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Research article

Climate, hydrology, and human disturbance drive long-term (1988–2018) macrophyte patterns in water diversion lakes

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ABSTRACT

Macrophytes are affected by many natural and human stressors globally but their long-term responses to these multiple stressors are not often quantified. We employed remote sensing and statistical tools to analyze datasets from both short-term (2017–2018) field investigations to explore seasonal patterns, and long-term (1988–2018) Landsat remote-sensing images to detect annual patterns of macrophyte distributions and study their responses to changes in climate, hydrology, and anthropogenic activities in a chain of water diversion lakes in eastern China. We found: 1) biomass and species richness of macrophytes peaked in summer with dominant species of submerged macrophytes *Ceratophyllum demersum*, *Potamogeton pectinatus*, and *Potamogeton maackianus* and floating macrophytes *Trapa bispinosa*, and non-native species *Cabomba caroliniana* spread in midstream Luoma Lake and Nansi Lake in summer, while *Potamogeton crispus* was dominant in all the lakes in spring; 2) water physicochemical parameters (chloride and water depth), lake characteristics (area and water storage), climate factors (air temperature and precipitation), and anthropogenic activities (commercial fishery and urban development) were significantly correlated to the seasonal distribution of macrophytes; 3) long-term data showed a significantly negative correlation between coverage of floating macrophytes and precipitation where the wettest year of 2003 had the lowest coverage of floating macrophytes; and 4) climate (air temperature) and hydrology (water level) were positively correlated with total macrophyte coverage, but human disturbance indexed by the gross domestic product was negatively driving long-term coverage of macrophytes. Our study has important implications for understanding the long-term succession of macrophytes under both natural and human stressors, and for future environmental management and ecological restoration of freshwater lakes.

1. Introduction

Climate change and anthropogenic activities are increasingly threatening the ecological integrity of freshwater lakes globally (Akasaka et al., 2010; Davis et al., 2010; Fares et al., 2020). The internal processes and hydrological regimes of lake ecosystems have also been greatly modified owing to increased anthropogenic pressures (e.g., water conservancy projects, aquaculture, agriculture, industry, and urbanization) (Kong et al., 2017; Kim and Nishihiro, 2020). Both climate change and anthropogenic activities could have significant impacts on the species composition of macrophyte communities and their spatial distribution in freshwater lakes (Foti et al., 2012; Wang et al., 2019).

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Climate factors affect species growth, multi-traits, and lineage compositions of macrophytes (García-Girón et al., 2020). Studies from both manipulative experiments and field investigations have shown that alterations in climate regimes may influence macrophyte interactions, germination rates, reproductive strategies, and species abundance, which could lead to changes in biodiversity, community structure, and ecosystem function of macrophytes (Li et al., 2017; Fares et al., 2020; Kim and Nishihiro, 2020). In addition to climate factors, various anthropogenic activities negatively affect macrophytes (Egertson et al., 2004; Davis et al., 2010). Manzo et al. (2020) indicated that isolated ponds with limited anthropogenic pressure were better for macrophyte conservation than those under high anthropogenic pressures. Also, eutrophication in lakes caused by nitrogen and phosphorus may trigger a transition from a macrophyte-dominant to a phytoplankton-dominant state (Scheffer et al., 1993; Akasaka et al., 2010; Zhang et al., 2016). High-intensity aquaculture activities such as intensive grazing by herbivorous fishes and crabs on macrophytes could greatly reduce the biomass and species diversity of macrophytes (Wang et al., 2019). However, few study that detected large-scale macrophyte patterns considered how multiple stressors and their interactions affected freshwater macrophytes (Zhu et al., 2007; Chappuis et al., 2012; Kennedy et al., 2015; Murphy et al., 2019). Further, the mechanisms driving these patterns are not clear (Birk et al., 2020; Chen et al., 2020).

The eastern plains basin of China is a region that has numerous freshwater lakes that are experiencing multiple human stressors such as industry, agriculture, fishery, and urbanization (Zhuang et al., 2019; Guo et al., 2020b). In addition, since 2013 the world's largest water diversion project, the South-to-North Water Diversion Project (SNWDP), has connected many freshwater lakes (including our study lakes Gaoyou, Hongze, Luoma, Nansi, Dongping Lakes) and the four largest Chinese river basins (e.g., Yangtze, Huai, Yellow, and Hai) through the Beijing-Hangzhou Grand Canal in this region (CMWR, China Ministry of Water Resources). Moreover, the climate characteristics of these freshwater lakes are divided by the Huai River: the southern lakes (i.e., Gaoyou and Hongze Lakes) have a subtropical monsoon climate whereas the northern lakes (i.e., Luoma, Nansi, and Dongping Lakes) have a temperate monsoon climate (Qu et al., 2020). Thus, these lakes represent great natural experimental units to detect how multiple human stressors and climate affect freshwater communities. Since the 1990s, there have been field investigations on macrophyte communities in some of these lakes, such as Hongze Lake, Nansi Lake, and Dongping Lake (Zhang, 1992; Pang, 1999; Shi, 2002; Qiu et al., 2017; Yu et al., 2017). As technology evolves, some studies used remote sensing technologies to interpret and identify wetlands and macrophyte distribution (Ozesmi and Bauer, 2002; Wang et al., 2019; Huang et al., 2021). However, we are not aware of any study that has attempted to assess the large spatial distribution patterns of macrophytes by considering all these water diversion lakes, or to detect both climate and multiple human stressors driving macrophyte changes over the long-term and over large spatial scale.

Here, we combined both short-term (2017–2018) field observations and long-term (1988–2018) remote-sensing data to investigate the patterns of macrophytes in the five diversion lakes along the eastern route of the SNWDP and their responses to both climate change and multiple anthropogenic stressors such as land use changes, water diversions, and fishery. The underlying hypothesis for our study was that both the macrophytes' short- and long-term distributions had clear spatiotemporal patterns and were strongly related to climate, hydrology, and anthropogenic activities. The objectives of the present study were to 1) clarify the short-term seasonal structure and biodiversity patterns of macrophyte communities in the lakes, 2) identify the long-term annual distribution of macrophytes in the water diversion lakes, and 3) assess the specific relationships between patterns of macrophytes (short-term, long-term) and three types of drivers, climate, hydrology, and human factors. Our study provides information on the effects of climate and anthropogenic disturbances on macrophyte communities in the eastern plain of China as well as guidelines for ecological management and restorations of macrophytes in freshwater lakes in China and elsewhere.

2. Material and methods

2.1. Study area and lakes

The eastern route of the South-to-North Water Diversion Project (SNWDP-ER) of China starts from the Jiangdu water control sluice gate in Yangzhou, Jiangsu Province, moves water from the lower reach of the Yangtze River in the south to the Yellow River in the north connecting four major river basins in China (i.e., the upstream Yangtze River, Huai River, Yellow River, and downstream Hai River) (CMWR, Guo et al., 2020a, b; Qu et al., 2020). From the south (upstream) to the north (downstream), the five water diversion lakes along the SNWDP-ER are Gaoyou Lake (GYL, 32°42′-33°41' N, 119°06′-119°25' E), Hongze Lake (HZL, 33°06′-33°40' N, 118°10′-118°52' E), Luoma Lake (LML, 34°00′-34°11′ N, 118°06′-118°18′ E), Nansi Lake (NSL, 34°27′-35°20′ N, 116°34′-117°21′ E), and Dongping Lake (DPL, 35°30′-36°20′ N, 116°00′-116°30′ E), with a surface area of 661, 2152, 285, 1176, and 209 km^2, respectively (Fig. 1, Table A.1). These lakes have a distance of 65–622 km to the source water near the Yangtze River (Qu et al., 2020). They provide multiple ecosystem services such as drinking water, navigation, fisheries, flood control, biodiversity conservation, and tourism in eastern China (Guo et al., 2020a; Qu et al., 2020).

Before the operation of the SNWDP-ER, Jiangsu Province had constructed and implemented the River Water to North Diversion Project in the 1960s, and some of these lakes in Jiangsu Province (e.g., GYL, HZL, and LML) have been used as water diversion lakes since then. The SNWDP-ER has been officially in operation since November 2013 where water is transferred annually from November to May (CMWR). By May 2022, a total of $5.4*10^9$ cubic meters of water have been transferred through the SNWDP-ER (CMWR).

2.2. Field sampling and laboratory analysis

Macrophyte samples were collected from the five water diversion lakes in both 2017 and 2018. In 2017, field sampling was conducted in four seasons: March for spring, June for summer, September for autumn, and December for winter. A total of 9–16 sites were sampled in each lake (GYL = 11, HZL = 16, LML = 9, NSL = 12, DPL = 11; Table A.1) depending on lake area, morphology, habitat, and macrophyte distribution. In 2018, we sampled in spring (April), summer (July), and autumn (September) and more sampling sites were added in addition to the sites in 2017 (GYL = 21, HZL = 32, LML = 17, NSL = 40, DPL = 16; Table A.1). At each site, three quadrats of approximately 2.5 m * 2.5 m were randomly selected within the range of 5 m around the sampling site to measure macrophyte species (Kanninen et al., 2013). Macrophytes were collected by a reaping hook (covering 0.2 m^2), then we washed, drained, identified, and measured the wet weight of each macrophyte species (Chen et al., 2012). Collected macrophytes were assigned to four life forms: emergent, free-floating, floating-leaved, and submerged. GPS and ArcGIS (10.6) were used to record and map the boundary and calculate the distribution area of macrophytes. In each site, macrophytes biomass was calculated as the wet weight per unit area (mean of three quadrats), and richness was calculated as the total number of species (total of three quadrats).

At each site, seven water quality parameters were measured in situ (Qu et al., 2020). Water temperature (WT, °C), conductivity (Cond, μS/cm), dissolved oxygen (DO, mg/L), and pH were measured with a portable multi-parameter water quality meter (YSI Professional Plus, USA). Water depth (WD, cm) and transparency (SD, cm) were measured with a Secchi disk. Turbidity (Tur, NTU) was determined with a portable turbidity meter (HACH 2100 Q). A 2-L water sample was collected, preserved, and transported with ice to the laboratory for further analysis within 48 h. This water was analyzed for 12 parameters (total nitrogen

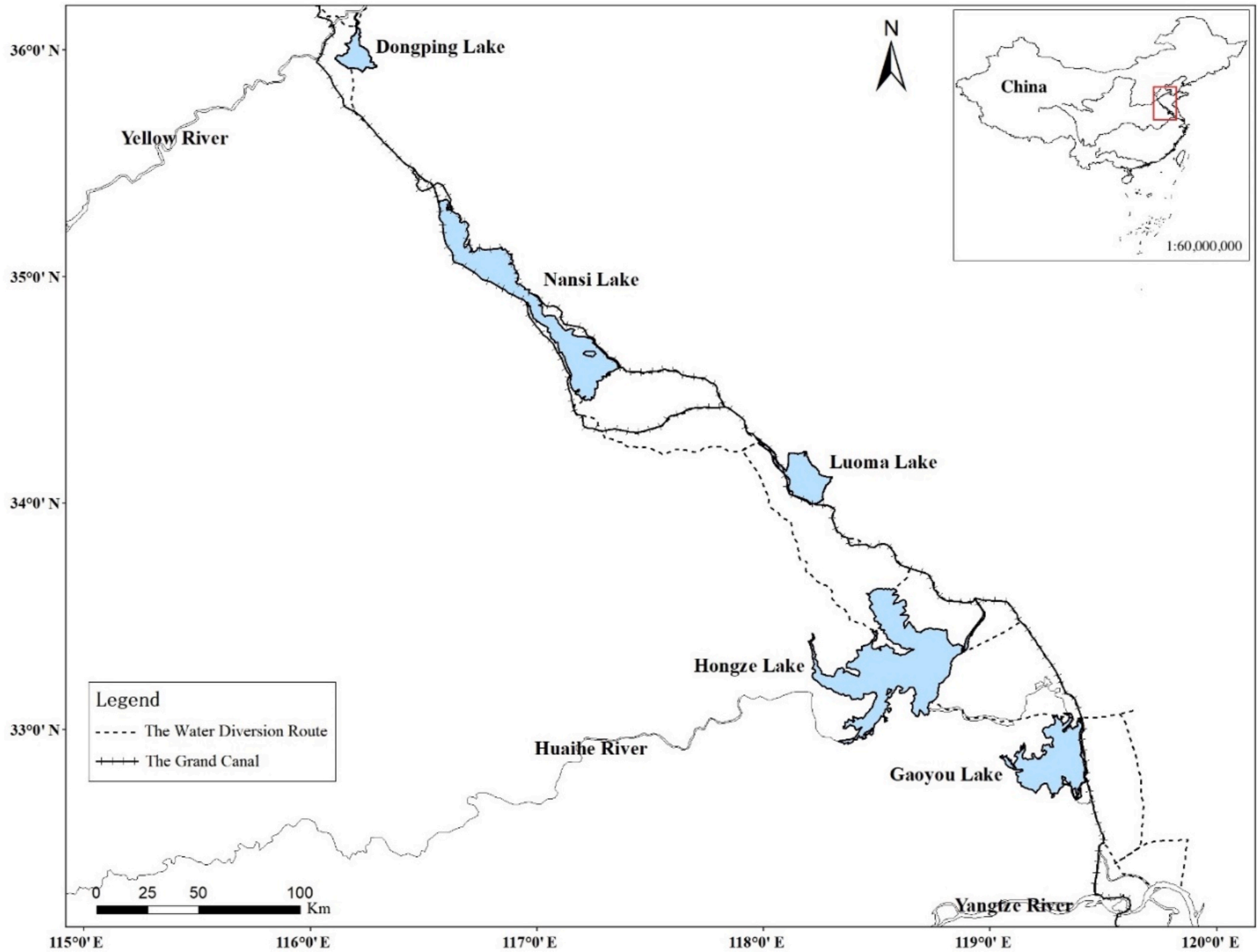

Fig. 1. Map of the five water diversion lakes along the Eastern Route of the South-to-North Water Diversion Project of China.

TN, ammonia nitrogen NH_4–N, nitrate nitrogen NO_3–N, NO_2–N, total phosphorus TP, phosphate PO_4, Chloride Cl^-, total hardness TH, total alkalinity TA, chlorophyll *a* Chl, chemical oxygen demand COD, and total suspended solids TSS) (APHA, 2005; Qu et al., 2020).

2.3. Remote sensing data collection and analysis

Remote sensing data, Landsat-5 TM and Landsat-8 OLI remote-sensing images, were used to analyze the long-term patterns of macrophyte coverage in the five water diversion lakes. We considered factors such as the growth period of macrophytes (June to September), climate events (e.g., drought or flood), and previous investigations about macrophytes in water diversion lakes, for remote-sensing image selection. In the end, a total of 42 scenes of Landsat-5/8 (TM/OLI) remote sensing images with lower cloud cover between June and September 1988, 1993, 1998, 2003, 2008, 2013, and 2018 were selected (Table A.2). All the Landsat images were downloaded from the USGS (United States Geological Survey).

Before extracting data on macrophyte coverage, we conducted data pre-processing (geometric correction, radiometric calibration, and atmospheric correction) and training sample selection (spatial coordinate random stratified sampling, visual interpretation) (Wang et al., 2019). Land covers were divided into macrophytes (emergent, floating, and submerged), water, and urban land. The classification and regression tree (CART) method was used to interpret and identify macrophytes (Marceau et al., 1990; Hansen et al., 1996; Deng, 2014). After macrophyte classification, we conducted an accuracy assessment (an overall accuracy and the kappa coefficient) to evaluate the accuracy and reliability of the classification results (Table A.3). ENVI 5.3 was used to analyze remote sensing data, and ArcGIS 10.6 was used to map the spatial distribution of macrophytes.

2.4. Climate and human-related data collection

Climate factors (air temperature AT, precipitation Pre, and average wind speed AWS), hydrological factor (water level WL), lake characteristics (lake area LA, lake water storage LWS), and anthropogenic activity factors (land-use types, gross output value of fishery GOVF, population, and gross domestic product GDP) between June and September of 1988, 1993, 1998, 2003, 2008, 2013, and 2018 of the five water diversion lakes were selected as the main explaining factors. Climate data were obtained from the China Meteorological Data Sharing Network. Data on lake characteristics, population, and GDP were obtained from the National Bureau of Statistics (NBS). Land-use types (areas of urban land as Urb, agricultural land as Agr, grassland as Gra, forest land as For, rough land as Rou or barren land, water as Wat) were obtained from the Resource and Environment Science Data Center. In each lake, we retrieved the above climate, population, GDP, and land use data from the corresponding datasets for the major city located in the lake area. Water level data were obtained for each lake from related lake hydrological monitoring departments that maintain fixed monitoring stations for these lakes.

2.5. Statistical analysis

2.5.1. Short-term patterns of macrophytes and driving factors

Two-way ANOVAs were used to test the effects of lake, season, and their interactions on biomass, richness, and diversity indices. No macrophyte sample was collected in HZL, LML, NSL, and DPL lakes in winter in 2017, thus the seasonal statistical analysis only included spring, summer, and autumn. If there was an interaction between lake and season, then one-way ANOVA was performed at different levels of the two factors; if there was no interaction, one-way ANOVA was performed for each of the two factors. Prior to the ANOVAs, all raw data were log10 transformed to meet the conditions of normality. Diversity indices were calculated using "vegan" and "BiodiversityR" packages in R software. Dominance was calculated according to the following equations:

$$B_{ri} = B_i / B_t \times 100\%$$

$$F_i = N_i / N_t \times 100\%$$

$$D_i = (B_{ri} + F_i) \times \qquad 2$$

Where B_{ri} is the relative biomass of the species i, B_i is the biomass of the species i, B_t is the total biomass of all the species; F_i is the frequency of occurrence of species i, N_i and N_t are the occurrence number of species i and the total sampling sites, respectively; Di is the degree of dominance.

Dominance of macrophytes (Guo et al., 2018) in lakes were used for principal component analysis (PCA) and canonical correspondence analysis (CCA). PCA was used to detect seasonal patterns of macrophytes using "FactoMineR" (Lê et al., 2008) and "factoextra" (Kassambara and Mundt, 2016) in R software. We used CCA to evaluate relationships between macrophytes and water physicochemical parameters (WD, WT, Tur, pH, DO, Cl-, COD, and TA), climate (Pre, AT, and AWS), anthropogenic factors (GOVF, Urb, and Gra), and lake characteristics (LA and LWS) (Guo et al., 2020a). The ordination analysis was carried out in R using "vegan", "ggplot2", and "ggrepel" packages. All the analyses were performed in the R platform (R Development core Team, 2019).

2.5.2. Long-term patterns of macrophytes and driving factors

The ANOVA was used to test macrophyte coverage differences among lakes and between years, respectively. Pearson correlation analysis was used to identify relationships between macrophyte coverage and environmental factors (climate, hydrology, and anthropogenic factors) and choose the appropriate factors for further analysis. To determine cause-effect relationships between explanatory factors and macrophytes, we used structural equation modeling (SEM). SEM is a statistical method based on the covariance matrix of variables to analyze the cause-effect relationships between variables (Bollen, 1989; Grace, 2006). SEM integrates factor analysis and path analysis, and can test the explicit variables (i.e., coverage of macrophytes, air temperature, precipitation, water level, population, urban land area, and GDP), latent variables (i.e., vegetation, climatic, hydrological, and anthropogenic factors), and the relationships between error variables in the model to get direct, indirect, and total effects of the explicit variables on the latent variables (Chen and Lin, 2010). The fitting degree (chi-square value CMIN, degree of freedom ratio CMIN/DF, value-added fit index NFI, IFI, CFI) of the SEM refers to the consistency between the theoretical model and the actual data. Path coefficient includes standard path coefficient and non-standard path coefficient, which have the same meaning as the path coefficients of regression analysis (Bollen, 1989; Grace, 2006). According to the assumptions and the principle of SEM, the initial conceptual model was constructed as shown in Fig. A.1. All statistical analyses were performed in R 3.5.3 (R Development core Team, 2019).

3. Results

3.1. Short-term patterns and drivers of macrophytes

3.1.1. Composition and diversity

A total of 20 species in 12 families of macrophytes were collected from the five water diversion lakes (Table A.4). A total of 20, 9, 15, 14, 19, and 11 macrophytes species were collected from Gaoyou Lake, Hongze Lake, Luoma Lake, Nansi Lake, and Dongping Lake, respectively. Only seven species occurred across all lakes, with some species endemic to specific lakes (Table A.4). No macrophyte sample was collected in HZL, LML, NSL, and DPL lakes in winter in 2017, thus the seasonal statistical analysis only included spring, summer, and autumn. There was no interaction between lakes and seasons in biomass and richness, and no significant difference between lakes (Table 1). Biomass and richness of macrophytes varied significantly among seasons and peaked in summer and autumn (One-way ANOVA, $P < 0.01$, Table A.5). Dominant species in four seasons varied greatly among lakes (Table A.6). We also collected a non-native submerged species *Cabomba caroliniana* in both Luoma Lake and Nansi Lake, with a dominance degree of 4.7% and 1.3%, respectively in summer, which was the first record of this species in Luoma Lake. There were significant effects of lake, season, and their interactions on diversity indices of macrophytes (Table 1). Shannon-Wiener index in Luoma Lake was significantly lower than that in the other lakes in autumn (Two-way ANOVA, $P < 0.05$, Fig. A.2).

3.1.2. Patterns of macrophytes communities

Species richness of submerged macrophytes in summer was significantly higher than that in spring (One-way ANOVA, $P < 0.05$, Table A.5). Species richness and biomass of floating-leaved macrophytes in summer and autumn were significantly higher than that in spring (One-way ANOVA, $P < 0.05$, Table A.5). Species richness and biomass of free-floating and emergent macrophytes did not differ significantly among seasons (Table A.5).

In spring, the first two principal components explained more than 34.1% of the total variance of macrophytes (Fig. 2a); PC1 had positive correlations with *P. crispus* (0.81) whereas *P. pectinatus* (0.86) was highly correlated with PC2. Hongze Lake and Nansi Lake differed from the others, with relatively high dominance of *P. crispus*, *P. maackianus* and *P. malaianus* in Hongze Lake, and high dominance of *P. crispus* and *P. pectinatus* in Nansi Lake. In the other lakes, *P. crispus* was dominated.

In summer, the first two principal components explained more than 21.6% of the total variance of macrophytes (Fig. 2b); PC1 had positive correlations with *N. minor* (0.76), *U. vulgaris* (0.75), and *N. nucifera* (0.60) whereas PC2 had negative correlations with *T. bispinosa* (−0.70), *S. natans* (−0.58), and *H. dubia* (−0.51). Composition patterns of macrophytes in the five lakes overlapped. The downstream lake, Nansi Lake had relatively high dominance of *N. minor*, *U. vulgaris*, *N. nucifera*, *P. lucens*, and *P. pectinatus*. In the two upstream lakes, Luoma Lake had high dominance of *T. bispinosa*, *P. maackianus*, and *V. natans* while Hongze Lake had relatively high dominance of *H. dubia*.

In autumn, the first two principal components explained more than 35.6% of the total variance of macrophytes (Fig. 2c); PC1 had positive correlations with *M. verticillatum* (0.95), *P. pectinatus* (0.91), *P. malaianus* (0.82), and *H. verticillata* (0.80). Two species *T. bispinosa* (−0.91) and *H. dubia* (−0.66) were highly correlated with PC2. Upstream Gaoyou Lake and Hongze Lake differed from others, which had relatively high dominance of *T. bispinosa* and *N. peltatum* in Gaoyou Lake and high dominance of *P. malaianus* and *C. demersum* in Hongze Lake. Downstream Luoma Lake, Nansi Lake, and Dongping Lake had relatively high dominance of *C. demersum*, *M. verticillatum*, *P. maackianus*, and *N. peltatum*.

3.1.3. Relationships between macrophytes and explaining factors

Water physicochemical parameters (WD, WT, Tur, pH, DO, Cl^-,

Table 1
Two-way ANOVAs on biomass, species richness, and Shannon-Wiener index of macrophytes in the five water diversion lakes during 2017–2018.

Parameters	Lake			Season			Lake × Season		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Biomass (g/km^2)	4	*0.781*	*0.540*	2	*2.501*	***<0.01***	8	*0.638*	*0.744*
Species Richness	4	*1.270*	*0.284*	2	*29.598*	***<0.01***	8	*1.078*	*0.381*
Shannon-Wiener	4	*9.672*	***<0.01***	2	*9.144*	***<0.01***	8	*7.885*	***<0.01***

COD, TA), climate (Pre, AT, AWS), anthropogenic factors (GOVF, Urb, Gra), and lake characteristics (LA, LWS) were significantly correlated with macrophyte dominance in the five lakes (CCA, $P < 0.05$) (Fig. 3). In spring, the first two CCA axes accounted for 26.9% of distribution of macrophyte dominance; Cl^-, COD, GOVF, Pre, AWS, and LA significantly correlated with distribution of dominant species (CCA, $P < 0.01$) (Fig. 3a). In summer, the first two CCA axes accounted for 19.1% of distribution of dominant species; Urb, WD, WT, LWS, GOVF, and Tur had significant correlations with dominance of macrophytes (CCA, $P < 0.01$) (Fig. 3b). In autumn, the first two CCA axes accounted for 36.0% of variability in macrophyte dominance; Gra, pH, DO, AT, and TA were significantly correlated with dominant species (CCA, $P < 0.01$) (Fig. 3c).

3.2. Long-term patterns and drivers of macrophytes

3.2.1. Patterns of macrophytes

There were significant differences among lakes for coverage of total, emergent, and submerged macrophytes (One-way ANOVA, $P < 0.05$, Table 2, Fig. 5, Fig. A.3). Coverage of total macrophytes in GYL, LML, and NSL were significantly higher than that in the HZL and DPL (One-way ANOVA, $P < 0.05$, Fig. A.3a); emergent macrophyte coverage in NSL were significantly higher than that in the LML and DPL (One-way ANOVA, $P < 0.05$, Fig. A.3b); coverage of submerged macrophytes in HZL was the lowest and was significantly lower than that in the other four lakes (One-way ANOVA, $P < 0.05$, Fig. A.3d). Coverage of floating macrophytes in 2003 was significantly lower than that in the other six years (One-way ANOVA, $P < 0.05$, Fig. 4b). There was no significant effect of year on coverage of total, emergent, or submerged macrophytes (One-way ANOVA, $P < 0.05$, Table 2, Fig. 4a).

3.2.2. Drivers of macrophytes

The Pearson correlation analysis revealed a significant negative correlation between coverage of floating macrophytes and precipitation in five water diversion lakes in eastern China (-0.62, $P < 0.05$); coverage of emergent macrophytes was negatively correlated with GDP (-0.64, $P < 0.05$); and a significantly negative correlation also existed between total macrophytes coverage and precipitation (-0.70, $P < 0.05$).

The modified SEM ($\chi^2 = 14.641$, df = 14.000 , $P = 0.403$; CFI = 0.992; NFI = 0.869; IFI = 0.993) showed strong relationships between coverage of macrophytes and environmental factors such as air temperature, precipitation, urban land area, GDP, and water level (Table A.7, Fig. 6). The SEM revealed positive relationships between macrophyte coverage and climate (air temperature and precipitation) (0.507, $P = 0.594$, Table A.7), and water level (0.442, $P = 0.069$, Table A.7). However, the coverage of macrophytes was negatively correlated with GDP (-0.349, $P = 0.527$, Table A.7).

4. Discussion

4.1. Short-term, seasonal patterns of macrophyte distribution

Our short-term investigation demonstrated a clear spatial and temporal pattern of macrophyte coverage in the water diversion lakes along the eastern route of SNWDP, characterized by biomass, species richness, diversity indices, and dominance of macrophytes. Increased biotic homogenization and risks of biological invasion were expected from the increased connectivity between watersheds associated with the SNWDP and through other human stressors. This trend was observed in the current study where macrophyte assemblages showed high similarity among the water diversion lakes and were dominated by the species of *Potamogeton crispus* in spring. This species is likely to disperse to other lakes and canals along the SNWDP. Due to its growth pattern (germination in autumn and winter and rapid growth in early spring), *P. crispus* has become the dominant spring species in lakes of both the United States and China (Tobiessen and Snow, 1984; Ditomaso and Barr, 2014; Tan et al., 2021). In summer and autumn, submerged macrophytes (other *Potamogeton* species, *Myriophyllum spicatum*, and *Ceratophyllum demersum*), floating-leaved macrophytes (*Trapa bispinosa*), and emergent macrophytes (*Nelumbo nucifera*) were dominant in Nansi Lake, Luoma Lake, and Hongze Lake. Most of the dominant macrophytes were highly tolerant to water eutrophication caused by a variety of anthropogenic activities (Qiu and Wu,). Historically, there were 81 and 73 species of macrophytes in Hongze Lake and Nansi Lake in the 1990s, respectively (Zhang, 1992; Liu et al., 2009). However, by employing the consistent sampling method, our current investigation found only 15 and 19 species and similar macrophytes communities in the above two lakes.

Water diversion leads to large amounts of water exchange and changes in water quality characteristics of water diversion lakes such as increase of water turbidity and decrease of clarity (Guo et al., 2020a, b; Qu et al., 2020). Local sources of pollution linked to specific agricultural and urban land-uses also resulted in increased nutrient concentrations in lakes (Egertson et al., 2004; Akasaka et al., 2010; Zhang et., 2019). Lake characteristics and water chemistry had strong influences on the distribution of macrophyte species and could determine the presence or absence of species in lakes (Vestergaard and Sand-Jensen, 2000; Heegaard et al., 2001; Jamoneau et al., 2021). Vestergaard and Sand-Jensen (2000) demonstrated that alkalinity and pH were the main factors responsible for the species distribution. In our study, the five water diversion lakes were mildly alkaline and pH was consistent from upstream to downstream lakes with 8.8 ± 0.4 in Gaoyou Lake and 8.6 ± 0.3 in Dongping Lake (Qu et al., 2020), which may be an important reason for macrophyte homogenization in water diversion lakes. Our results showed high similarities of macrophyte communities among water diversion lakes as the SNWDP has promoted water exchange and diffusion of macrophytes' propagules between previously isolated or partially connected lakes. Moreover, many anthropogenic activities such as mechanic removal of macrophytes, enclosure culture of fish, and artificial bank revetment projects may have reduced habitat heterogeneity and contributed to the decline in coverage and homogenization of macrophyte communities in water diversion lakes (Wang et al., 2019).

Alternatively, water diversion may have provided invasion opportunities for non-native species (Liu et al., 2017). For example, *C. caroliniana*, a submerged macrophyte species native to North and South Americas (Ding et al., 2003), was found for the first time in Luoma Lake. In China, *C. caroliniana* was first found in rivers in Ningbo city, Zhejiang Province in 1993 (Ding, 2000) and then was found in the Taihu Lake basin in Jiangsu Province (Ding et al., 2003). Hou et al. (2012) discovered *C. caroliniana* in Nansi Lake. Also, during the continuous monitoring of the eastern route of SNWDP in November 2020, we observed the presence of *C. caroliniana* in the Beijing-Hangzhou Grand Canal, the section from Gaoyou Lake to Hongze Lake (Xia et al., unpublished data). Such results are consistent with previous studies that inter-basin water transfer creates major pathways for freshwater

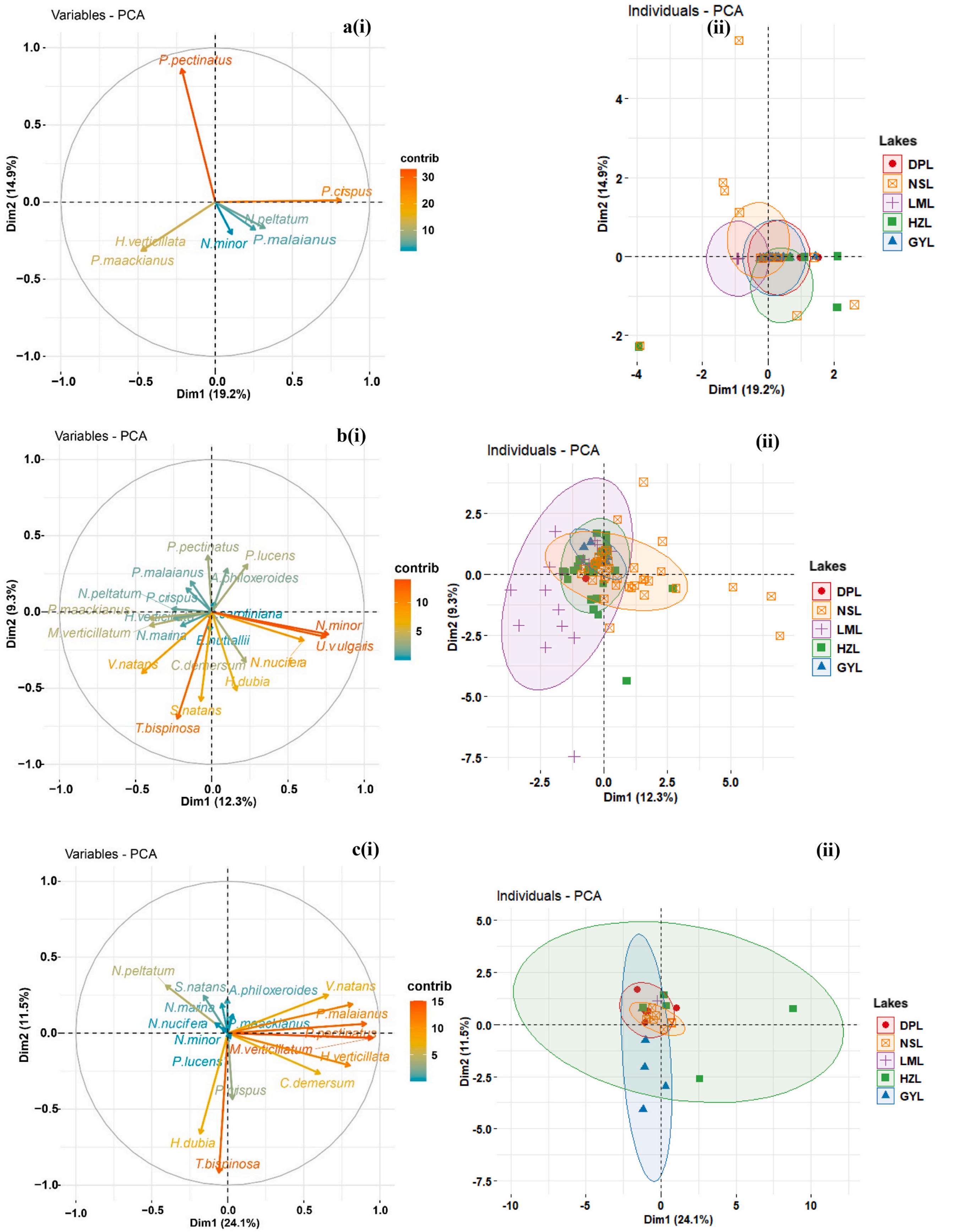

Fig. 2. Macrophyte patterns in (a) spring, (b) summer, and (c) autumn in the water diversion lakes. Note: (i)The PCA plot of dominant species, (ii) the PCA plot of individual lakes. DPL, Dongping Lake, NSL, Nansi Lake, LML, Luoma Lake, HZL, Hongze Lake, and GYL, Gaoyou Lake.

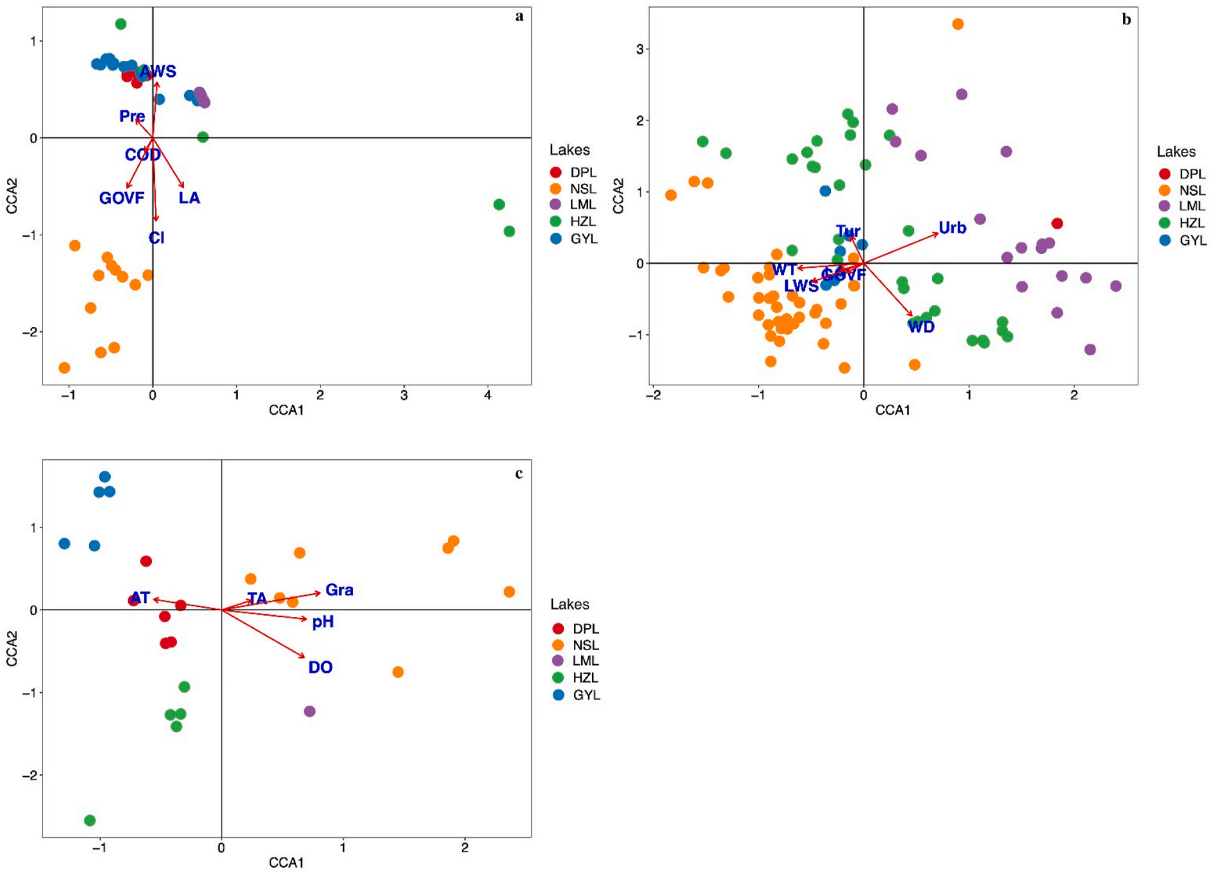

Fig. 3. Canonical correspondence analysis of macrophytes and environmental variables from 2017 to 2018 in (a) spring, (b) summer, and (c) autumn. Note: Only significant environmental variables $P < 0.05$ were depicted in the figure. Points indicated the sampling sites; Cl: chloride, AWS: average wind speed, GOVF: gross output value of fishery, LA: lake area, Pre: precipitation, COD: chemical oxygen demand, Urb: urban land area, WD: water depth, WT: water temperature, LWS: lake water storage, Tur: turbidity, AT: air temperature, Gra: grass land area, DO: dissolved oxygen, TA: total alkalinity.

Table 2
One-way ANOVAs on macrophyte coverage for the five water diversion lakes from 1988 to 2018.

Macrophyte coverage (%)	Lake			Year		
	Df	*F*	*P*	df	*F*	*P*
Total	4	*6.227*	***0.001***	6	*0.370*	*0.891*
Emergent	4	*3.854*	***0.012***	6	*0.787*	*0.587*
Floated	4	*2.398*	*0.072*	6	*3.538*	***0.01***
Submerged	4	*3.455*	***0.019***	6	*0.249*	*0.956*

invasions by providing a direct link between previously isolated catchments and modifying the habitat conditions of the receiving waters to become more favorable to invasive species establishment (Zhan et al., 2015; Guo et al., 2020a).

4.2. Long-term (1988–2018) patterns of macrophytes

Based on the distribution area and coverage, we found a clear distribution pattern of macrophyte communities in the water diversion lakes along the eastern route of SNWDP. Macrophyte coverage in the water diversion lakes varied from year to year. For example, in the 1980s, the macrophyte coverage in Hongze Lake was 550 km^2 (Zhang, 1992), it was 196.5 km^2 in 2003 and 449 km^2 in 2018. Previous studies showed that macrophyte coverage in Hongze Lake, Luoma Lake, Nansi Lake, and Dongping Lake fluctuated annually, at least since the 1980s (Liu and Tang, 1986; Zhang, 1992; Xu et al., 2013; Qiu et al., 2017; Yu et al., 2017). This is consistent with our results. Changes of lake habitat caused by multiple anthropogenic activities may be the main reasons for the changes in macrophyte communities. Long-term variations of macrophyte coverage do occur in freshwater lakes (Zhu et al., 2007; Wang et al., 2019; Sø et al., 2020). For example, macrophyte coverage in Taihu Lake increased by a factor 9 from 1980 to 2014 and then sharply decreased from 2015 to 2017. This recent decrease was primarily due to anthropogenic activities in the lake (Wang et al., 2019). Macrophyte richness in 24 Danish lakes were also found declined in old lakes (lake age >20 years) due to the increase of nutrient and decrease of lake characteristics (Sø et al., 2020).

4.3. Drivers of macrophytes

The short- and long-term patterns of macrophytes in water diversion lakes are likely the results of a combination of many factors, such as changes in climate, lake characteristics and water quality, and disturbance from anthropogenic activities (e.g., industry, agriculture, aquaculture, and urbanization). The literature also indicates that climate warming, water quality, and different land use types affect morphology of individual plants and diversity, and structure of macrophyte communities (Kosten et al., 2009; Akasaka et al., 2010; Gillard et al., 2017; Kim and Nishihiro, 2020).

Macrophytes in water diversion lakes were positively correlated with climate factors, especially air temperature. These can be reflected by the seasonal differences in macrophyte biomass, richness, diversity, and dominance in our study. Regional climate usually was the fundamental factor in biological and physiological metabolism and biological processes in freshwater ecosystems (Mooij et al., 2005; Li et al., 2017). Li

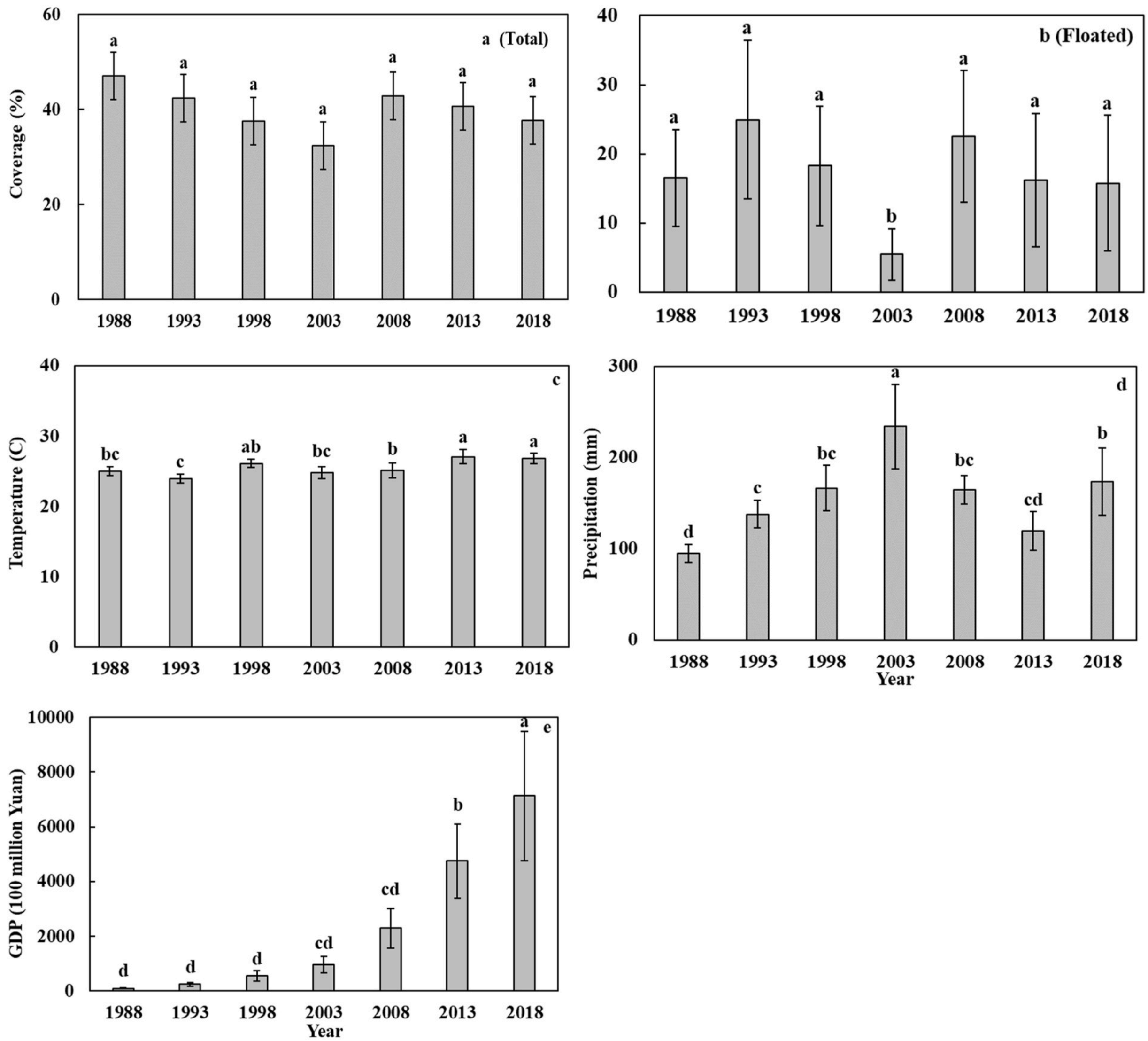

Fig. 4. Coverage of (a) total macrophytes species, (b) floating macrophytes, (c) average air temperature, (d) average precipitation, and (e) GDP (gross domestic product) of five water diversion lakes from 1988 to 2018. Note: errors bars represent the ±SD and different letters above bars indicate significant differences ($P < 0.05$).

et al. (2017) confirmed the decisive role of temperature and light as drivers of biomass and density of macrophytes. A few studies have reported that an increase in air temperature led to algae outbreak and decrease of water transparency in the freshwater lakes, which could change the lake habitat and reduce biomass and coverage of macrophytes (Kosten et al., 2009). However, the high water flow occurring during the water diversion period could reduce potential algal blooms (Qu et al., 2020).

We found that heavy precipitation in 2003 was correlated with decreased coverage of macrophytes, especially floating macrophytes (Fig. 5). This was consisted with a previous study in Nansi Lake where significant negative correlations were observed between precipitation and wetland vegetation indices (Yu et al., 2017). After the 2003 wet year, the macrophytes recovered in all the studied lakes (Fig. 5). However, significant variations of precipitation among years (Fig. 4d) did not cause significant variations of the water level (Fig. A.3e), which may instead partially result from the lake impoundment and water diversions (Qu et al., 2020). The limited variations in water level may explain the overall positive relationship between water level and macrophyte coverage in the current study (Zhang et al., 2015). Effects of water level on macrophytes are species-specific. For example, dominant species *C. demersum* and *M. spicatum* in water diversion lakes were more tolerant to water depth than *H. verticillata*, and lower water level fluctuations can facilitate the establishment success of the submerged macrophyte communities (Li et al., 2015).

The gross output value of the fishery, urban land area, and GDP were all negatively correlated with the coverage of macrophytes in the water diversion lakes in our study. This suggests macrophytes in the lakes along the SNWDP-ER were heavily affected by anthropogenic activities around the lakes. Rapid development of the economy, disturbance from land use, lake reclamation, enclosure culture, and various other anthropogenic activities around these lakes can lead to habitat fragmentation and affect patterns and succession of macrophyte communities in freshwater lakes (Akasaka et al., 2010; Wang et al., 2019; Fares et al., 2020; Kim and Nishihiro, 2020). Area of open water and aquaculture on Hongze Lake increased by 224% and 755% respectively whereas the coverage of macrophytes was reduced by 45% from 1979 to 1988 (Ruan et al., 2005). Results of the short-term investigation showed that pollution-resistant species *C. demersum*, *M. verticillatum*, *P. crispus* and *T. bispinosa* were dominant in the water diversion lakes and the lakes were in a state of mild to moderate eutrophication. With the expansion of urban land area around the lakes, a large amount of industrial,

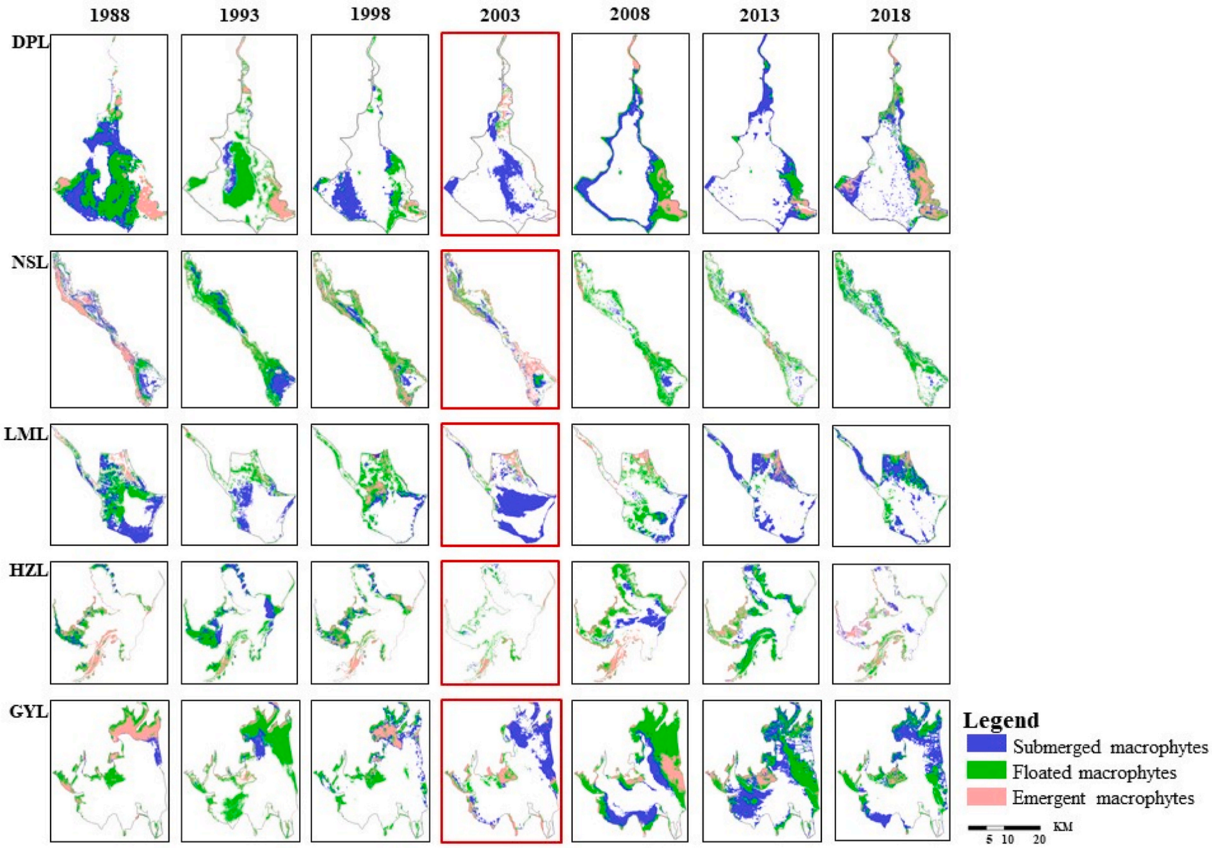

Fig. 5. Spatio-temporal dynamics of macrophytes coverage in the water diversion lakes in eastern China.

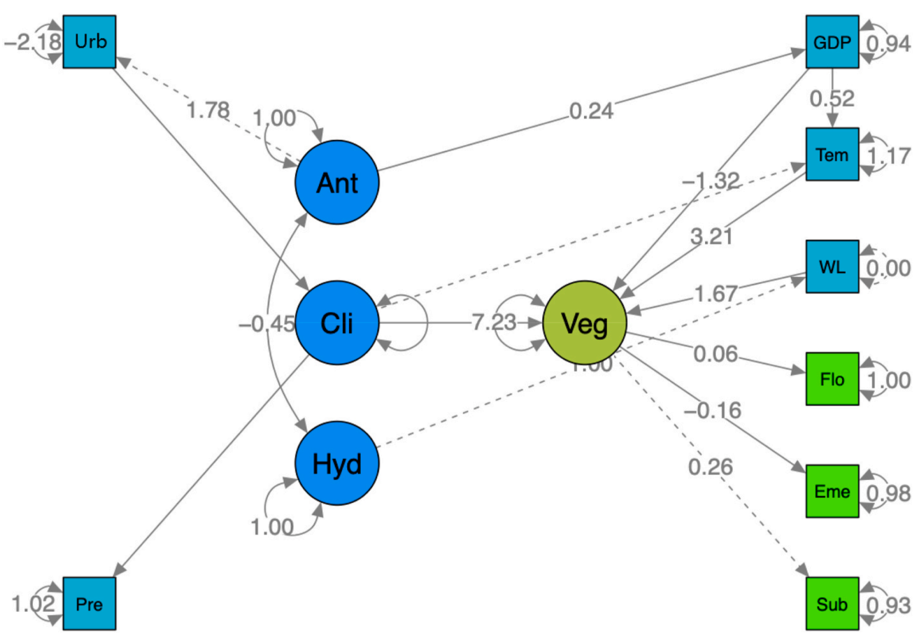

Fig. 6. Structural equation model (SEM) for the coverage of macrophytes and environmental factors in the five water diversion lakes in Eastern China. Note: Sub: coverage of submerged macrophytes; Eme: coverage of emergent macrophytes; Flo: coverage of floating macrophytes; WL: water level; Tem; average air temperature; Pre: average of precipitation; Urb: urban land area; GDP: gross domestic product; Veg: vegetation; Hyd: hydrological factor; Cli: climate factor; Ant: anthropogenic activity factor; $\chi 2 = 14.641$, df = 14.000, p = 0.403; CFI = 0.992; NFI = 0.869; IFI = 0.993.

agricultural and urban wastewater could enter into the lakes through surface runoff, which increases the nutrient level of the lakes and has a direct negative effect on macrophytes and/or an indirect negative effect through stimulation of phytoplankton and epiphytic algae, which intercept light needed by the macrophytes (Guo et al., 2020b; Zhang et al., 2019b; Sø et al., 2020). Since the 1980s, multiple human activities associated with rapid development of industry, urbanization, agriculture, and fishery in the eastern plains of China had destructive impacts on macrophytes in the studied lakes. In recent years, however, the concept of the green economy (i.e., economic development with less impact on the environment) has been initiated in China, which may change the relationship between the GDP and ecological conditions that we observed in the current study.

In freshwater lakes, macrophyte species succession during eutrophication typically change from slow-growing, clear-water groups (e.g., *Chara* and *Najas*) to tall, pollution-resistant groups, such as *C. demersum*, *M. verticillatum*, and species of *Potamogeton* species (Sø et al., 2020). With the increase of nutrient and organic materials, as well as the combined action of climate and hydrological factors, macrophytes eventually disappeared as the lake changes to an algal-dominated stable state of turbid water (Scheffer et al., 1993; Egertson et al., 2004; Feuchtmayr et al., 2009; Zhang et al., 2016). In our study lakes, the species composition and macrophyte community structure indicate that these lakes may move towards to a tipping point when the lakes will revert to a stable turbid state with little macrophytes.

If these lakes continue to suffer from expanding human stressors, which is most likely as they are in the fastest development region of China, the loss of macrophyte could be rapid and large (Chen et al., 2017). Urbanization, intensive commercial fishery, and the introduction of non-native species can all cause declines of macrophyte. As the global climate change proceeds, especially for extreme conditions such as increased frequency and intensity of floods and droughts, macrophyte could experience added stress. Moreover, as the water diversion increases the amount of water transferred and the time period of diversion to meet northern China's development in the coming decade as planned, hydrological and water quality conditions could be further affected and pose potential risks for macrophyte in these lakes (Qu et al., 2020). It is therefore urgent to restore macrophyte communities in these lakes to maintain the stable state of clear-water. The plains of eastern China where the studied lakes are located is a rapidly developing region with multiple human activities (e.g., water diversion, fishery, agriculture, and industry) and latitude differences, and therefore a great region for studying the combined disturbances of human stressors and climate change on lake ecosystems. Our study provides literature support and valuable reference to clarify the changes of macrophytes in freshwater lakes in rapidly developing regions and to understand the relationships between macrophytes and multiple stressors such as climate, hydrology, and anthropogenic activities. Furthermore, our findings may be relevant to other regions with interests in managing macrophytes to mitigate biodiversity loss, non-native species dispersal, and other ecological issues. Although our study is the first and most comprehensive investigation on macrophytes in water diversion lakes in the SNWDP to date, there are still some limitations to be improved in future studies. These include more sampling sites, longer -term of field observations, and consideration of other potential driving factors.

5. Conclusions

In this study, we investigated both short-term (seasonal) and long-term patterns of macrophytes and their driving factors in five water diversion lakes along the SNWDP in eastern China. We reached the following conclusions:

1. In the short-term period (2017–2018), biomass and richness of macrophytes varied significantly between seasons and peaked in summer and autumn. The non-native species *Cabomba caroliniana* was first recorded in Luma Lake. Water physicochemical parameters (WD, WT, Tur, pH, DO, Cl-, COD, TA), climate (Pre, AT, AWS), anthropogenic factors (GOVF, Urb, Gra), and lake characteristics (LA, LWS) were significantly correlated with macrophyte dominance.
2. In the long-term period (1988–2018), a significantly negative correlation was observed between coverage of floating macrophytes and precipitation where the coverage of floating macrophytes was the lowest while the precipitation was the highest in 2003. The SEM revealed positive relationships between macrophyte coverage and air temperature and water level, and a negative one between macrophyte coverage and GDP, an index of anthropogenic activities.

Overall, our study revealed both the short- and long-term patterns of macrophytes in water diversion lakes in the eastern plains of China, and identified key factors correlated with the changes in community structure and distribution of macrophytes. As important feeding and refuge habitat for aquatic organisms, the decline in species number and coverage of macrophytes would have serious impacts on freshwater ecosystems. Therefore, lake management may need to focus on maintaining and restoring macrophytes in the lakes to respond to future land use changes, water diversion, and climate change.

Authorship contribution statement

Wentong Xia: Resources, Data collection, Formal analysis, Writing – original draft, Writing – review & editing.
Bin Zhu: Formal analysis, Writing – review & editing.
Shuanghu Zhang: Data collection.
Han Liu: Resources, Data collection.
Xiao Qu: Resources, Data collection.
Yinglong Liu: Resources, Data collection.
Lars G. Rudstam: Writing – review & editing.
James T. Anderson: Writing – review & editing.
Leyi Ni: Writing – review & editing.
Yushun Chen: Conceptualization, Advising, Data collection, Formal analysis, Writing – original draft, Writing – review & editing.
All authors approved the final version and submission.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2022.115726.

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