



# Functional Responses of Phytoplankton Assemblages to Watershed Land Use and Environmental Gradients

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Watershed land-use changes have been identified as major threats to lake fauna, subsequently affecting ecosystem functioning. In this study, the functional-based approach was used to examine the effects of land use and environmental changes on phytoplankton communities in four selected lakes in Northeast China. We also identified the sensitive functional traits as indicators of environmental stressors. The integration of RLQ analysis with the fourth-corner approach significantly identified five of 18 functional trait categories, including flagella, filamentous, unicellular, mixotrophic, and chlorophyll *c*, as potential indicators to changes in watershed land-use intensity and environmental gradients. Significant relationships between traits and land use and water quality highlighted the consequential indirect impact of extensive agricultural and urban development on phytoplankton via allochthonous nutrient inputs and various contaminants. In addition, the functional richness of phytoplankton assemblages generally increased along with surface area and forests, but decreased along with intensive agricultural and urban land use, implying that functional homogenization may cause a reduction in ecosystem productivity and reliability to land-use intensity. Given the superior performance of the functional-based approach, our findings also highlighted the importance of the application of both the biological traits and functional diversity index in monitoring programs for lake ecosystems.

**Keywords:** algae, community structure, eutrophication, functional-based approach, human disturbance

## INTRODUCTION

Agriculture and urbanization have drastically transformed complex natural ecosystems into simplified managed ecosystems in many locations (Flynn et al., 2009; Hooke and Martín-Duque, 2012). By changing contaminant, sediment, nutrient, and organic matter loading (Williamson et al., 2008), land-use changes have far-reaching consequences for aquatic ecosystems (Foster et al., 2003). Lakes can be sensitive to land-use changes because they often occupy low points in landscapes, effectively accumulating effects across watersheds (Arbuckle and Downing, 2001;

Stachelek et al., 2020). For example, intensive and extensive agricultural practices, and specifically the application of fertilizer or manure within watersheds, are strongly responsible for lake eutrophication (Bennett et al., 2001; Carpenter, 2005), in conjunction with the proliferation of harmful algal blooms, decrease in dissolved oxygen (DO) levels, and loss of aquatic biodiversity (Carpenter et al., 1998), while watershed urban development is associated with several environmental consequences, including nutrient pollution, and sewage, pathogen and other contaminants (Bai et al., 2018). The strong linkage between lake ecosystems and their watershed (Williamson et al., 2008) highlights the effects of watershed land use exerted on lake habitats and biota and their consequential indirect impact on ecosystem functioning.

Several studies described the decline in species diversity as a consequence of habitat degradation due to watershed development (Lenat and Crawford, 1994; Dodson et al., 2005; Xu et al., 2019). Changes in the structure and composition of regional habitats may lead to local extinction through changes in nutrient loading and runoff of pollutants from surrounding areas (Ricciardi and Rasmussen, 1999; Meador and Goldstein, 2003). Moreover, as watershed land-use types are likely to influence greenhouse gas emissions that can affect the regional climate (Smith et al., 2008), community structure is expected to respond significantly to differences in thermal conditions (Dell et al., 2011). Species should be shaped by environments based on their niches, which are better conceptualized by their morphological, behavioral, or life-history traits that impact their fitness via growth, reproduction, and survival, rather than their taxonomical identity (McGill et al., 2006). Thus, functional trait-based approaches can be informative for understanding the biotic communities in response to environmental gradients (Mouillot et al., 2013).

Phytoplankton, the foundation of aquatic food webs, are a highly diverse group of eukaryotes and cyanobacteria. As phytoplankton in aquatic systems have fast growth rates and short-generation times (Sommer, 1989), they are highly influenced by a multitude of factors, including nutrients, temperature, light, carbon dioxide (CO<sub>2</sub>), and grazers (Sarnelle, 1992; Elliott et al., 2006; Burson et al., 2018), and they are known to be sensitive and predictive to environmental changes. Ecological studies investigating the effects of environmental gradients often assess phytoplankton community changes based on taxonomy-based approaches such as species composition, biomass, or diversity. Some evidence suggests that urban and agricultural land use within a watershed, indirectly representing increased nutrient inputs and various contaminants (Carpenter et al., 1998; Nielsen et al., 2012; Beaver et al., 2014), may influence the composition of phytoplankton assemblages by favoring the growth of cyanobacteria toward the agricultural and artificial land-use types (Sánchez et al., 2021). Phytoplankton biomass and production in the lakes surrounded by urban areas or agricultural land tend to be increased by anthropogenic nutrient enrichment (Peng et al., 2021). Despite substantial progress in the understanding of the changes in phytoplankton communities due to watershed land-use changes, studies using trait-based

approaches and exploring the consequential functional outcomes following land-use change are still scarce.

In this study, we evaluate how environmental stress gradients, representing a range of land uses and trophic conditions, affect phytoplankton functional traits and the diversity of lakes in northeast China. We used RLQ and fourth-corner analyses to assess the bivariate relationships between environmental stress gradients and species traits. The aims of this study were to: (1) examine the patterns of species composition and trait distribution of phytoplankton in the selected lakes in relation to environmental changes and (2) identify the sensitive functional traits as indicators of environmental stressors. We hypothesized that the phytoplankton communities in lakes vary along a land use and environmental gradient. The assumed variation in communities could be promoted by environmental filtering for specific traits. In addition, we hypothesized with increasing agricultural and urban land-use pressure and nutrient enrichment, there would be a corresponding decrease in functional diversity of phytoplankton communities.

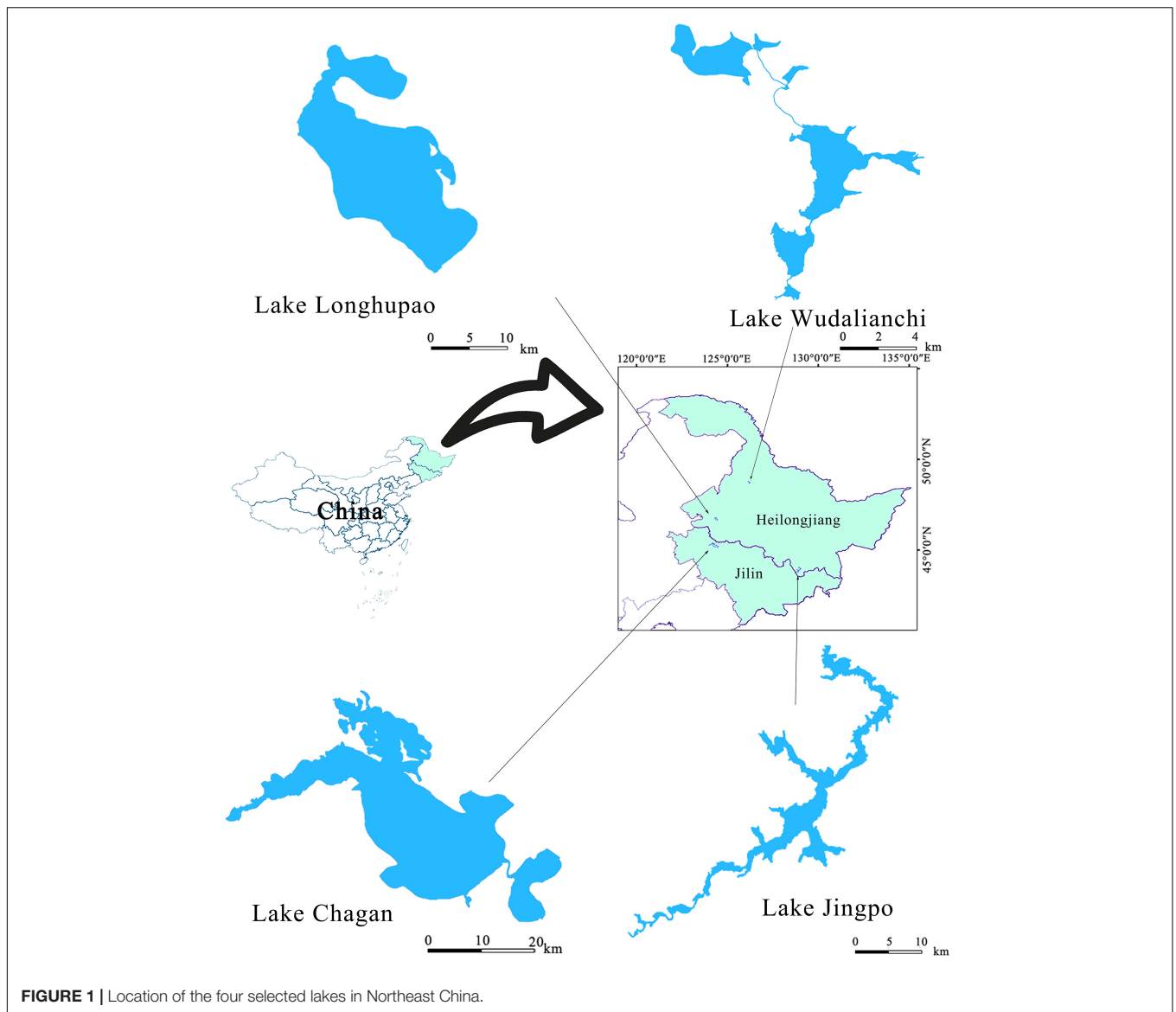
## MATERIALS AND METHODS

### Study Area

The study was conducted in four natural lakes in northeast China: the Chagan, Jingpo, Longhupao, and Wudalianchi (**Figure 1**), all belonging to the Songhua River Basin. The region is characterized by a temperate continental monsoon climate, with a mean annual temperature of 2.8°C and average annual precipitation of 531.1 mm. During the last several decades, the region has undergone massive changes in land cover and a large amount of land has formed sparse grassland and reed land which has become a place for local farmers to graze (Liu et al., 2005). Lake Chagan and Longhupao belong to the lowland part of the Songhua River Basin with loamy soils as the dominant geological features, while Lake Wudalianchi and Jingpo are lava-dammed lakes with sandy and loamy soils. The selected lakes varied in both development in their catchments and represented different morphometric and water quality conditions (**Table 1**).

### Land Use and Environmental Gradients

The land-use variables comprised proportions of the forest, grassland, wetland, and agricultural and urban areas within lake watersheds. These were determined at the whole topographic catchment scale. The Geographic Information System (GIS) program ArcGIS (version 10.7) was used to analyze the percentage of different land cover types. Environmental gradients were described in terms of lake morphology and water quality. Lake morphological variables comprised surface area and maximum depth. The surface area was drawn with ArcGIS software based on physical barriers and topographical features. Maximum water depth was obtained from Jing et al. (2014). Water quality variables comprised DO, water temperature, and pH that were measured in site at the subsurface (~0.5 m) using the YSI Professional Plus Multi-meter (YSI Incorporation, Yellow Springs, OH, United States) and variables related to trophic status including total nitrogen (TN), total phosphorus (TP), and



**FIGURE 1** | Location of the four selected lakes in Northeast China.

chemical oxygen demand (COD). TN and TP were analyzed using the persulfate digestion method and COD was determined with open reflux method (American Public Health Association [APHA], 1992).

### Functional Trait Selection

Phytoplankton were collected from the four lakes seasonally in May (spring), August (summer), November (autumn) 2019, and February (winter) 2020. Composite water samples combining euphotic depth-integrated subsamples were collected for phytoplankton at 12 locations in each lake. Phytoplankton counts and cell volume estimates were performed using the inverted microscope method (Utermöhl, 1958). Phytoplankton was identified at the species or genus level according to Hu and Wei (2006). A total of 18 functional traits (Table 2) that are considered crucial for reproduction, resource acquisition, and predator avoidance (Weithoff, 2003; Litchman and Klausmeier,

2008) were assigned for each of the 279 phytoplankton species. Cell size and greatest axial linear dimension (GALD) ( $\mu\text{m}$ ) were obtained by averaging measurements from at least 10 individuals for each taxa. Other traits were compiled based on scientific literature, web search, and expert knowledge (Jones, 2000; Weithoff, 2003; Hu and Wei, 2006; Litchman and Klausmeier, 2008; Klais et al., 2017; Loewen et al., 2021).

### Statistical Analysis

To demonstrate the location of different algal groups in relation to their functional traits, principal component analysis (PCA) was conducted on trait matrix of species. Species in the PCA plot were phylogenetically grouped in major taxonomic groups (phyla): chlorophytes, chrysophytes, cryptophytes, cyanobacteria, diatoms, dinoflagellates, and euglenophytes.

Two complementary multivariate analyses, the RLQ analysis (Dolédéc et al., 1996) and the fourth-corner approach

**TABLE 1** | Information on watershed land use and environmental gradient parameters in four selected lakes.

Variables	Lake	Lake	Lake	Lake
	Chagan	Longhupao	Jingpo	Wudalianchi
Surface area (km <sup>2</sup> )	366.8	128.4	84.6	20.7
Maximum depth (m)	3.5	3.5	48	12
Agricultural area (%)	46.51	28.55	25.22	54.92
Urban area (%)	2.63	1.20	0.96	1.21
Forest (%)	0.04	0.13	67.43	20.41
Grassland (%)	28.80	49.25	4.07	14.33
Wetland (%)	1.54	1.36	0.90	0.00
Water temperature (°C)	14.9	14.7	14.1	11.8
Dissolved oxygen (mg/L)	8.96	10.38	9.43	10.17
pH	9.18	8.58	8.35	8.60
Total phosphorus (mg/L)	0.229	0.289	0.147	0.162
Total nitrogen (mg/L)	1.617	1.003	2.124	1.783
Chemical oxygen demand (mg/L)	8.189	5.889	7.420	7.650

**TABLE 2** | Phytoplankton functional traits used in this study.

Traits	Abbreviation
Cell size < 100 μm <sup>3</sup>	Small
Cell size 100–1,000 μm <sup>3</sup>	Medium
Cell size > 100 μm <sup>3</sup>	Large
Greatest axial linear dimension > 35 μm	GALD > 35 μm
Unicellular life form	Unicellular
Colonial life form	Colonial
Filamentous life form	Filamentous
Coenobium life form	Coenobium
Mucilaginous-producing	Mucilage
Nitrogen fixation	N-fixation
Silica requirement	Si-requirement
Chlorophyll <i>b</i> -containing	Chlorophyll <i>b</i>
Chlorophyll <i>c</i> -containing	Chlorophyll <i>c</i>
Phycobilins-producing	Phycobilins
Mixotrophy	Mixotrophy
Toxin-producing	Toxin
Flagellar motility	Flagella
Buoyancy-regulating	Buoyancy

(Dray and Legendre, 2008; Dray et al., 2014), were conducted to investigate the covariation between environmental characteristics and functional traits. RLQ (R, sites by environmental variables; L, sites by species abundance data; Q, species by traits) analysis performs a double inertia analysis between the Q and R through L ordination (Dolédec et al., 1996). Thus, it is possible to identify the effects of land use and environmental gradients on the traits based on the phytoplankton community structure. As suggested by Dray and Legendre (2008), we combined two permutation models for both the analyses tested the null hypotheses that “species assemblages are randomly attributed to sites, irrespective of the site characteristics” (model 2) and that “species are distributed according to their preferences for site conditions, but irrespective of their traits” (model 4). Finally, the fourth-corner approach was used to evaluate the specifically

predictive role of functional traits in watershed land-use intensity and environmental gradients.

We calculated three multidimensional functional diversity indexes: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). Increases in these three index values indicate that more niche space is occupied by species, a more evenly abundance distribution in niche space, and a larger divergence in the abundance distribution in niche space, respectively (Mason et al., 2005). The relationships between functional diversity index and land use and environmental gradients were examined using Pearson correlation.

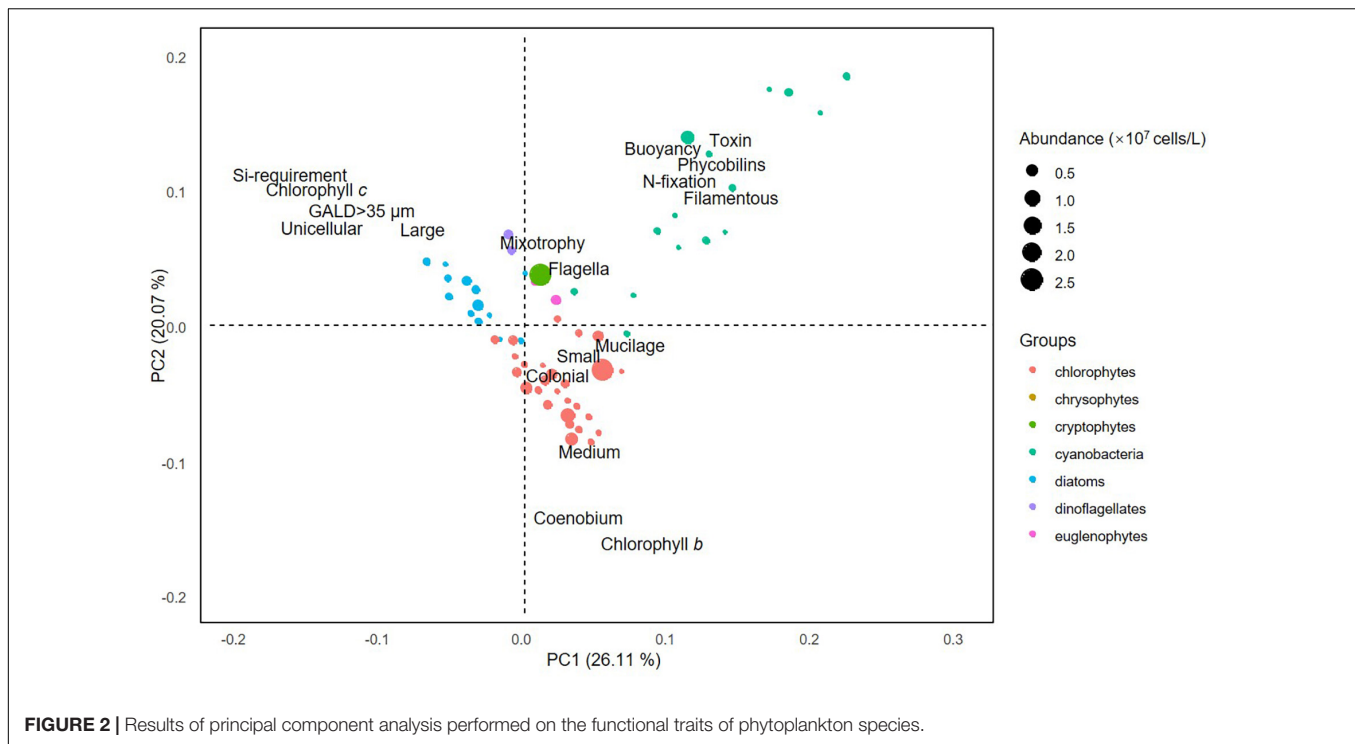
All the analyses and graphics were performed in R version 4.0.3 (R Core Team, 2020) with the *ade4* (Dray and Dufour, 2007), *vegan* (Oksanen et al., 2020), *FD* (Laliberté and Legendre, 2010), *corrplot* (Wei and Simko, 2021), and *ggfortify* (Tang et al., 2016) packages.

## RESULTS

The first two axes of the PCA performed on phytoplankton functional traits explained 26.11 and 20.07% of the variation, respectively (Figure 2). Of the four general trait groups, the first was dominated by species that are small to medium sized and chlorophyll *b*-producing and form colonies or coenobiums (i.e., chlorophytes); the second comprised filamentous and toxin-producing species with the ability of buoyancy regulation and nitrogen fixation (i.e., cyanobacteria); the third consist of large-sized species that are unicellular, chlorophyll *c*-producing, and require silica (i.e., diatoms); the fourth contained species that are mixotrophic and flagellate (i.e., dinoflagellates, crypto-, and euglenophytes).

The RLQ analysis revealed that land use and environmental gradients influence the distribution of phytoplankton species with specific traits (model 2,  $p < 0.001$ ) and that the composition of phytoplankton assemblages is dependent on the land use and environmental gradients of studied lakes and influenced by species traits (model 4,  $p = 0.028$ ). The first two RLQ axes accounted for 97.44% of the variation in relationships between land use and environmental gradients and functional traits. The first RLQ axis was positively correlated with urban and agricultural land use, surface area, pH, and TN. Grassland, wetland, DO, and TP loaded positively onto the second RLQ axis, while forest cover, maximum depth, and water temperature loaded negatively onto the second RLQ axis (Figure 3A). The traits filamentous, phycobilins, toxin-producing, and nitrogen fixation occurred in cyanobacteria and the traits chlorophyll *b*-producing, medium sized, and coenobium generally occurred in chlorophytes positively correlated with the first RLQ axis, whereas the traits unicellular, mixotrophic, and chlorophyll *c*-producing negatively correlated with the first RLQ axis. The traits flagella, large sized, and the silica requirement were negatively related to the second RLQ axis (Figure 3B).

The fourth-corner analysis provided the significant interactions between individual traits and land use and environmental gradients. Of the 18 traits examined in this study, five were deemed indicators of morphological, land



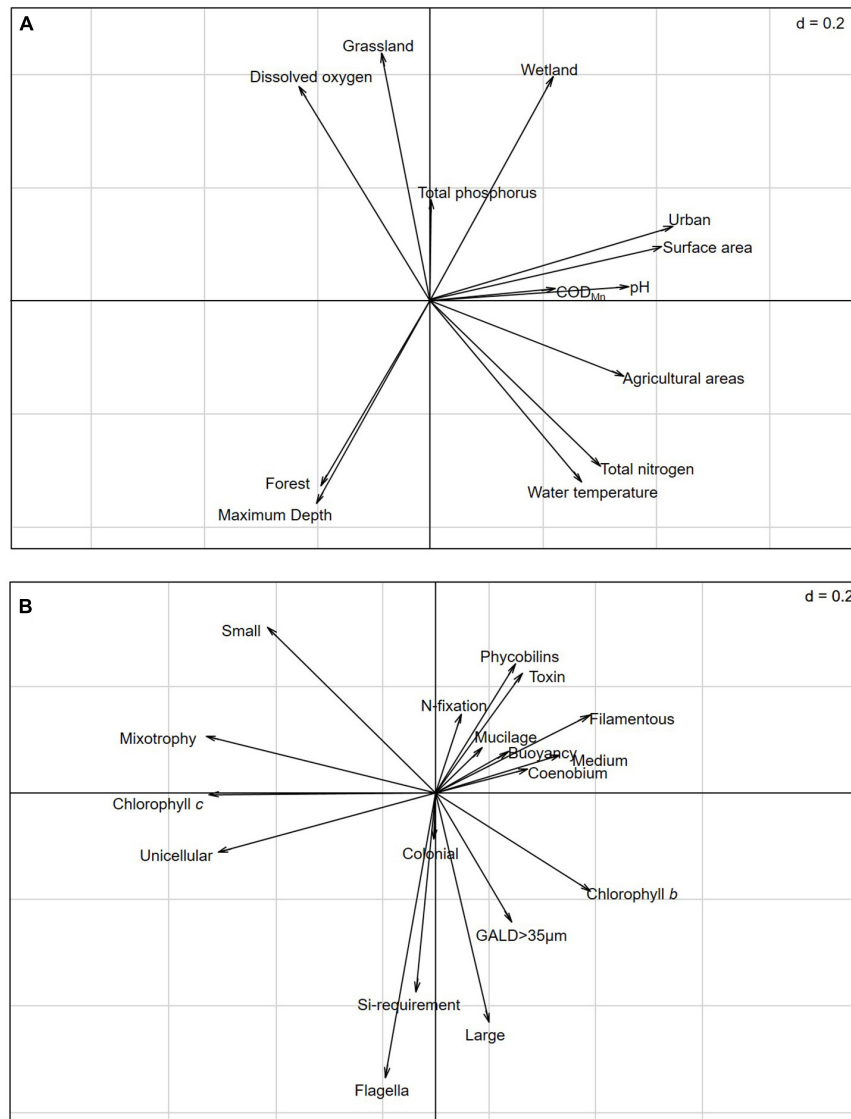
use, and environmental variables (Figure 4). Filamentous taxa possessed flagella were significantly positively associated with surface area, maximum depth, and urban areas, whereas unicellular, mixotrophic, chlorophyll *c*-containing taxa were significantly negatively associated with surface area, agricultural, and urban land use.

Functional richness of phytoplankton assemblages generally increased along with surface area and forests, but decreased along with intensive agricultural and urban land use (Figure 5). There were no relationships between FEve and morphological and environmental variables. FDiv was positively correlated with wetland and higher TP, but negatively with agricultural land use (Figure 5).

## DISCUSSION

Lakes provide for a wide range of valuable ecosystem services, including provisioning, regulation, and maintenance, as well as cultural services for instance, by improving human well-being (Reynaud and Lanzanova, 2017; Custódio et al., 2020). To this end, conventional approaches to lake restoration and preservation have typically focused on the mechanisms and factors regulating species assemblages. The observable functional differentiation of the traits of phytoplankton community revealed that of the stress gradients studied, human land-use activities had a consistent and strong influence upon phytoplankton functional structure via their consequences for nutrient loading. In addition, land-use transformations due to extensive agricultural and urban development cause a reduction of the FRic in phytoplankton assemblages.

Our results indicate significant relationships between traits and environmental stress variables, which provide a framework to link phytoplankton communities of lakes to environmental filtering. More specifically, increased agricultural and urban areas around lakes associated with changes in physicochemical properties, such as the increase in nitrogen, pH, or decrease of DO generally favored filamentous and toxin-producing algae as opposed to mixotrophic algae. These results are in agreement with other studies, which found that agricultural or urban land use could increase nutrient inputs from the watershed and in turn influence phytoplankton functional traits (Phillips et al., 1978; Carpenter and Waite, 2000; Bosch et al., 2009; Loewen et al., 2021). However, different anthropogenic land-use types have changing effects on lake N and P stoichiometry, with agricultural runoffs generally having a higher nitrogen-to-phosphorus ratio than those from urban areas or grasslands (Carpenter et al., 1998). In this study, agricultural lands were positively associated with TN, but negatively associated with trait nitrogen fixation. These results suggest a reduction of N:P ratio under generally eutrophic conditions that may favor the dominance by nitrogen-fixing cyanobacteria due to their competitive advantage under nitrogen-limited conditions (Smith, 1983; Sharpley and Withers, 1994). We also found that increased phosphorus inputs from grassland and wetland were positively associated with toxic cyanobacterial species, providing further support for the role of phosphorus load in fueling toxic cyanobacterial blooms (Bormans et al., 2016). As the water sources of Lake Chagan and Longhupao pass through manured grassland and a large number of wetlands were transferred to irrigation ditches for rice fields (Liu et al., 2021), a higher level of phosphorus loading to lakes and low N:P ratios can be expected.

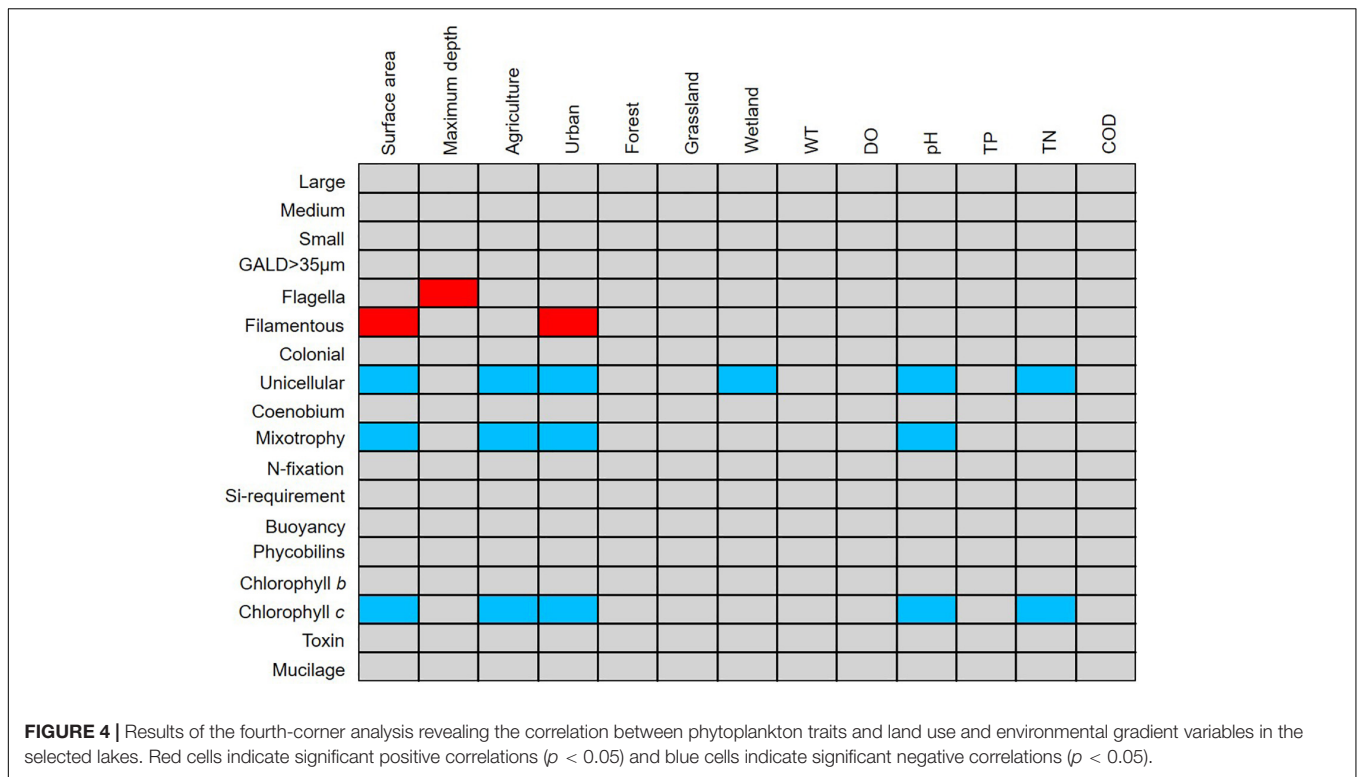


**FIGURE 3** | RLQ analysis revealing the correlations between land use and environmental gradient variables (R table  $101 \times 13$ ) and functional traits (Q table  $279 \times 18$ ), constrained by species abundance (L table  $101 \times 279$ ): **(A)** Coefficients for the land use and environmental gradient variables and **(B)** coefficients for the functional traits.

Our results also showed that land use and environmental gradients could potentially influence resource acquisition traits of phytoplankton. Mixotrophy, which is an important trait related to nutrient acquisition (Litchman and Klausmeier, 2008), is advantageous under low nutrient conditions (Troost et al., 2005). Mixotrophic taxa increased in lakes with relatively low land-use intensity and nutrient conditions, suggesting a competitive advantage of these taxa under low nutrient supply. In addition, differences in pigment composition allow differences in spectral utilization patterns that can provide opportunities for species coexistence under light limitation (Stomp et al., 2004). Experimental studies with chlorophyll *c*-containing species *Stephanodiscus hantzschii* have shown negative effects of light intensity on chlorophyll *c*, especially under high

nutrient conditions (Marzetz et al., 2020). We observed the opposite pattern with high chlorophyll *c*-containing species under nitrogen-limitation conditions. This might be due to decreasing light availability in deeper lakes with more forested dominated watershed, which favors the growth of chlorophyll *c*-containing species, as has been found in other north-temperate lakes (Loewen et al., 2021).

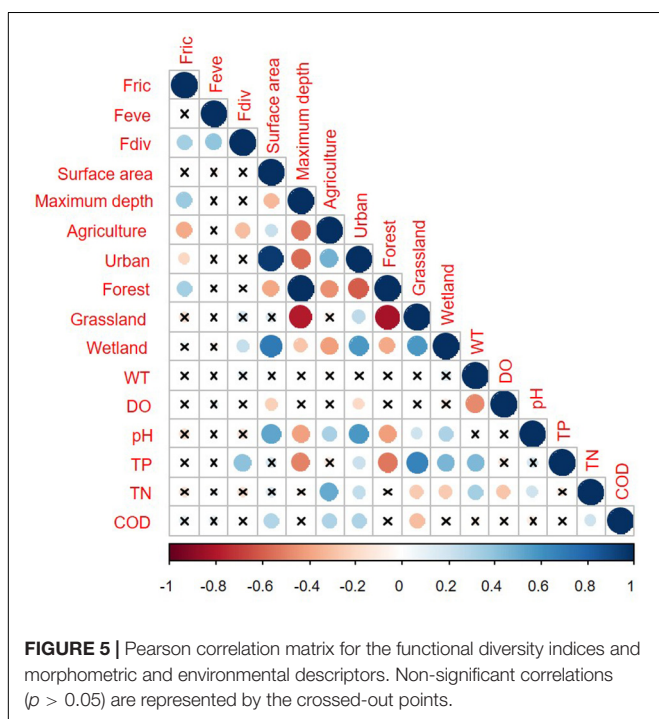
We revealed significant morphological factors (maximum depth and surface area) constraining the composition of phytoplankton communities. Our results indicate deeper water favoring flagellated algae. These results further demonstrate that the physical factors related to lake morphology influence functional strategies to survive in terms of functional traits related to motility (Wentzky et al., 2020). For instance, lake



depth exerts a strong influence on the stability of the water column (e.g., mixing and thermal stratification) and thus on the light and oxygen condition and the internal nutrient loading from sediment into the hypolimnion (O'Brien et al., 2003;

Yang et al., 2016). The flagellates possess active motility that enable them to alter position within the water column to alleviate any spatial limitation or segregation of resources and select optimum conditions (Salmaso and Padisák, 2007; Litchman and Klausmeier, 2008; Wentzky et al., 2020). Deep lakes where turbulence and internal nutrient loading were relatively low that may give a competitive advantage of flagellated algae to overcome nutrient deficiency and sedimentation losses by adjusting the position in the water column. In contrast, the negative association between maximum depth and traits nitrogen fixation and toxin production is possible because the increasing internal phosphorus loading with decreasing N:P ratios in shallow lakes is the main driver of the nitrogen-fixing cyanobacterial blooms (Smith, 1983; Sharpley and Withers, 1994). We also observed links between water temperature and algal traits in deep lakes. In this study, the higher water temperature may increase the prevalence of flagellated algae. Similar to water depth, the water temperature could influence the vertical distribution of oxygen and upward mixing of nutrients (Straile et al., 2003) and thus mediate physiological processes and behavioral responses of phytoplankton. The other morphological factor that was positively associated with the filamentous nitrogen-fixing algae is lake surface area. As larger lakes in this study are common in urban areas and have relatively shallow sloped basins and high phosphorus loadings, their phosphorus-rich conditions and conducive environment for germination of akinetes may promote the proliferation of nitrogen-fixing cyanobacteria (Kovács et al., 2012).

In aquatic systems, land-use changes are major driving forces of biodiversity loss (Allan, 2004). Increasing environmental



stress gradient in our study, representing intensive urbanization or agricultural practices generally reduce FRic. Several studies have previously identified the significant effect of environmental disturbance upon freshwater biodiversity, and land-use changes have been identified as further significant factors influencing lake ecosystems (Arbuckle and Downing, 2001; Light and Marchetti, 2007; Nielsen et al., 2012; McGoff et al., 2013). Watershed land-use development has often been cited as having a negative effect upon the biodiversity of lakes (Dudgeon et al., 2006; van Soesbergen et al., 2019). Functional diversity has been shown with potential applications for predicting environmental disturbance. In this study, FRic of phytoplankton communities decreased with increasing land-use intensity. Similar patterns of functional changes of community in response to environmental disturbance have been reported, for instance, a reduction in functional diversity of aquatic insects in southeastern Brazil (Castro et al., 2018), and of fishes in Malaysia (Wilkinson et al., 2018), and of benthic diatoms in Italy (Falasco et al., 2021). Potentially higher functional diversity represented much higher levels of productivity and reliability (Diaz and Cabido, 2001; Vallina et al., 2017). Our result of a significant decline in FRic with increasing land-use intensity suggests that homogenization may cause a reduction in ecosystem productivity and reliability to human disturbance. Given the importance of functional diversity to productivity and reliability (Mason et al., 2013; Gherardi and Sala, 2015), we suggest that management at the watershed and local scales such as mitigating grazing and cultivation practices can help to ensure a stronger determinant of ecosystem processes in face of anthropogenic disturbances.

Functional richness represents the amount of functional space occupied by a species assemblage (Mouchet et al., 2010). We suggest that the significant decrease in FRic along the agricultural and urban land-use gradients may imply a low degree of niche differentiation among species, reflecting the occupation by species with similar traits inhabiting the area, in response to extensive habitat degradation due to increased intensity of land use. Although increasing nutrient loadings from watershed are likely to favor cyanobacteria bloom (Doubek et al., 2015; Richardson et al., 2019), the results suggest that increasing land-use intensity is to the detriment of FRic, indicating that the functional community structure of phytoplankton is susceptible to agriculture and urbanization-driven disturbances. In this study, a possible explanation for a reduced functional diversity along the environmental stress gradient is eutrophication and anthropogenic contamination by agriculture and urbanization. For example, eutrophication of lakes is characterized by a potential deficit of oxygen, blooms of cyanobacteria, decrease water transparency, and deterioration of water quality (Carpenter et al., 1998). Other detrimental consequences of converting natural land covers include pesticides and other toxic chemicals from agricultural and urban areas. For instance, urban runoffs are widely recognized as transport vectors of salts, pharmaceuticals, and trace metals such as cadmium, copper, and lead (Müller et al., 2020), while agricultural runoffs are widely recognized as transport vectors of pesticides and phosphorus and nitrogen in forms of fertilizers and manure (Carpenter et al., 1998; Munz et al., 2017). These contaminants will lead to the loss of biodiversity directly through simple toxicity effects

on physiological, developmental, and reproductive processes (Burant et al., 2018) or indirectly by altering the environmental conditions (Yang et al., 2022).

## CONCLUSION

In this study, we considered the effect of land-use changes and environmental gradients upon the functional response of phytoplankton assemblages. The integration of RLQ analysis with the fourth-corner approach significantly identified functional traits as potential indicators to aquatic environments. Furthermore, anthropogenic disturbance such as agricultural and urban land use can modify phytoplankton traits which consequentially decreased functional diversity of phytoplankton assemblages. Moreover, declines in FRic representing functional homogenization may cause a reduction in ecosystem productivity and reliability. Given the superior performance of functional-based approach, our findings also highlighted the importance of the application of both the biological traits and functional diversity index in monitoring programs for lake ecosystems.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

## AUTHOR CONTRIBUTIONS

XD and DS designed and orchestrated the research and wrote up the findings. KM, JY, and XJ providing help for field sampling. HW, HL, LW, and CZ provided review and comments and edited the manuscript. TH revised the content of the manuscript and responsible for the overall submission. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.819252/full#supplementary-material>



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