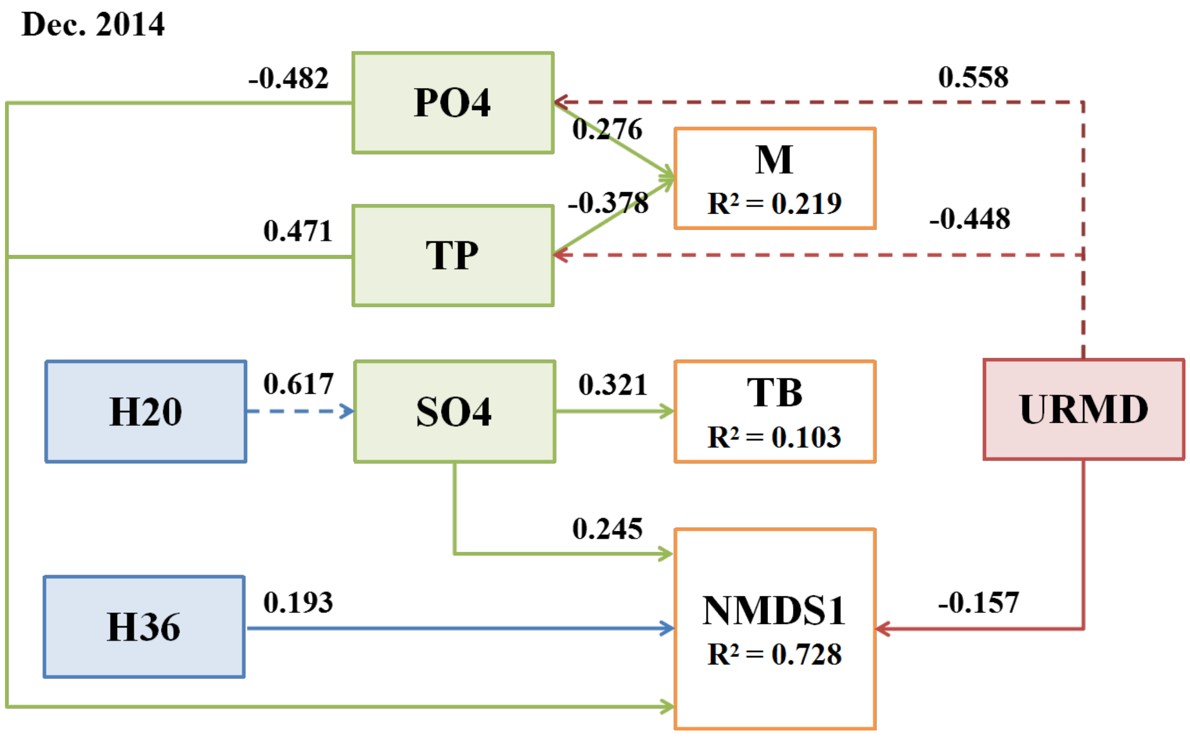
3.3.2. Relationships described by structural equation model

From the general linear model results (supporting information Table A. 4), we got a general idea about the effects of the multiple stressors. For further investigation of the causal relationship between the abiotic and biotic variables, we fitted structural equation models (SEMs) to infer the direct and indirect effects of specific abiotic variables on bio-indicators (indicated by NMDS1 and phytoplankton functional groups **M**, **TB**) (Fig. 5).

In high flow period (Dec. 2014), SEMs indicated that group **M** was directly governed by

PO_4^{3-}-P and TP (β=0.276, 0.378, respectively, standardized coefficient), while indirectly affected by URMD via PO_4^{3-}-P and TP (β=0.558, -0.448, respectively, standardized coefficient). The hydrological variable H20 (skewness of 7 days' discharge) was mediated through sulfate (SO_4^{2-}) effect on **TB**. The SEM explained 72.8% of the variation of NMDS1. The explanations come from H36 (skewness of 30 days' discharge), PO_4^{3-}-P, TP, SO_4^{2-} directly, and URMD indirectly via H20.

During the low flow period (Sep. 2015), the strongest relationship (β=0.525, standardized coefficient) was observed in the SEM analysis between functional group **TB** and dissolved oxygen (DO). H20 exerted an indirect effect on **TB** via DO (β=-0.465, standardized coefficient). Area covered by water (WATR) appeared as the key variable for the group **M**, directly (β=0.503, standardized coefficient) and indirectly through NPR (β=-0.318, standardized coefficient). The SEM explained 31% of the community variation (represented by NMDS1) was negatively affected by DO, and positively affected by WT and WATR.



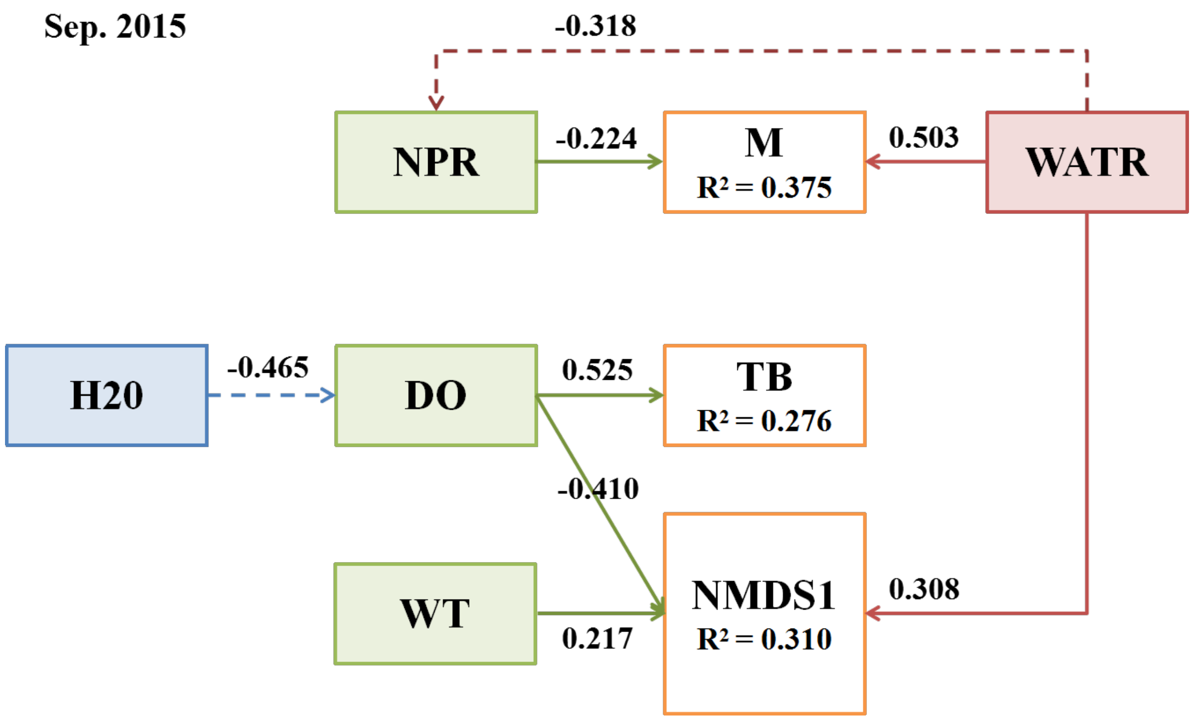


Fig. 5 Structural equation models embody the causal relationships between hydrological regime (H), land-use pattern (L), physicochemical condition (P) and phytoplankton bio-indicators. Solid arrows represent direct paths ($p<0.05$), and dashed arrows represent indirect paths. The values corresponding to the path coefficients have standardized effect size. The models are evaluated using R^2. The hydrological parameters are in blue squares, physicochemical parameters in green squares, land-use parameters in red squares, and the orange squares represent phytoplankton functional groups (**M**, **TB**) and community index (NMDS1). The analysis includes two scenarios: the upper one illustrates the situation in December of 2014 (n=59), the lower one shows the results on September of 2015 (n=59). The environmental variables included: H20: skewness of 7 days' discharge (including the sampling day); H36: skewness of 30 days' discharge (including the sampling day); WATR: area covered by water; URMD: urban area with residential-medium density; PO4: phosphate- phosphorus; TP: total phosphorus; SO4: sulfate; NPR: nitrogen to phosphorus ratio; DO: dissolved oxygen; WT: water temperature.

4. Discussion

*4.1. Response of **TB** to multiple stressors*

We observed a higher contribution of hydrological regime during high water period (Fig. 4). The result demonstrated the importance of flow regime in shaping phytoplankton community population and composition, which was also supported by previous results in the study region (Qu et al., 2018a). Among the hydrological variables, skewness of discharge in 7 days (H20) emerged as the key factor in shaping the pattern of **TB** both in wet and dry periods of the study (Fig. 5). The index H20 provided two opposite trends across different hydrological periods. One river could present two types of hydrograph on skewness depending on the hydrological conditions, such as in the river Piquiri, South Brazil, where small (large) floods present positive (negative) skewness (Fleischmann et al., 2016). The maximum value of skewness of flow in the studied catchment was observed in the tributary Jerrisbek during the wet season. As we know, the Jerrisbek tributary is in the flatter hill region. Additionally, the region had a higher share of forest and pasture, which turned to interfluvial wetland during flooding, which leads to low flood wave attenuation (Junk et al., 2011). A larger skewness implied higher discharge and runoff variability (Poff and Zimmerman, 2010).

Higher percentage of **TB** was observed in the tributary of Jerrisbek compared to other areas of the river (Table A. 2). The PFG **TB** as typical potamal phytoplankton better dominated in high flow condition of small rivers (Stanković et al., 2012). The result support the hypothesis that increased water discharge can trigger higher share of **TB** in the community, due to their relatively high tolerance to flushing and turbulence (Borics et al., 2007). Phytoplankton communities were co-dominated by planktic and benthic algae. The proportion of silicified benthic diatoms increased when water residence time decreased (Beaver et al., 2013). Consistent with this, Wang et al. (2018) demonstrated that the community composition of benthic diatoms in river plankton was not randomly distributed. Additionally, it could be related to algal hydrological constraints based on their morphological and functional traits aspects in a meaningful way. Likewise, B-Béres et al. (2016) also emphasized that the trait of guild was a sensitive indicator for the environmental conditions in the lowland rivers and streams.

Furthermore, we also observed a significant positive relationship between sulfate and benthic diatoms. The results revealed the possible importance of sulfate for diatoms growth. Based on a controlling experiment, sulfate is likely to be a promotion factor, which would be a benefit to the photosynthetic characteristics of benthic diatoms (Lengyel et al., 2015).

*4.2. Response of **M** to multiple stressors*

During high flow period, domestic area (URMD) is selected as an indirectly structuring factor to **M** via essential nutrient phosphorus (Droop, 1974), and the soluble phosphate was positive related with **M** (Fig. 4). It was surprisingly against with our hypotheses that the key factor would be the major land-use of agriculture. However, the results are consistent with other previous findings. In the Taizi River basin (China), they reported the pollution sources from built-up land areas were existing in both rainy and dry seasons as a point source, where the population is dense and industrial activities are intensive (Bu et al., 2014). It was reported that the urbanized land-use had better production of water quality than agricultural land-use, indicating that urbanized land-use is the primary contributor to degraded water quality rather than agricultural land-use (Baker, 2003; Schoonover and Lockaby, 2006). Additionally, it was reported a continuous high supplement of nitrogen, while controlled phosphorus in the rural area (Mischke et al., 2011). The condition of phosphorous showed as an important nutrient factor, especially for the growth of **M**.

During the low flow period, the area covered by water body (WATR) appeared as another key factor for controlling the functional group **M** with a direct positive relationship (Fig. 5). The result indicated that the lake act as a source of *Microcystis* rather than a sink of purification in the catchment. The biomass of the percentage of **M** was the highest on the sites after lakes. On the contrary, Lake Durowskie (west Poland), which is also located in a farmland-dominant catchment, has suffered inflow with severe cyanobacteria blooms by the linked Struga Gołaniecka River. However, the outflow water quality recovered by three restoration methods in the lake (Gołdyn et al., 2014; Kowalczewska-Madura et al., 2018). As a typical planktic group, **M** has been regarded as a group with the preference of small, eutrophic lacustrine habitat (Borics et al., 2007), while sensitivities to flushing and low light (Reynolds et al., 2002). In lentic area, high phytoplankton bio-volume may dominate by bloom-forming cyanobacteria occurring due to high water residential time (Rangel et al., 2016). The upstream dam resulted in lake type eutrophic, epilimnetic *Microcystis* dominance, while replaced by benthic diatoms in the middle sections of the River Loire (France) in late summer (Abonyi et al., 2012).

Moreover, we also observed that the ratio of nitrogen to phosphorous was directly negative related to group **M** during the dry season (Fig. 5). On one hand, the result showed that the content of phosphorous acted as the shaping factor for *Microcystis* development (Schindler et al., 2016). On the other hand, the negative relationship between NPR and **M** consistent with the previous studies that cyanobacteria bloom was favored by low NPR (Orihel et al., 2015; Smith, 1983).

Finally, we are specially facing a high biomass of **M** on the low flow period, when local farmers fertilized crops and used pesticides more extensively in the study region (Ulrich et al., 2018). Cyanobacteria had been noticed by higher tolerance to herbicides than other phytoplankton taxa (Bérard et al., 1999), particularly under status of enhanced nutrient supply (Harris and Smith, 2016), indicating pesticides might potentially stimulated the dominance of **M** during low flow period.

4.3. Response of phytoplankton community to multiple stressors

During the high flow period, the phytoplankton community pattern had a higher influence from hydrological indexes compare to the dry period (Fig. 5). The hydrological regime mainly contributed to the low biomass and high similarity of the phytoplankton composition during the high flow period, due to the high connectivity and extensive dispersal stochasticity (Rodrigues et al., 2018). On the contrary, there was a relative high level of total biomass during the dry season (Fig. 3), and a high share of contribution from physicochemical condition in structuring the phytoplankton community (Fig. 4). Firstly, it can be expected a light limitation in winter months in the Northern Hemisphere. In addition, we could infer even higher light availability in the dry season due to the low water level (Nõges et al., 2016). Moreover, water temperature had a positive contribution to the phytoplankton population development in September (Fig. 5). This phase of the year had more suitable temperature for algae growth compared to December. Warm autumn water temperatures combined with anthropogenic eutrophication attributed to the cause of riverine algal blooms during drought period (Bowling et al., 2016).

Overall, our findings suggest that the impacts of flow regime, land-use pattern, physicochemical condition and their potential interactions on riverine PFGs (**TB**, **M** and the community) varied greatly across hydrological periods. However, traditional biomonitoring campaigns and management practices, which focused on improving local abiotic variables to increase local biodiversity, were often based on one-time sampling data and fairly ignored the potential bias resulting from temporal variations, particularly different hydrological periods (Stubbington et al., 2017b). The designation was probably one of the reasons that have resulted into many problems and delays in implementation of recent international water framework directive policies such as EU WFD (Voulvoulis et al., 2017).

We therefore advocate that sampling programs and analyses that target future environmental policies should take different hydrological periods into account (Stubbington et al., 2017a). Furthermore, studies address that detailed causal relationships between changing environment and aquatic organisms could significantly improve our basic understanding of ecological responses to multiple stressors. Sustainable watershed management requires holistic approaches that assess collective biotic and abiotic data to better predict the impacts of anthropogenic activities and climate change on aquatic ecosystems (Dudgeon et al., 2006).

5. Conclusions

In this study, the phytoplankton biomass and functional groups composition vary spatiotemporally during two contrasting seasonal hydrological periods. Their responses to physicochemical conditions, hydrological regime and land-use pattern are different during different hydrological periods. we detect that:

(1) The hydrological regime contributes more during the high flow period in structuring the phytoplankton community. The skewness of 7 days discharge emerged as a key driver of hydrological regime, and it always had an indirect effect on functional group **TB** during two hydrological periods.

(2) Anthropogenic stressor by urban land-use acted as a critical driver for functional group **M** especially during high flow period. The group **M** was directly related to phosphorous relevant indicators indicating its sensitivity to the concentration of phosphorous. The area with a higher share of water bodies was also a key cause factor during the low flow period, guide the lacustrine zone as its origin.

Our results provide evidence that, for a more comprehensive and accurate understanding of the aquatic status, we should also take consideration of different hydrological periods. Secondly, we recommend functional groups as effective indicators of phytoplankton dynamics to simplify the pattern and seize the key issue to achieve a better knowledge of the relationship between phytoplankton and multiple environmental stressors. Climate change and anthropogenic activities, for instance altering flow regime and land-use pattern, act as an important ecological filter of riverine phytoplankton community via physicochemical conditions. Further studies across lake-river continuums are needed to enhance our understanding toward incorporating hydrological regime, land-use pattern, as well as physicochemical conditions into investigation designs, which would enable us to keep the pace with increasing demand for sustainable watershed management. Structure equation model disentangled the contribution of multiple stressors. It would be an outperforming method to generalize results, identify common patterns, and predict response of phytoplankton to environmental changes in future studies.

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