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**Identifying the main drivers of change of phytoplankton community
structure and gross primary productivity in a river-lake system**

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Abstract: The management of river-lake systems is hindered by limitations in the
applicability of existing models that describe the relationship between environmental
factors and phytoplankton community characteristics but rarely include common and
indirect effects on algae dynamics. In this study, we assumed that the interaction of
light, water, temperature, pH, and nutrients, including direct and indirect effects, are

the potential factors affecting phytoplankton dynamics. We determined which of these are the main drivers of phytoplankton community structure and production in a river-lake system by using three different models based on the partial least squares structural equation modeling method. Our results indicated that the models achieved more than 60% of the overall explanatory power of various environmental factors on phytoplankton characteristics, including indirect and direct effects. In particular, light, pH, and nutrient content and ratios commonly control phytoplankton dynamic characteristics rather than a single nutrient, but light is the main driving force of phytoplankton community characteristics. Controlling the underwater light conditions, and nitrogen and phosphorus pollution load could effectively regulate algal blooms, increase productivity, promote ecological balance, and reduce water pollution. Our findings provide a scientific and theoretical basis for water resource management and pollution control.

Key words: phytoplankton community; gross primary productivity; biodiversity; environmental factor; Poyang Lake

1. Introduction

Phytoplankton, a principal primary producer in aquatic ecosystems and the basic link in the aquatic food web (Havens.,2014), can play a key role in the basic functions including energy flow, material circulation, and information transmission (Lakshmi et al., 2014; Deines et al., 2015; Cai and Kong., 2013). Phytoplankton characteristics,

such as community structure, diversity, and gross primary productivity (GPP), are influenced and regulated to a certain extent by external environmental conditions (Kumar et al., 2018). Generally, light conditions, nutrient concentrations (Siegel et al., 2013), pH (Jakobsen et al., 2015), water temperature (Jiang et al., 2014; Deng et al., 2017), and predation by zooplankton and grazers (Silva et al., 2014) are primary factors that affect the growth and reproduction of phytoplankton in an aquatic ecosystem.

Several forecasting models have been constructed to depict the functional relationship between nutrients and phytoplankton community structure (Thrane et al., 2014; Čado et al., 2017; Santiago and Roel., 2014). These models show linear or nonlinear relationships between nutrients and phytoplankton biomass, abundance, and species as a proxy of phytoplankton community structure (Kong et al., 2015; Miao et al., 2016; Sun et al., 2019). Similar findings are found between nutrients and phytoplankton diversity (Cao, Wang et al., 2016) and primary productivity (Sugimoto et al., 2017; Li et al., 2016; Yin et al., 2017; Wilkerson et al., 2015). Browning et al. (2017) also found that nutrient composition will change the phytoplankton growth pattern and chlorophyll *a* content.

Scholars have also found that phytoplankton characteristics are affected by other factors, including pH (Cony et al., 2017), water temperature (Liu et al., 2015), suspended solids (Cao, Wang et al., 2016), salinity (Liu et al., 2015; Ke et al., 2014), light (Sugimoto et al., 2017; Matsumoto et al., 2014), transparency (Wu et al., 2014a), hydrologic features, and human activities (Wang et al., 2015; Gao et al., 2019), not

just nutrients. However, this relationship is either influenced by a single factor or the common factor was identified by neglecting to take into consideration any indirect effects. In addition, the explanatory power of the models that were used do not effectively explain dependent variables. This suggests that no single variable (including collective nutrients) can effectively describe the complex dynamics of phytoplankton ecology, which leads to the question: what factors can better influence and predict phytoplankton characteristics? Water resource managers need an answer to this question as it has an important theoretical and practical value for understanding the impact of environmental changes on aquatic ecosystems and providing scientific evidence for water quality assessment and pollution control. Traditional theories suggest that macronutrients, such as nitrogen and phosphorus, mainly influence the dynamic characteristics of phytoplankton, although some studies (Cao, Wang et al., 2016; Sugimoto et al., 2017; Cony et al., 2017; Liu et al., 2015; Wu et al., 2014a; Wang et al., 2015) indicate that other environmental factors have a greater impact on phytoplankton growth.

Many linear regression models are often used to construct the relationship between environmental factors and phytoplankton ecology (Čađo et al., 2017), but for the first time, partial least squares structural equation modeling (PLS-SEM) technique replacing regression modeling and correlation analysis has been applied in water resources management. Previous studies have been applied in management information systems, education, agriculture, social sciences, engineering technology, and other fields (Ringle et al., 2012). Partial least square method is a set of principal

component analysis, canonical correlation analysis and multiple linear regression analysis of the advantages of a body (Ramli et al., 2018; Tian et al., 2008; Fan., 1997). It not only can handle the causal relationship between potential variables simultaneously while disposing measurement errors in the structural model (Farooq et al., 2016, 2018; Hair et al., 2017), but also can solve the problems of small sample size, non-normal data and single-item constructs which are involved in the proposed model of this study (Ringle et al., 2012).

Poyang Lake, the largest freshwater lake in China, is recognized as the Wetland of International Importance due to its ecological-economical function (Sun et al., 2015; Zhang and Chen., 2017). There exists numerous functions and values, including regulating water source, improving vegetation growth and organic matter production (Liu et al., 2017), soil protection, CO₂ fixation and O₂ release, pollution degradation, and maintaining the ecosystem health in the Poyang Lake basin, and its ecosystem service value reaches 1.38×10^{11} yuan every year (Xie et al., 2011). For Poyang Lake basin, a river-lake system with strong hydrologic characteristics and one that is affected largely by environmental conditions, the applicability of existing models that describe the relationship between nutrients or other environmental variables and phytoplankton characteristics for water quality assessment and resource management is limited. We hypothesize that the interaction of light, water temperature, pH, and nutrients, including direct and indirect effects, is the potential influence of phytoplankton dynamics in the Poyang Lake basin. We therefore used the partial least squares structural equation modeling (PLS-SEM) method to verify whether this

assumption is supported by evidence, to determine which factor(s) is the main driving force of phytoplankton community structure and production in a river-lake system, and to promote our understanding of a large eutrophic lake.

2. Materials and Methods

2.1 Study area

The study was carried out in the Poyang Lake basin, which is located in the central and northern area of Jiangxi Province in China along the south bank of the middle and lower reaches of the Yangtze River (26°44'48"-29°44'40" N, 115°4'13"-116°24'6" E) (Figure 1). Poyang Lake (PYL, Figure1c), Gan River (GR, Figure1d) and Jiazhu River (JZR, the second tributary, Figure1e) are regularly monitored by the Qianyanzhou Experimental Station of the Chinese Academy of Sciences (CAS), Beijing, in Taihe County, Jiangxi Province (Gao et al., 2016; Hao et al., 2017). Poyang Lake is the largest freshwater lake in China and five tributaries, the Gan River, Fu River, Xin River, Rao River, and Xiu River, drain radially into Poyang Lake, which then drains into the Yangtze River (Yao et al., 2015). It plays an important role in regulating the water level of the Yangtze River, conserving water resources, improving vegetation growth and local production, and maintaining the ecosystem health (Liu et al., 2017). Due to the natural variation in lake morphometry, climate, hydrology conditions, and physical and chemical properties, the Poyang Lake basin forms a highly variable lake type (Borics et al., 2012) that belongs to a seasonal lake with high water exchange rate and large fluctuation of water level (Chen et al., 2016).

The area has a continental, subtropical, monsoon climate with an annual mean precipitation of about 1400-1600 mm. The annual mean temperature and sunshine hours are 16-18°C and 1894-2085 h, respectively (Jin et al., 2012). Seasonal variation of the water level is consistent with precipitation, with the annual mean water level ranging from 9.59 to 15.36 m (Chen et al., 2016). Poyang Lake is a lacustrine face at the high water level(> 15 m) and a fluvial face at the low water level(< 10 m) (Lai, G.Y., 2012; Ouyang and Wang., 2018). Due to the unique feature of aqueous phase, Poyang Lake only preserves the lacustrine phase from July to September, and has a river feature in the other nine months (Ouyang and Wang., 2018), which is regarded as a river-lake system (Gan River- Poyang Lake system, RLS). The abundant precipitation, natural complex terrain, hydrological connectivity of the river-lake system, and the hydrological heterogeneity and short water residence time (59 days in Poyang Lake (Chen et al., 2011)) of the existing lake water body are simultaneously endogenous and exogenous (Borics et al., 2013).

In general, the annual average runoff of the Poyang Lake basin is 149.4 billion m³, which accounts for 16.7% of the annual runoff at the control station of the Yangtze River basin. The Gan River in particular accounts for 40.4% of the total runoff to Poyang Lake (Yao et al., 2015). Due to the geology and hydrology of the region (Borics et al., 2012), most macronutrients fluxes from the surrounding areas, particularly the Gan River, drain into Poyang Lake, and this may lead to natural eutrophication of the lake. Simultaneously, the high hydrological connectivity of the river-lake system, water yields of lake and various natural conditions result in diluted

nutrient concentrations and diversified phytoplankton (Wang et al., 2015). Consequently, the phytoplankton communities respond rapidly to changes in environmental conditions, such as hydrological conditions and nutrients (Siegel et al., 2013).

2.2 Sample collection and laboratory analysis

2.2.1 Sampling and data collection

Taking into consideration land-use type, spatial distribution, and sampling process, 15 sampling points to measure base flow in the Poyang Lake watershed were established (Figure 1). The sampling period was based on the climatic cycle as follows: autumn (September) in 2017 and 2018, winter (January and December) in 2018, spring (May) in 2018, and summer (July) in 2018. A total of 144 surface (0.5 m depth) water samples were taken using 100-mL polyethylene bottles; these were then stored in a refrigerator until analysis. 14 sampling points in Poyang Lake (P1, P3-P15) and eight in the Gan River (G2, G5, G7-G12) were sampled for phytoplankton and chlorophyll *a* (Figure 1). But due to low water level, some samples could not be collected in some seasons. The phytoplankton samples according to Hu and Wei. (2006) were collected from 0-50 cm of surface water in 1-L polyethylene bottles and fixed with 15mL-Lugol's reagent prior to standing for 48 h at room temperature. Extracting the supernatant without algae from the upper part using rubber hose is based on siphon principle. The remaining 60mL sample sediment were transferred into 100-mL polyethylene bottle prior to storage in 40% formaldehyde solution (Hu and Wei., 2006) and were transferred to Nanjing Institute of Geography and

Limnology, CAS, for determination of algal biomass, density, and species composition.

Water samples for chlorophyll *a* were collected at the surface (0.5 m depth) in 500-mL polyethylene bottles, fixed in 1% MgCO₃, and sent to the Institute of Geographic Sciences and Natural Resources Research Laboratory for test analyses. pH was measured in situ using an ultrameter (Myron L Company), and water temperature, water level, runoff, and precipitation data were obtained from the Qianyanzhou Experimental Station and Hydrological Yearbook of the People's Republic of China: Hydrological Data of the Yangtze River Basin (Poyang Lake Area). Data on solar radiation and the number of hours of sunlight were obtained from the RETScreen (Canada) <https://retscreen-international.updatestar.com/> and <https://sunrise.supfree.net/>, respectively.

2.2.2 Sample analyses

The preserved water samples were analyzed as soon as possible after collection, using standard spectrophotometric techniques. Different forms of carbon concentrations (dissolved inorganic carbon [DIC], dissolved organic carbon [DOC], and dissolved total carbon [DTC]) were determined with the TOC Analyzer II (Vario EL III, Germany); nitrogen concentrations (total nitrogen [TN], dissolved total nitrogen [DTN], nitrate nitrogen [NO₃⁻-N], and ammonia nitrogen [NH₄⁺-N]) were measured with a segmented continuous flow analyzer (Futura, France); phosphate concentrations (total phosphate [TP], dissolved phosphate [DTP], and nitrate phosphate [PO₄³⁻]) and silicon (SiO₄⁴⁻) concentrations were measured using an

automatic chemical analyzer (Smartchem 200, Italy). For determination of species composition classification, population abundance (cells/L) of each species, and the mean volume of cells (μm^3), we referred to Hu and Wei. (2006), and for the determination of chlorophyll *a*, we used the hot ethanol method (Lorenzen., 1967).

2.3 Data calculation and statistics

2.3.1 Gross primary productivity

Gross primary productivity calculation was based on Vertically Generalized Production Model (VGPM Model) (Behrenfeld and Falkowski., 1997a).

$$PP_{eu} = 0.66125P_{opt}^B \cdot \frac{E_0}{E_0 + 4.1} \cdot Z_{eu} \cdot C_{opt} \cdot D_{irr} \quad (1)$$

where PP_{eu} is the primary productivity of the euphotic zone ($\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$); C_{opt} is the Chla concentration of surface water ($\text{mg} \cdot \text{m}^{-3}$) (Deng et al., 2017); E_0 is photosynthetically available radiation intensity of the water surface ($\text{mol} \cdot \text{m}^{-2}$), for this study, $E_0 = 20\text{--}23 (\text{mol} \cdot \text{m}^{-2} \cdot \text{d}^{-1})$ (Zhu et al., 2010); D_{irr} is the photoperiod (h), based on the latitude and longitude, the sunrise and sunset times can be calculated (<https://richurimo.51240.com/>).

P_{opt}^B was the maximum photosynthesis rate of water ($\text{mgC} \cdot \text{mgChla}^{-1} \cdot \text{h}^{-1}$), a function of temperature and calculated as follows (Behrenfeld and Falkowski., 1997a, b).

$$P_{opt}^B = \begin{cases} 1.13 & T \leq -1.0 \\ 4.00 & T \geq 28.5 \\ P_{opt}^{B'} & -1.0 < T < 28.5 \end{cases} \quad (5)$$

$$P_{opt}^{B'} = 1.2956 + 2.749 \times 10^{-1}T + 6.17 \times 10^{-2}T^2 - 2.05 \times 10^{-2}T^3 + 2.462 \times 10^{-3}T^4 - 1.348 \times 10^{-4}T^5 + 3.4132 \times 10^{-5}T^6 - 3.27 \times 10^{-8}T^7 \quad (6)$$

where P_{opt}^B is the maximum photosynthesis rate of water ($\text{mgC} \cdot \text{mgChla}^{-1} \cdot \text{h}^{-1}$); $P_{opt}^{B'}$

is the maximum photosynthesis rate of water, when $-1.0 < T < 28.5$; T is the temperature of water surface ($^{\circ}\text{C}$).

Z_{eu} was euphotic depth(m) and calculated by the empirical formula (Yin et al., 2017).

$$Z_{eu} = 4.605 / (0.062C_{tripton} + 0.011C_{Chla} + 1.430) \quad (r^2=0.954, n=199, P<0.001) \quad (7)$$

where C_{Chla} is the Chlorophyll a content of water($\text{mg}\cdot\text{m}^{-3}$). $C_{tripton}$ is the concentration of non-pigment particles, also known as suspended solids, obtained by using the data of Landsat 8 30m spatial resolution remote sensing reflectance in the band 5 (Zhou et al., 2016), and coefficient of determination of the model was 0.93 (Cui et al., 2013).

GPP was plotted with Arc map (version 10.2) by adding attribute and modifying properties (Symbology: Charts) and One-way ANOVA in IBM SPSS (version 22.0) was used to analyze seasonal differences of GPP. Moreover, multivariate linear regression model (IBM SPSS (version 22.0)) was also used to analyze the relationship between GPP and environmental variables.

2.3.2 Phytoplankton diversity index

Shannon-Wiener Index (H') (Tian et al., 2017), Simpson Diversity Index (D_s) (McLaughlin et al., 2016), Marglef Richness Index (D_M), and Pielou Evenness Index (J) (Amir et al., 2015) were as a dependent variable to represent phytoplankton diversity and their calculation methods as Table S1. Phytoplankton diversity, species and environmental factors were analyzed using Origin (version 9.1). R (version 3.5.1) was used to analyze phytoplankton density and its normalization by the Scale function in order to remove the unit limitation of data and eliminate the influence of dimension

on data processing and analysis.

2.4 Partial least squares structural equation modeling (PLS-SEM)

We adopted the PLS-SEM approach using SmartPLS version 3.2.8 (Ringle et al., 2015) to analyze relationships between environmental factors and phytoplankton characteristics. We used three models, the Environmental Factor–Phytoplankton Community Model (EF-PC Model), Environmental Factor–Phytoplankton Community-Phytoplankton Diversity Model (EF-CD Model), and Environmental Factor–Gross Primary Productivity Model (EF-GPP Model), to describe the relationship between environmental factors and phytoplankton characteristics. Conceptual models of this study belonged to the Reflective-Formative type (Ringle et al., 2012), which has characteristics of reflective measurement models (outer models) and formative structural models (inner models), which all models were consist of latent variables and measurable variables (Figure S1).

In three models, environmental factors as independent variables encompassed four dimensions i.e. pH, light, nutrient concentration and nutrient ratio and three dependent variables were phytoplankton community, diversity and gross primary productivity, respectively. The EF-PC Model (Figure S1a), which consisted of 7 reflective measurement models and 2 formative structural models, identified the casual relationships between four latent variables (pH, light, carbon concentration and C/N/P) and one latent variable (phytoplankton community, whose measurable variables included species number, total biomass, and total density). We used a two-stage approach to operate and test the model, namely given priority to the

reflective model, and the structural model should be operated and test by using the obtained latent variable scores in first-stage (Ringle et al., 2012) and its test results were shown in Figure S3. On the basis of the EF-PC Model, a potential variable of phytoplankton diversity was added, and its observed variables included the D_M , D_S , H' , and J , which constituted the EF-CD Model (Figure S1b). The EF-CD Model and EF-GPP model involved 8, 5 reflective measurement models and 3, 1 formative structural model, respectively. In the EF-GPP Model, the latent variable of GPP, which had observed variables of chlorophyll a and estimated primary productivity, was converted as a dependent variable substitute for Phytoplankton Community. The casual relationship between GPP and C/N (DTC concentration /DTN concentration), light (Solar radiation, Sunshine hour, Water temperature), and pH was determined. Moreover, carbon and nitrogen concentration are the latent variables of identifying C/N in the formative model (Figure S1c). In addition, the hypothesizes of all the models in this study are based on the existing research results and aforementioned introduction, which provided support for the main drivers of change of phytoplankton characteristics, this study proposes following hypotheses seeing Table S2-S4, our models are explanatory in nature.

3. Results

3.1 Variations in the phytoplankton community

3.1.1 Phytoplankton species and density

We identified a total of 133 species of phytoplankton from the samples taken in the Poyang Lake basin. These species belonged to eight phyla and 77 genera (Figure

2). Among the species, 20 species belonging to eight genera in the phylum Cyanophyta represented approximately 15.04% of the total species, 64 species belonging to 32 genera in Chlorophyta represented 48.12%, and 32 species belonging to 22 genera in Bacillariophyta represented 24.06%. In addition, the species richness of Cyanophyta, Chlorophyta and Bacillariophyta in Gan River were lower than that in Poyang Lake. In the whole river-lake system, the species richness of cyanobacteria was the highest, followed by Bacillariophyta. The phytoplankton species richness was greatest in summer. An increase then decrease in species numbers occurred from spring to summer and then ultimately to winter.

Phytoplankton density and biomass varied substantially seasonally in the Poyang Lake basin (Figure 3). The highest algal density (up to 1.50×10^7 cells/L) occurred in summer, whereas the lowest density (3×10^5 cells/L) occurred in winter. The average algal densities for the lake ranged from 3.80×10^5 to 9.38×10^6 cells/L. High algal densities occurred at P5 and P4, both within the Nanjishan Nature Reserve, yet the dominant phyla differed: Cyanobacteria in spring and summer, Bacillariophyta in autumn, and Chlorophyta at P3 in winter. Moreover, the standardized data of phytoplankton density showed that both common and dense populations of the Bacillariophyta, Cyanobacteria, and Chlorophyta were mainly concentrated in Poyang Lake, while the uncommon populations of Cryptophyta and Euglenophyta were distributed in the Gan River.

3.1.2 Phytoplankton Diversity

The highest Shannon-Wiener Index of phytoplankton community diversity in the

Poyang Lake basin occurred in spring ($H' = 2.54$), with a lowest value appearing in summer ($H' = 0.58$). The trend for temporal variation as shown by the Simpson Diversity Index and Marglef Richness Index is consistent with H' (Figure 4). In spring, the highest values of D_S and D_M were 0.82 and 14.74, respectively, showing that community diversity was relatively high and species were abundant in spring. However, the Pielou Evenness Index differed from the other diversity indexes, with the highest value found in autumn (0.52), demonstrating a more even distribution of individuals in autumn than in spring. On a spatial scale, D_M of Gan River was higher than that of Poyang Lake in spring, and there was no significant difference H' , D_S , D_M , and J in the river-lake system in other seasons.

3.1.3 Gross primary productivity

The GPP of phytoplankton, calculated by the VGPM for the period, differed greatly over the sampling period, with higher values during spring and summer for most of the study area and lower values during autumn and winter (Figure 5). The highest GPP ($1864.81 \text{ mg m}^2 \text{ d}^{-1}$) and greatest increase occurred in spring. Seasonal GPP fluctuations also varied; we saw small variations in winter from 39.80 to $393.43 \text{ mg m}^2 \text{ d}^{-1}$, a larger wave in spring from 82.86 to $1864.81 \text{ mg m}^2 \text{ d}^{-1}$, and moderate variations in summer ($26.72\text{-}1217.85 \text{ mg m}^2 \text{ d}^{-1}$) and autumn ($22.55\text{-}972.85 \text{ mg m}^2 \text{ d}^{-1}$), and GPP of the Gan River - Poyang Lake system in spring and summer was significant different from that in autumn and winter (Figure S2). Some differences between Poyang Lake, a lacustrine system, and Gan River, a fluvial system, were also apparent. The mean GPP in Poyang Lake was higher than in the Gan River during

autumn and winter but was lower in spring and summer, and this difference was particularly significant in autumn (Figure S2).

3.2 Variations in environmental factors

3.2.1 Nutrients

Figure 6 shows a large influx of nutrients flowing from the second tributary (Jiazhu River) to the first tributary (Gan River) and ultimately to Poyang Lake. The different forms of carbon and nitrogen concentrations trended higher in winter and lower in spring, which was consistent with variations in rainfall. Both the mean SiO_4^{4-} and TN concentrations were highest in autumn, but the mean DTC and TP concentrations were highest in winter. NH_4^+ and PO_4^{3-} concentrations were low, particularly PO_4^{3-} , which fell close to zero; however, DTC and SiO_4^{4-} concentrations ranged from 9.04 to 19.01 mg/L and 2.47-19.38 mg/L, respectively. In the view of the spatial distribution, there existed a significant difference of DTC in autumn and SiO_4^{4-} during the four seasons between the river and lake, and the mean SiO_4^{4-} concentrations in the Gan River were higher than Poyang Lake (Table S5). However, TN and TP concentration during the four seasons (except for TP in winter) had no difference in the Gan River and Poyang Lake (Table S5).

3.2.2 Physical and hydrological factors

Solar radiation, sunshine hour, water temperature, and pH in the study area are shown in Figure 7. Water temperature ranged from 7.47 to 30.95 °C at Poyang Lake and 10.95 to 29.94 °C in the Gan River. There was little variation in the small basin area of the Jiazhu River (tributary of the Gan River). Furthermore, the mean solar

radiation ranged from 6.30 to 18.90 MJ m⁻² d⁻¹ over the year in the study area, with highest levels in summer and lowest in winter (Figure 7a). The mean pH was between 6.88 and 7.66 during all seasons, indicating fluctuations between weak acidity, neutrality, and alkalinity (Figure 7b). Solar radiation and pH of Poyang Lake reached higher than other rivers in spring, and water temperature and sunshine hours of Poyang Lake were highest in summer.

3.3 Model Result

3.3.1 PLS Model result

The EF-PC, EF-CD, and EF-GPP Model results are shown in Figure 8. In the EF-PC Model (Figure 8a, Table S6), a strong, positive, direct relationship between light, carbon concentration and phytoplankton community (path coefficient = 0.866, 0.391; T = 5.873, 2.789; p = 0.000, 0.005) were highly significant, providing support for H1 and H2, respectively. Findings of the PLS model also supported H3 and H4, indicating a negative direct relationship (path coefficient = -0.411, -0.165; T = 4.325, 2.030; p = 0.000, 0.043) between pH, C/N/P and phytoplankton community, separately.

Figure 8b and Table S7 describe the test results and decisions of the hypothetical paths in the EF-CD Model. Phytoplankton community was therefore shown as an endogenous variable with a direct relationship (highly significant, strong negative correlation) with phytoplankton diversity (path coefficient = -0.760; T = 10.377; p = 0.000), supporting H1; pH (H2) and C/N/P (H3) both had a significant negative effect on phytoplankton diversity. The results also indicated six significant positive or

negative indirect effects (Table S9), carbon concentration/light/pH → phytoplankton community → phytoplankton diversity, carbon/nitrogen/phosphorus concentration → C/N/P → phytoplankton diversity, that were supported in the EF-CD Model.

The test results of hypothetical paths demonstrated that all hypotheses were supported in the EF-GPP Model (Figure 8c and Table S8). Thus, light and C/N ratio had a significant, positive, direct effect on GPP, with the effect of light being stronger. In contrast, a highly significant, negative, direct relationship between pH and GPP (path coefficient = -0.553; $T = 3.936$; $p = 0.000$) supported H2, whereas the C/N ratio as an indirect latent variable supported H4 and H5, indicating that carbon and nitrogen concentrations both had a significant effect on C/N. Furthermore, a negative indirect effect between nitrogen concentration and GPP was significant (nitrogen concentration → C/N → GPP [coefficient = -0.266; $T = 2.051$; $p = 0.040$] (Table S10).

Measurements for all three models satisfied all requirements for constructing a unidimensional, valid, and reliable model and passed the Bootstrap test for outer model loading, outer weight, and path coefficient, and overall explanatory power and goodness of fit (GoF) indicated that all three models had good model fits (details can be found in Section S1, Supporting Information). The three models demonstrated the validity of assessing phytoplankton growth in response to various environmental variables. The representative model of the EF-PC Model could explain 63.4% of the factors affecting phytoplankton community ($R^2 = 0.634$), and its GoF reached a high of 0.726 (Table 1). Similarly, the EF-CD Model of phytoplankton diversity based on

the EF-PC Model also had a 57.3% explanatory power of factors affecting phytoplankton diversity ($R^2 = 0.573$) and a GoF index value > 0.7 (Table 1). In addition, for GPP (i.e., the EF-GPP Model), the overall explanatory power of constructs was 25.6% ($R^2 = 0.256$), but the GoF index value of $0.469 > 0.36$ and standardized root mean square residual value of $0.048 < 0.08$ belong to a good fit model (Table 1). Due to the basic features of PLS Model, the three models can be applied on a small sample size, large proportion of predictors, and non-normal data case study (Farooq et al., 2016, 2018; Hair et al., 2017; Ringle et al., 2012).

3.3.2 Linear regression analysis of the GPP simulation

There may be a relationship between GPP and phytoplankton community structure and biodiversity (Napoléon et al., 2014), but we used the PLS method to express three dependent variables with latent variables. This led to the finding that individual observed variables in latent variables had little relationship with GPP. A single observation variable as an independent variable, using multiple linear regression, was an effective method to simulate and predict GPP. Table 2 provides information on modeling GPP with biological or both biological and physical factors. The overall explanatory rate of GPP was as high as 94.3%, which was simulated by endogenous variables. GPP was significantly correlated with biodiversity, which was negatively correlated with the H' , in contrast to the D_M and J . Species number was another endogenous variable that was one of the observed variables of phytoplankton community structure. In addition, physical parameters of light, temperature, and pH also had a significant impact on GPP; this was consistent with the results of the

PLS-SEM method.

4.Discussion

4.1 Seasonal difference of phytoplankton

Table S20 and S21 describe the regional and seasonal difference in the Gan River and Poyang Lake during the four seasons, respectively. Diversity indexes had no regional difference during the four seasons and algae density in spring had a significant difference in the Gan River and Poyang Lake (Table S20). There were significant differences in the diversity indexes of four seasons and density in spring and summer was significantly different from that in autumn and winter (Table S21). There is a phenomenon that higher algae density and diversity indexes in spring and summer but lower in autumn and winter (Figure 3 and 4), which is caused by different external environment. Meanwhile, the change trends of phytoplankton were consistent with the solar radiation and sunshine hour (Figure 7a) and opposite to the nutrients (Figure 6), which showed the light and nutrient drive phytoplankton growth and this was confirmed by the EF-PC and EF-CD Model.

The highest GPP and greatest increase occurred in Gan River (G9) in spring (Figure 5). While algae density reached highest in Poyang Lake during the four seasons (Figure 3). But D_M was the highest in G9 in spring (Figure 4), which indirectly shows that phytoplankton density is not the only standard to measure primary productivity, which is confirmed by our Regression Model of GPP (Table 2). However, nutrient concentrations, hydrological and light conditions of G9 all belong to a moderate range (Figure 6 and 7) and result in a suitable ecological environment

which also indicates that a variety of environmental factors affect phytoplankton ecology together, rather than driven by a single factor.

4.2 Driving-force analysis

Phytoplankton respond to environmental variables, such as nutrients, light, pH, and water temperature. We found light, rather than nutrients, to be the greatest driving force of phytoplankton community structure. Because light supplies the energy needed for photosynthesis and light transmission is affected by turbidity produced by suspended particles, light is more crucial than nutrients for limiting phytoplankton growth and blooming in turbid ecosystems (Domingues et al., 2011). The Poyang Lake basin is a turbid ecosystem as a result of the sediment transport project on the Gan River and the high levels of suspended solids in Poyang Lake. Light availability is known to be a vital factor in restricting phytoplankton growth and GPP (Wu et al., 2013, 2014b), and this is consistent with the significant positive relationship between light and phytoplankton density and GPP that we found in this study. It also indirectly reflects the possible reason that the phytoplankton density in the exogenous river was lower than that in the endogenous lake, which was caused by the different underwater light conditions, namely the slight disturbance of river leads to the turbidity of water body (Wang et al., 2016).

However, we found light conditions have a significant indirect effect on diversity, which is similar to the findings of Gao and Sun (2016). Water temperature as an observed variable of the reflective measurement model of light has the same mechanism of influence on phytoplankton characteristics as that of light. A strongly

significant negative relationship occurred in pH and phytoplankton ecology. pH affects phytoplankton photosynthesis and respiration by influencing the equilibrium of the carbonate system and controlling the partial pressure of carbon dioxide (Jakobsen et al., 2015). The optimum range of pH for various phytoplankton is different, so pH can significantly affect species composition (Cony et al., 2017)

As basic biogenic elements, the proportion and concentration of nutrients can play an important role in phytoplankton growth (Kane et al., 2014). Compared with nitrogen and phosphorus concentrations, the effects of carbon concentration and the C:N:P ratio on the structure and diversity of the phytoplankton community are significant, although the relationship between carbon concentration and phytoplankton diversity is indirect. DOC concentrations have a significant effect on phytoplankton GPP in lakes (Seekell et al., 2015), which is consistent with our study. A significant direct relationship between GPP and C:N ratio, and an indirect relationship with nitrogen concentration. Therefore, not all aspects of phytoplankton growth will be limited by the concentrations of nitrogen and phosphorus, which are closely linked to human activities, land use, and hydroclimatic conditions (Borics et al., 2013). A significant correlation between chlorophyll *a* and nutrient concentrations in the lake has been reported (Wu et al., 2014b). However, the ability to predict phytoplankton characteristics by nutrient concentration alone is limited, so phytoplankton characteristics should be assessed in combination with other environmental conditions.

Phytoplankton community structure can be used as an endogenous variable to

influence biodiversity and GPP, and the relationship between GPP and biodiversity has been documented (Napoléon et al., 2014; Jia et al., 2019). Phytoplankton community has a significant negative relationship with the diversity index and conforms to the regular pattern reported in Tian et al. (2017). In eutrophic lakes, phytoplankton communities are dominated by several dominant species; single dominance and limited species outbreaks result in lower diversity and evenness and higher community structure (Gao and Sun., 2016; Filstrup et al., 2014). We found the impact of phytoplankton diversity on GPP to be more prominent than that of community structure.

Our findings not only exist in Poyang Lake basin, but also many scholars have found similar conclusions in other places. In coastal waters (Santiago and Roel., 2014), ocean (Matsumoto et al., 2014), reservoirs (Silva et al., 2014), estuary (Domingues et al., 2011), light has a close relation with phytoplankton ecology. pH had a significant effect on phytoplankton growth in the reservoirs (Silva et al., 2014) and ocean (Jakobsen et al., 2015). Furthermore, nutrients also limited phytoplankton growth in the estuary (Wilkerson et al., 2015), ocean (Ke et al., 2014; Kumar et al., 2018) and lakes (Seekell et al., 2015; Thrane et al., 2014; Kane et al., 2014). In the strong hydrological river-lake system such as estuary, river, and lake, our findings are general applicability.

4.3 Implications for lake management

In this study, we investigated the response of phytoplankton dynamics to environmental factors and identified the main drivers that dominate phytoplankton

dynamics in a river-lake system. We can therefore specify different water resource management strategies based on the management objectives. Phytoplankton growth and blooms are sensitive to light, pH and nutrients, and therefore size and species composition of the phytoplankton community can be effectively controlled by regulating underwater illumination conditions, pH and exogenous nitrogen and phosphorus contaminants. Algal blooms should, in fact, be caused by excessive nutrient input (Rapport and Hildén., 2013; Vilmi et al., 2015), but nutrient content is diluted in fast-flowing waters (Cao, Chu et al., 2016), and the Poyang Lake basin does not belong to a highly eutrophic area. To maximize the regional ecological function, it is necessary to promote primary productivity meanwhile prevent the occurrence of water bloom. Three measures, regulating the underwater light conditions, the inflow of exogenous nutrients, and pH of water body, can achieve this goal. However, pH regulation needs to balance algae and bacteria, which is difficult to implement and destroys the ecological balance in the original system.

There are three ways to control the underwater light conditions, using plastic floating plate to block the light and control algae (Sun., 2008), installing the diving lamp manually to compensate the light (Cao et al., 2014), which consumes a lot of manpower and material resources. A underwater light regulating device (Yu., 2018), which is based on the principle of collecting natural sunlight and diffusing it to the blocked area by using the light path device (concave lens) floating on the water surface, is suitable for large-scale application, due to less layout area and quantity, ensuring the self-purification ability of a natural water body and low cost. In addition,

controlling nitrogen and phosphorus fluxes in aquatic system is mainly to reduce the emission of nitrogen and phosphorus pollution sources (Sun., 2008). Therefore, it is feasible and effective for alleviating or avoiding algal blooms and improving productivity to control non-point source nitrogen and phosphorus pollution load and install the underwater light control device. Our research, therefore, provides a scientific and theoretical basis for water resource management and pollution control.

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Table 1. R^2 , SRMR, and GoF of Structural Model in EF-PC, EF-CD, EF-GPP Model

	Latent Variable	R^2 of Initial Sample	T-Statistic	P-Statistic	SRMR	GoF
EF-PC Model	Phytoplankton Community	0.634	7.085	0.000	0.052	0.726
	C/N/P	0.206	3.241	0.001	-	0.426
	C/N/P	0.206	3.288	0.001	-	0.426
EF-CD Model	Phytoplankton Community	0.493	5.799	0.000	-	0.661
	Phytoplankton Diversity	0.573	7.247	0.000	0.079	0.703
	Gross Primary Productivity	0.256	2.411	0.016	0.048	0.469
EF-GPP Model	C/N	0.733	14.681	0.000	-	0.764

Note: C/N/P represented a value of DTC concentration: DTN concentration: DTP concentration, namely $DTC/DTN/DTP = [DTC \text{ concentration}] / [DTN \text{ concentration}] / [DTP \text{ concentration}] = [DTC \text{ concentration}] / ([DTN \text{ concentration}] \times [DTP \text{ concentration}])$. And C/N/P represented a simplified form of DTC/DTN/DTP in the model. $C/N = DTC/DTN = [DTC \text{ concentration}] / [DTN \text{ concentration}]$.

Table 2. Multivariate Linear Regression Model of Gross Primary Productivity

Model	R^2	Adjusted R^2	p Value
$GPP = 0.957 \text{ Chla}^{***} + 0.213 \text{ Species Number}^* - 0.405 \text{ H}^{***} + 0.214 \text{ D}_M^* + 0.395 \text{ J}^{**} - 152.286$	0.943	0.937	0.000
$GPP = 0.991 \text{ Chla}^{***} + 0.138 \text{ Species Number}^* - 0.379 \text{ H}^{***} + 0.274 \text{ D}_M^{**} + 0.352 \text{ J}^* + 0.178 \text{ Solar Radiation}^* - 0.169 \text{ Water Temperature}^* + 0.116 \text{ pH}^{**} - 1107.861$	0.955	0.947	0.000

Note: Chla, chlorophyll *a*; H', Shannon-Wiener Index; D_M , Marglef Richness Index; J, Pielou Evenness Index.

Significance of the independent variable: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Figure 1. Sampling point distribution of watersheds and different land-use types in the Poyang Lake basin

Figure 2. Phytoplankton species richness during the four seasons in the Poyang Lake basin. JZR: Jiazhu River, GR: Gan River, PYL: Poyang Lake, RLS: the river-lake system (Gan River - Poyang Lake system).

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Figure 3. Phytoplankton density by phylum and its standardized density for all seasons in the Poyang Lake basin. Phytoplankton density by phylum (10⁴ Cells/L): a. Spring. c. Summer. e. Autumn. g. Winter. Standardized density of phytoplankton by phylum: b. Spring. d. Summer. f. Autumn. h. Winter. JZR: Jiazhu River, GR: Gan River, PYL: Poyang Lake.

Figure 4. Phytoplankton diversity for all seasons in the Poyang Lake basin. D_s : Simpson Diversity Index, H' : Shannon-Wiener Index, D_M : Marglef Richness Index, J : Pielou Evenness Index. JZR: Jiazhu River, GR: Gan River, PYL: Poyang Lake.

Figure 5. Gross primary productivity ($\text{mg m}^2 \text{d}^{-1}$) during the four seasons in the Poyang Lake basin.

Figure 7. Hydrological and physical factors of the Poyang Lake basin. JZR: Jiazhu River,
GR: Gan River, PYL: Poyang Lake

Figure 8. PLS model for the relationship between environmental factors and phytoplankton dynamic characteristics.a. PLS for the EF-PC Model. b. PLS for the EF-CD Modelc. PLS for the EF-GPP Model. (The circular is the latent variable, it could not be observed directly, while the square is the observed variable, the actual monitoring index. C/N/P represented a value of DTC concentration: DTN concentration: DTP concentration, namely $\text{DTC}/\text{DTN}/\text{DTP} = [\text{DTC concentration}] / [\text{DTN concentration}] / [\text{DTP concentration}] = [\text{DTC concentration}] / ([\text{DTN concentration}] \times [\text{DTP concentration}])$. And C/N/P represented a simplified form of DTC/DTN/DTP in the model. $\text{C}/\text{N} = \text{DTC}/\text{DTN} = [\text{DTC concentration}] / [\text{DTN concentration}]$.)

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