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# Long-Term Succession in Cyanobacteria and Aquatic Plant Communities: Insights from Sediment Analysis

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ABSTRACT

Historical legacy effects and the mechanisms underlying primary producer community succession are not well understood. In this study, environmental DNA (eDNA) sequencing technology and chronological sequence analysis in sediments were utilized to examine long-term changes in cyanobacterial and aquatic plant communities. The analysis results indicate that the nutritional status and productivity of aquatic ecosystems have been relatively high since 2010, which could reflect a period of eutrophication due to high long-term rates of organic matter deposition (33.22–42.08 $g \cdot kg^{-1}$). The temporal and spatial characteristics of community structure were related to environmental filtering based on trophic status between 1849 and 2020. Turnover in the primary producer community was confirmed through change-point model analyses with regime shifts toward new ecological states. On the basis of ecological data and geochronological techniques, it was determined that the quality of habitats at a local scale may affect ecological niche shifts between cyanobacterial and aquatic plant communities. These observations suggest how primary producers respond to rapid urbanization, serving as an invaluable guide for protecting freshwater biodiversity.

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## 1. Introduction

Rapid urbanization and climate change have greatly altered the biodiversity and community dynamics of lake ecosystems worldwide, which is one of the most worrisome issues worldwide [1]. Aquatic plants and phytoplankton, as essential primary producers in lake ecosystems, provide energy for the food web [2] and contribute to the maintenance of the trophic state gradient in water bodies [3,4]. Ecosystem regime shifts are believed to occur when external disturbances and/or internal drivers lead to the exceedance of threshold critical points, ultimately resulting in changes in the trophic levels of an ecosystem [5,6]. However, research has shown that a decreasing trend exists in the populations of 41% of submerged plants due to changes in land use and the eutrophication of water bodies [7]. For example, in the largest urban lake in China, Donghu Lake in Wuhan, a decreasing trend has been demonstrated in the diversity and coverage of aquatic plants [8]. Eutrophication and climate change-induced cyanobacterial blooms have become a global phenomenon, leading to economic losses, ecological imbalances, and the deterioration of water quality [9–11]. For example, eutrophication can cause a decrease in light intensity, which in turn affects species diversity and ultimately disrupts the transition of lake ecosystems to a "clear-water" state [12]. The growth and reproduction of phytoplankton significantly influence the structure and function of aquatic ecosystems by influencing the food web [2]. However, owing to the lack of long-term historical data spanning a century, our understanding of lake evolution remains unclear.

In traditional cross-taxa monitoring systems, organisms are detected through visual and/or acoustic recognition or through manual collection methods [13]. However, at present, problems such as high sampling/analysis costs, the risk of identification errors, detection errors caused by phenotypic plasticity, the inability to identify cryptic species, and potential errors in distinguishing individuals at the larval stage still exist [14–16]. In contrast to traditional survey methods, environmental DNA (eDNA) provides a

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new powerful tool to survey aquatic biodiversity and reveal the long-term dynamics of ecosystems [17,18]. In this monitoring method, DNA barcoding (focusing on individual species) and metabarcoding (a combination of barcoding and high-throughput sequencing methods) are mainly used [13,19]. Increasing work is being conducted to extract and analyze ancient DNA from lake sediment deposits to understand the historical population and community changes in terrestrial and aquatic organisms, such as fish [20], vascular plants [21], prokaryotes [22], and phytoplankton [9].

The results of standard aquatic plant surveys in freshwater ecosystems may be strongly influenced by seasonal and hydrological changes, making sampling challenging and resulting in limited historical data on aquatic plants in a region or watershed. Additionally, aquatic plants can reproduce through both sexual and asexual means to adapt to a dynamically changing environment [23,24], making species identification difficult. We chose Wuhan Donghu Lake as our research subject and examined the complex eutrophic and biological community succession patterns of this lake [25]. Our focus was on ① analyzing the temporal trends in aquatic plant and cyanobacterial communities in this urban lake; ② exploring the contributions of element content, temperature, and land use to aquatic plant and cyanobacterial community succession; and ③ determining the key factors that influence the stability of primary producer communities.

## 2. Materials and methods

### 2.1. Study area and sampling

This study focuses on the Guozheng Lake area in Donghu (China; 30.5880°N, 114.4045°E), and factors such as underwater topographical changes, lake morphology, and surrounding urban clusters were considered to determine sampling locations. In September 2021, three sediment cores were collected using a gravity corer (Fig. 1). The sediment cores were sliced into sections at 1 cm intervals using a sampler, and the sediment samples were sealed in self-sealing bags and stored in a refrigerator for freezing. The remaining two cores were freeze-dried and homogenized in the laboratory. One core was used for chronological dating and basic physicochemical property analysis, while the other core was segmented and stored at –80 °C for eDNA extraction.

The dried and ground samples weighing approximately 5 g were placed in 10 mL polyethylene centrifuge tubes and sealed. The samples were left undisturbed for more than 30 days until they reached radioactive equilibrium. After radioactive equilibrium was reached, the excess activities of $^{210}$Pb and $^{137}$Cs were measured using a high-purity germanium gamma spectrometer (GCW1522, Canberra, USA). The measured activity of $^{210}$Pb was used to calculate the ages of the sediment cores using the constant rate of supply (CRS) model [26], establishing a chronology of sediment layers and calculating the standard errors. Environmental variables of interest were measured from the same sediment core. The total nitrogen (TN) and total organic carbon (TOC) contents were measured using a FlashSmart elemental analyzer (Thermo Fisher Scientific, USA). The total phosphorus in the sediment cores was determined using the soil total phosphorus determination method (GB 9837-88). The $\delta^{13}$C values of $CO_2$ were analyzed using a stable isotope mass spectrometer (Delta, Thermo Fisher Scientific, USA) after comparison with an international standard (Pee Dee Belnite (PDB)). The $\delta^{15}$N values of the samples were calculated by comparing the $^{15}$N/$^{14}$N ratio of $N_2$ with an international standard (Atm-$N_2$) [27].

### 2.2. eDNA extraction and analysis

In accordance with the kit instructions, ancient eDNA was extracted from sediment samples using a PowerSoil DNA extraction kit (MoBio, USA). To prevent contamination, all eDNA extraction and polymerase chain reaction (PCR) amplification were

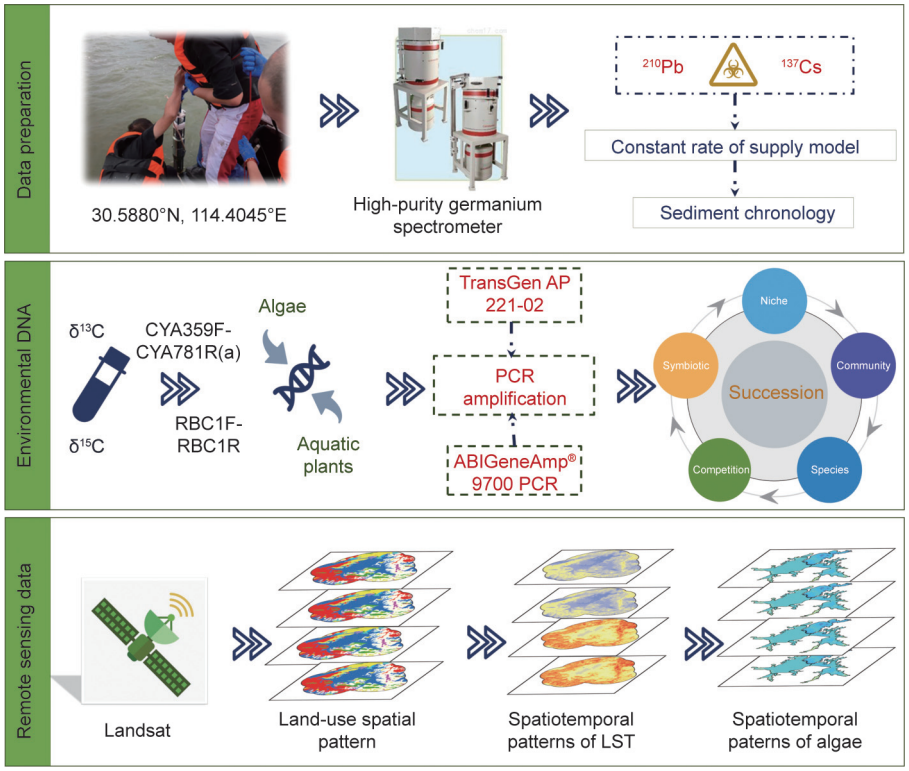


**Fig. 1.** Flow diagram of the sampling process and data analysis. LST: land surface temperature; PCR: polymerase chain reaction.

conducted in a clean workspace where no previous DNA extraction had taken place. To sequence the bacterial 16S ribosomal RNA (rRNA) gene fragment, we used the specific primers CYA359F (5'-GGGGAATYTTCCGCAATGGG-3') and CYA781R (5'-GACTACTGGGG TATCTAACATT-3') [28]. For sequencing aquatic plant-specific DNA, we used the primers RbclF (5'-ATGTCACCACAAACAGAGAC TAAAGC-3') and RbclR (5'-GTAAAATCAAGTCCACCRCG-3') [21]. We isolated cyanobacterial and aquatic plant using their taxonomy and conducted PCRs following proven methods [29]. The raw reads were demultiplexed, quality filtered using Trimmomatic, and then merged using FLASH. The operational taxonomic units (OTUs) were clustered using UPARSE (version 7.1) [30], with a cutoff of 97% similarity. The taxonomic identification of species was based on aquatic plant life types [31].

### 2.3. Remote sensing data collection

The dataset for land use/land cover remote sensing was based mainly on remote sensing data from the US satellites Landsat-multispectral scanner system, thematic mapper (TM)/enhanced thematic mapper (ETM), and Landsat 8. The data were extracted on the basis of interactive visual interpretation by humans and interpretation by computers. Single-band information extraction was performed to obtain standard false-color images, which were then optimized and adjusted to obtain vector data. For multitemporal land use/land cover remote sensing monitoring in China, the land resource classification system proposed by the Chinese Academy of Sciences was adopted [32]. Land surface temperature (LST) data acquisition was primarily based on remote sensing data from the Landsat TM/ETM and Landsat 8 satellites in August (1985–2020). The split-window method was used for temperature inversion, which is suitable for two thermal infrared bands, whereas the multiband algorithm is suitable for multiple thermal infrared bands [33].

All available surface reflectance data provided by the 30-meter resolution Landsat TM and Landsat 8 operational land imager (OLI) reflectance products spanning 1986 to 2018 were obtained from the Google Earth Engine platform [34]. The presence of blue–green algae blooms was identified through the floating algae index (FAI) [35], and the spatiotemporal distribution of algal blooms was then visualized and analyzed.

### 2.4. Statistical analysis

Correlation analysis (element contents (TN, TP, TOC, and N/P), Cyanobacteria, and aquatic plant genera (richness, diversity, evenness, and coverage)) was performed in SPSS 22.0 (USA), and a $p$ value < 0.05 was considered significant. All change-point analyses of aquatic plants and cyanobacterial communities from 1849 to 2020 were performed using a change-point analyzer (version 2.3) [36]. The R software "ggalluvial" package was used to construct Sankey diagrams.

## 3. Results and discussion

### 3.1. Ancient environmental change patterns in a typical urban lake

The TN content in Donghu Lake varied from 998 to 4665 $mg{\cdot}kg^{-1}$. Before 1972, it remained relatively stable, but after that, it rapidly increased (Fig. 2). The TOC content in the samples exhibited patterns similar to those of the TN content, ranging from 5.88 to 42.08 $g{\cdot}kg^{-1}$ (Fig. 2 and Fig. S1 in Appendix A). However, the TOC gradually increased around 1972, with an increasing trend in the TOC content of the sediments, particularly after 2009. In contrast, the TP content in the sediments remained stable between 1849 and 1855, with an average value of 350.33 $mg{\cdot}kg^{-1}$. After 1966, the total phosphorus content in the sediments increased to 589.77 $mg{\cdot}kg^{-1}$. In early 2014, it further increased to the range of 653.8 to 971.25 $mg{\cdot}kg^{-1}$ (Fig. 2). Starting in the 1950s, the phosphorus levels in the water of Donghu Lake increased, reaching a peak in the mid-1980s, and then declined [37]. The N/P ratio in the sediments ranged from 1.69 to 3.80 between 1849 and 1972. It has increased annually since 1993 and reached a value of 10.67 in 2010 (Fig. S1), and the N/P ratio in adjacent years was approximately 7. Overall, the trends in the TOC, TN, and TP contents in the sediment columns of Donghu Lake indicate a relatively high nutritional status and productivity in the aquatic ecosystem over the past 20 years (Fig. 2 and Fig. S1). The gradual increase in the N/P ratio is attributed mainly to the excessive input of nitrogen and phosphorus from urban activities [38], and most phosphorus in lake ecosystems is stored in bottom sediments. Consequently, phosphorus cycling from the sediment to the water column can have a significant and adverse impact on water quality [39]. Thus, from the 1970s to the summer of 1984, algae proliferated in Donghu Lake due to changes in water quality [37]. High-intensity human activities lead to the input of large amounts of nutrients into lakes, resulting in alterations to the nutrients in the sediments [18,40,41]. Excessive phosphorus inputs can lead to submerged plant-dominant species succession and ultimately reduce the stability of the macrophyte community [42].

The indices of sediment $\delta^{13}C$ and $\delta^{15}N$ are widely applied to evaluate the origins of organic matter in sediment in aquatic environments [43,44]. From 2020 to 2009, the $\delta^{13}C$ in Donghu Lake sediment showed a relatively stable trend, but from 2009 to 1849, it exhibited fluctuations with an overall decreasing trend (Fig. S2 in Appendix A). This trend was due to ① changes in hydrological conditions, productivity, climate, and so forth [45]; and ② depletion or decomposition of isotopes [46]. This could be attributed to the effect of diagenesis on the accumulation of carbon isotopes [47]. Compared with those of the bottom sediment, the $\delta^{13}C$ values in the top layer of Donghu Lake sediment significantly increased (Fig. S2), indicating an increasing input of terrestrial materials [48]. The $\delta^{15}N$ in Donghu Lake sediment exhibited a decreasing trend from 1966 to 1849, with the variation mostly between 5.44% and 6.88% (Fig. S2). However, from 1993 to 2020, the $\delta^{15}N$ in the sediment significantly increased, ranging from 7.71% to 8.81% (Fig. S2), suggesting that the variation in $\delta^{15}N$ may be attributed to the application of fertilizers and discharge of domestic wastewater [49,50]. Nutrient inputs also lead to changes in nitrogen cycling processes involving microorganisms [51], and internal nutrient loading in shallow lakes is known as a key driver of eutrophication [52].

### 3.2. Historical patterns of cyanobacterial and aquatic plant community composition in Donghu Lake

The research was conducted using eDNA technology to analyze the cyanobacterial community in the urban lake [53]. Between 1849 and 2020, a total of 20 genera belonging to the phylum Cyanobacteria were identified in the sediment columns of Donghu Lake (Fig. 3). Cyanobacteria were analyzed in low-latitude highland lake sediments over a time scale of 148 years using eDNA technology, and on the basis of sequencing results, it was determined that the Cyanobacteria belong to five main taxonomic orders [9]. In this study, *unclassified_Cyanobacteria* 16S rRNA genes dominated, with contributions ranging from 28.2% to 95.83%. From 1900–1919, the average proportion of *unclassified_Cyanobacteria* 16S rRNA genes was 88.83% (Fig. 3). In 1963 and 1909, the average proportions of *unclassified_Oscillatoriales* and *unclassified_Oculatellaceae* 16S rRNA genes were 1.14% and 5.05%, respectively. *Unclassified_Oscillatoriales* dominate eutrophic lakes in central Europe

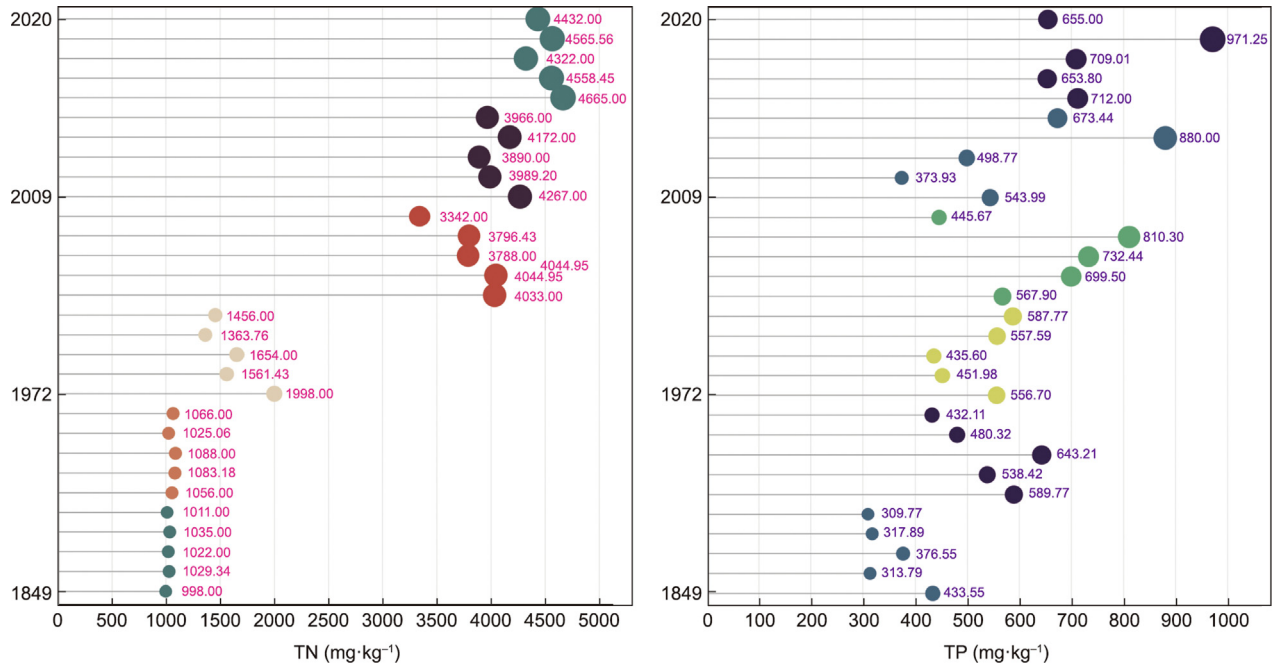


**Fig. 2.** Temporal trends in sediment TN and TP.

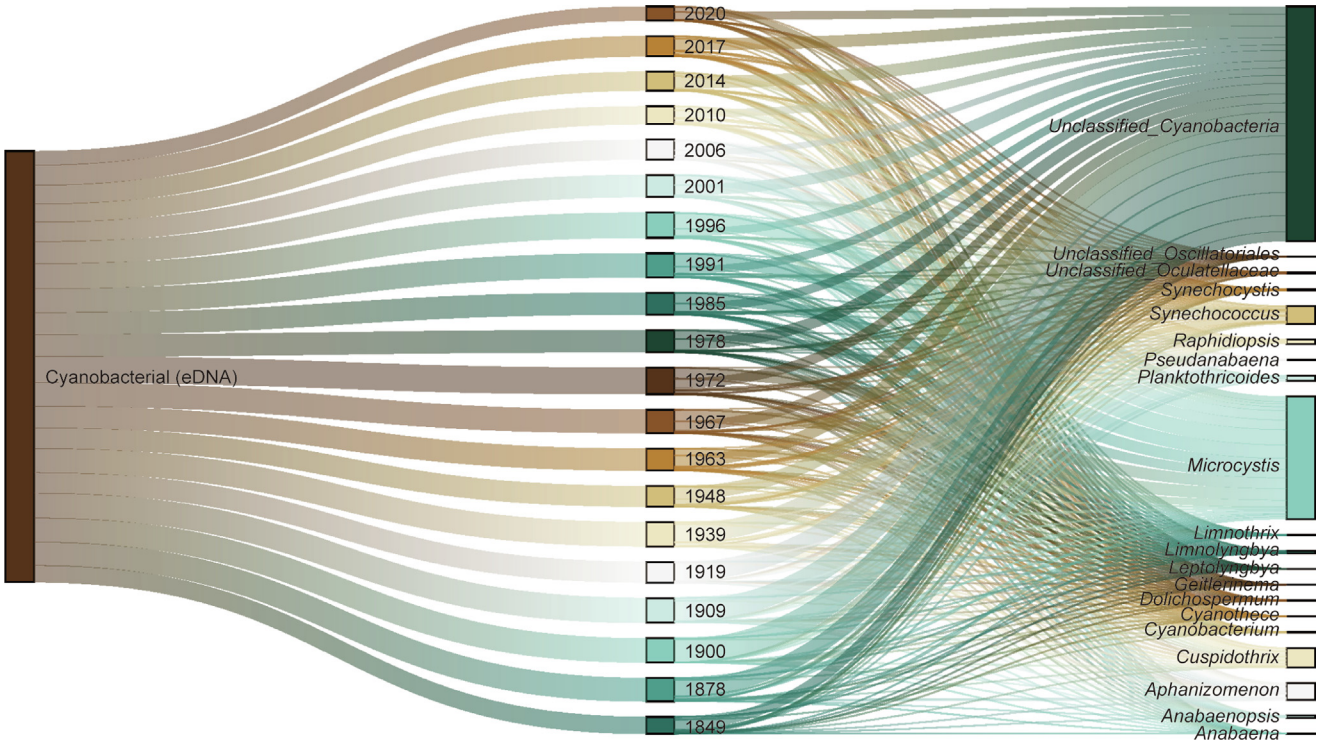


**Fig. 3.** Shifts in the taxonomic profiles of cyanobacterial communities in Donghu Lake.

during summer and autumn [54]. The genus *Synechocystis*, a single-celled cyanobacterium capable of carrying out oxygenic photosynthesis, had an average OTU value of 1.31%. The genus *Synechococcus*, representing Picocyanobacteria, had an average OTU value of 4.39%, with proportions of 9.52% and 8.95% in 1972 and 1849, respectively (Fig. 3). *Synechococcus* is frequently detected in lake sediments with different trophic states, and diverse genera are vulnerable to climate warming [55]. The genus *Raphidiopsis* had an average OTU value of 1.06%, while the genus *Pseudanabaena* was detected mainly in 1996, 2010, and 2014, with an average proportion of less than 1% (Fig. 3). The genus *Planktothricoides* had an average OTU value of 1.32%, whereas the genus *Microcystis*, a common freshwater Cyanobacterium [56], was detected in samples from 1849 to 2020, with an average OTU value of 28% and a proportion of 55.79% in 1991. Other genera, such as *Limnothrix*, *Limnolyngbya*, *Leptolyngbya*, *Geitlerinema*, *Dolichospermum*,

*Cyanothece*, *Anabaenopsis*, and *Anabaena*, had average OTU proportions ranging from 1.49% to 6.67% (Fig. 3). The cyanobacterial communities in lakes exhibit different characteristics during different successional periods, and these trends are related mainly to environmental conditions. The direction of community succession may be linked to the community's characteristics and its individual member traits. Moreover, nitrogen-fixing filamentous Cyanobacteria can drive eutrophication in mesotrophic states [4].

Between 1849 and 2020, a total of eight genera of aquatic plants were identified in the sediment cores of Donghu Lake (Fig. 4). Among them, unidentified aquatic plants accounted for approximately 0.1% of the 16S rRNA genes. In 1957, the aquatic plants in Donghu Lake belonged to 41 genera [57]. *Potamogeton*, a genus of widely distributed aquatic plants with a wide range of ecological amplitudes [58,59], was the dominant aquatic plant between 2015 and 2020, with an average proportion of 99.48% in Donghu Lake (Fig. 4). *Zizania*, a genus of monocotyledonous plants in the grass family, had an OTU proportion ranging from 15.67% to 99.74%, with the highest proportions occurring in 2010, 1978, 1976, and 1967 (Fig. 4). In 1935 and 1961, *Vallisneria* replaced *Potamogeton* as the dominant species, with an OTU proportion of 99%. The proportions of *Melica*, a genus of monocotyledonous plants in the grass family, ranged from 14.39% to 30.2% between 1991 and 2003. *Cyperus*, a genus of monocotyledonous plants (emergent life forms) in the sedge family, was detected in the sample cores from Donghu Lake in 1995, accounting for 19.98% (Fig. 4). *Vallisneria* does not alter the structure and function of ecosystems because it has a highly plastic response to biotic factors (such as biological predation or competition) and abiotic conditions (water level, new pollutants, etc.), which also promotes the gradual succession of *Vallisneria* as a dominant species [60,61]. During community assembly at severely disturbed sites, succession, and priority effects impact plant assembly and succession [62], and the early presence of *Vallisneria* likely results in its dominance. Under early succession, plant species diversity usually increases with the emergence of new species, but later succession is characterized by the elimination of opportunistic species and the dominance of native species [63].

The characteristics of aquatic plants in Donghu Lake identified over time using eDNA technology differed from those documented in the literature [8], probably because of the degradation of eDNA in the natural environment [17]. In addition, the accuracy of identification can be affected by a lack of maturity of sequencing technology [64] and the inadequacy of databases for aquatic plants. Research has revealed differences in the number and types of aquatic plants identified in urban rivers using traditional survey methods and eDNA methods [21].

The results indicate that the TN and TP contents in the sediments of Donghu Lake significantly influence the abundance and coverage of the genus *Cyanobacteria* ($p < 0.05$) (Fig. 5). Human activities and climate change are factors contributing to increased nutrient load in water, which in turn leads to changes in algal community abundance and succession. Furthermore, the total phosphorus content in the sediments significantly influenced the growth and reproduction of algal populations. For example, the content of 11 pigments detected in reservoir sediments was positively correlated with TP content [41], and dissolved reactive phosphorus in cyanobacterial blooms was also affected by water flow and seasonality [65]. This may be due to the alteration of geochemical cycles caused by reservoir engineering measures, which affect the release flux and migration processes of elements such as nitrogen and phosphorus, particularly resulting in the interception of particulate elements, which ultimately enhances algal growth and development [66,67].

The growth and development of algae are not only limited by the concentrations of nitrogen and phosphorus nutrients but also influenced by the concentration of total organic carbon in the aquatic environment [68]. Algae can absorb and utilize carbon dioxide and convert nutrients in water into organic matter for absorption, utilization, and reproduction using external energy sources [69]. In the sample cores from Donghu Lake, it was found that the TOC content of the sediment significantly affected the abundance, evenness, and coverage of Cyanobacteria (Fig. 5). Additionally, there was a significant correlation between the N/P ratio in the sediments and the abundance and coverage of Cyanobacteria (Fig. 5). The occurrence of algal blooms in freshwater ecosystems is related to the N/P ratio. In addition to these thresholds, the utilization efficiency of nutrients, differences in N/P ratios, and morphological characteristics need to be considered to understand transitions in algal growth dynamics [70,71]. For example, when the nutrient utilization efficiency in water changes, algal cells of

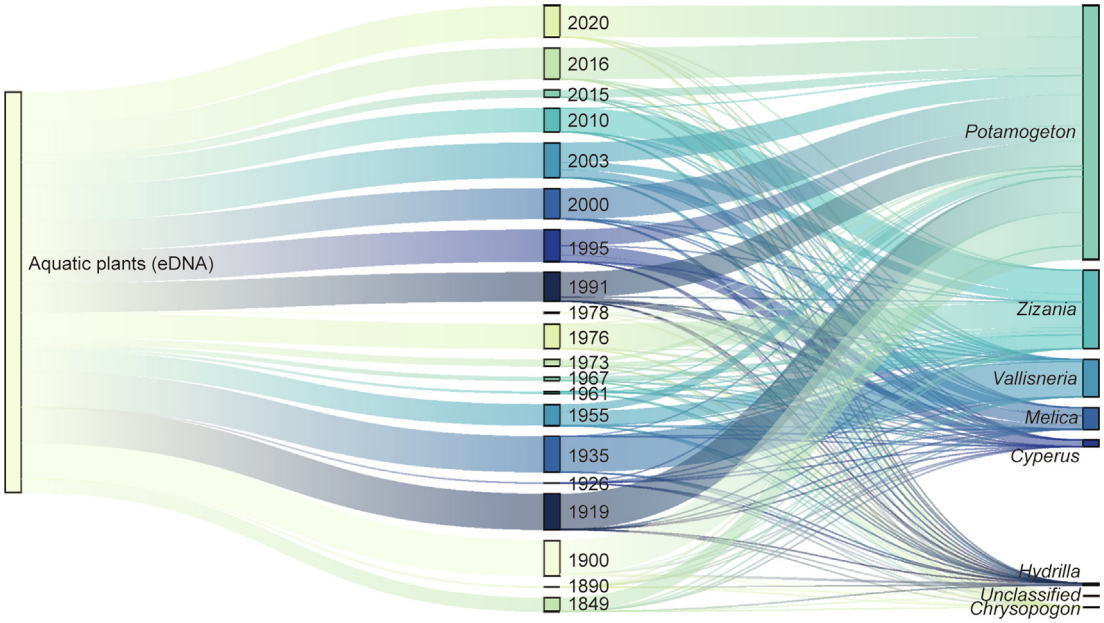


**Fig. 4.** Shifts in the taxonomic profiles of aquatic plants in Donghu Lake.

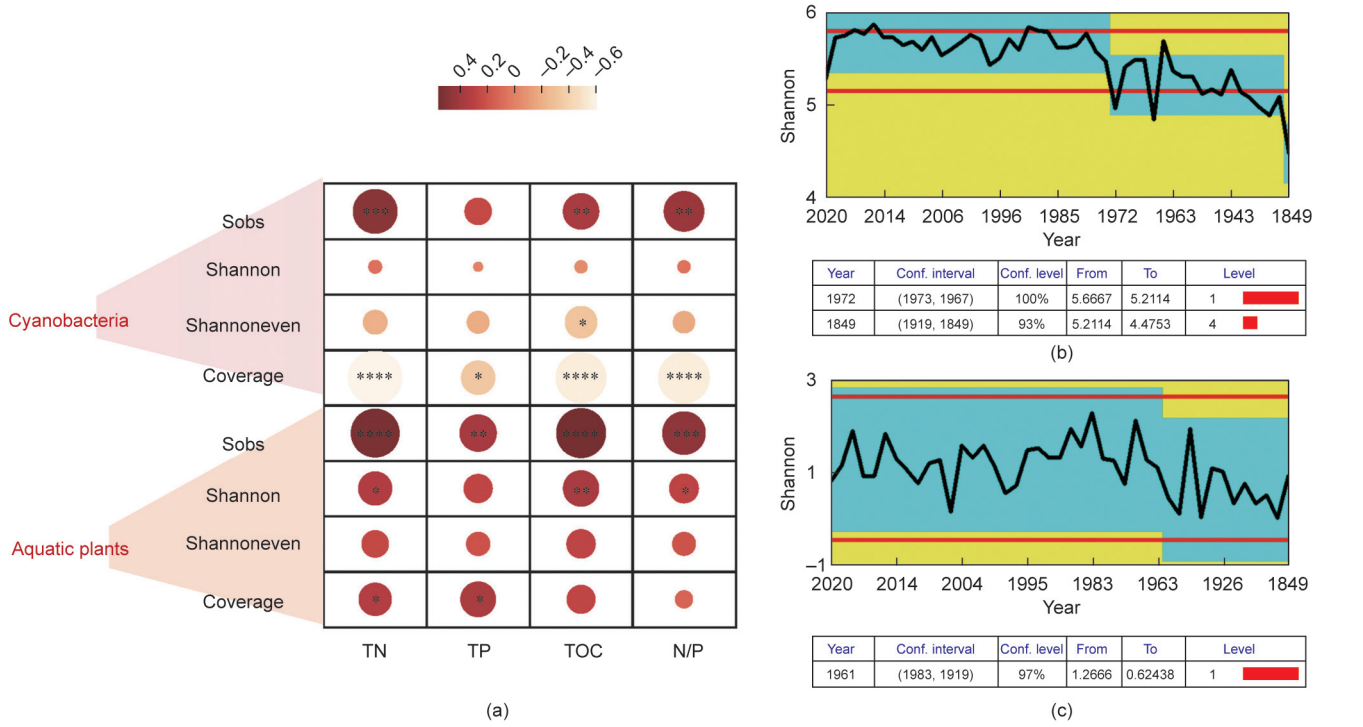


**Fig. 5.** (a) Relationships between element contents (TN, TP, TOC, and N/P), Cyanobacteria, and aquatic plant genera (richness, diversity, evenness, and coverage; $p$ values for significance: $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$, $^{****}p < 0.0001$); identification of change points in (b) *Cyanobacteria* and (c) aquatic plants OTU richness at the temporal scale. Conf.: confidence.

different compositions experience physiological stress [72]. The N/P ratio in the aquatic environment can change the stoichiometric allocation of cellular biochemical components, thereby affecting cell physiological functions and inhibiting cell growth and development [71]. TOC and TN are essential for the formation of algal protein components and the functioning of chloroplasts, whereas TP affects the synthesis of ribosomal RNA [73]. Therefore, the impact of exogenous organic carbon on algal cells is related mainly to the concentration of nutrients.

The results indicate that the contents of TN and TP in the sediment column of Donghu Lake significantly affect the structure of aquatic plant communities ($p < 0.05$) (Fig. 5). The growth and reproduction process of aquatic vegetation involves the process of aquatic plant community establishment and evolution, which reflects the coupled relationship between plants and environmental factors, with the core factors influencing community composition. Aquatic plants play a crucial role in nutrient exchange between lake sediments and overlying water because they can directly absorb and utilize nutrients from sediments through different organs during their growth, development, and maturation stages, thereby reducing the overall release of nutrients into the overlying water [74,75]. Some accumulated nutrients, such as nitrogen and phosphorus, in the sediment cores of Donghu Lake, may be derived from the decomposition of aquatic plants. Similarly, algae gradually replace aquatic plant communities as the dominant species, leading to the accumulation of mobile nitrogen and phosphorus in the sediment [76]. The decay of aquatic plants is also a key link in the material cycling of lakes because it releases nitrogen, phosphorus, and other species into the water, and this process is lengthy. For example, the study have shown that the decay of submerged plants increases the content of phosphorus in sediments in different forms, especially Ca–P within plant tissues, which accumulates in sediments as plant residues decompose [77]. The decay of aquatic plants also promotes the mineralization of organic matter in sediments, with colloidal substances covering the interfacial area, which reduces the strength of interaction between particulate sediments and phosphate ions and decreases the fixation of metal ions with phosphate ions, leading to changes in the nutrient elements present in the sediments [78,79].

Due to continuous urbanization, large amounts of nutrients enter the water environment, leading to an increase in nutrient levels in lakes and an increase in the growth and productivity of primary producers in lakes [80]. The accumulation of aquatic biomass in lake sediments increases the content of organic carbon, which, after a lengthy decomposition process, eventually becomes deposited as sediment at the bottom of the lake in the form of carbon [81]. The TOC content in the sediment cores of Donghu Lake is significantly correlated with the abundance of genetic sequences of aquatic plants (Fig. 5), which also confirms that aquatic plants are an important source of stored carbon in sediments. For example, the continuous input of exogenous total nitrogen leads to an increase in the biomass of aquatic organisms, which in turn increases the accumulation of organic and inorganic carbon [82]. Therefore, the degree of land development and utilization in the watershed surrounding a lake and the nutrient level of the water have significant impacts on the trends in carbon accumulation in sediments and the synergistic pattern, and it is also important to consider the sources of carbon in the carbon cycling process of urban lakes.

### 3.3. Mechanisms of regime shifts in the Donghu Lake ecosystem

A "steady state" means that the existing structure and function of an ecosystem remain unchanged over space and time. In response to biological or nonbiological disturbances, a lake ecosystem can undergo structural transformations leading to corresponding changes in the system's functional characteristics; this is known as a regime shift [83,84]. Regime shifts usually occur without clear warning signals, but the process itself is often catastrophic [85]. Exploring the mechanisms driving regime shifts in

urban lake ecosystems is beneficial for better understanding the response of lakes to rapid urbanization and for proposing more practical and effective lake ecosystem warning and management strategies. The term "alternative stable states" indicates that ecosystems can have multiple stable states, and regime shifts involve the dynamic process of transitioning from one trend or state to another [83]. Urban lake ecosystems are relatively fragile, with frequent exchange of substances between the overlying water and sediments and slow accumulation of suspended matter, resulting in relatively low pollutant load capacity. Most lake ecosystems have two states: a "clear-water state" dominated by aquatic plants or a "turbid-water state" dominated by algae [4,11]. The alternation between the "clear" and "turbid" water states is a common occurrence, likely because external pressures lead to dynamic transitions between the two states [86]. In many cases, the loss of aquatic plant populations is caused primarily by critical internal factors related to state transitions [87,88]. For example, once the nutrient concentration in the water exceeds a certain threshold due to increasing inputs of pollutants, algae blooms occur, leading to adverse conditions for submerged plants and causing massive die-offs [20,89,90]. On the basis of these results, it is inferred that changes in the conditions of the environment surrounding the lake may have led to a change in the state of the lake ecosystem, but threshold quantification is still needed to determine the key time points of the change.

On the basis of significant changes ($p < 0.05$) in the richness and corresponding cumulative sum of Cyanobacteria and aquatic plant OTUs between 1849 and 2020, a change point analysis was conducted (Fig. 5(b)). The results revealed that the cyanobacterial community structure remained relatively stable from 1849 to 1943. However, in 1972, a significant change point was observed in the cyanobacterial community, with increases in cyanobacterial OTU numbers (Fig. 5(b)). Donghu Lake was clear and full of aquatic plants until 1972 but then underwent a destabilizing transition (Fig. 5(c)). For the aquatic plant community, a significant change point was observed in 1961, followed by increases in the community from 1963 to 1995. However, since 1999, there has been a declining trend in the aquatic plant community (Fig. 5(c)). According to the literature records, the coverage of aquatic plants in Donghu Lake was high before the 20th century, particularly from 1962 to 1963, when the number of aquatic plant species reached 83, which belonged to 29 families and 53 genera. The dominant species included *Potamogeton pectinatus*, *Hydrilla verticillata*, and *Ceratophyllum demersum* [91,92]. However, from 1988 to 2014, the number of aquatic plant species decreased, with submerged plants being the most affected and consisting mainly of pollution-intolerant species [92,93]. On the basis of the survey of sample points and eDNA sequencing results, we found that the aquatic plant community structure in Donghu Lake has undergone varying degrees of succession, and this change may be closely related to the hydrological conditions and nutrient status of the lake.

### 3.4. Analysis of the trends in environmental conditions in Donghu Lake basis on remote sensing images

Land use represents the process of development and utilization of resources and the environmental conditions resulting from human activities [94]. Due to rapid urbanization and socioeconomic factors, there have been dynamic changes in land use within the Donghu Lake region, which can affect the functionality and structure of ecosystems [41]. Based on remote sensing data, it was determined that the main land use types around Donghu Lake include urban areas, industrial and mining construction sites, paddy fields, and forests, while beach and grassland areas are relatively small and sporadically distributed (Fig. S3 in Appendix A). In terms of changes in land use from 1985 to 2020, the scale of construction sites has continuously expanded due to rapid economic and societal development, whereas farmland area has continued to decrease (Fig. S3). Over the past 40 years, diverse and dynamic transitions have occurred in land use around Donghu Lake, with land conversion from paddy fields into construction sites being the highest and drylands mainly being converted into urban areas. Therefore, a reduction water surface area (Fig. S3) affects the diversity and abundance of aquatic plants [7].

The rapid development of urban areas not only led to changes in land use types around Donghu Lake but also affected the LST of the study area, especially in 2010 and 2015, when the expansion of urban and industrial construction sites resulted in higher land surface temperatures (Fig. 6). This caused the land surface temperature in the Donghu Lake area to increase to 35.5–40.0 °C (Fig. 6). In a previous study, researchers investigated the relationship

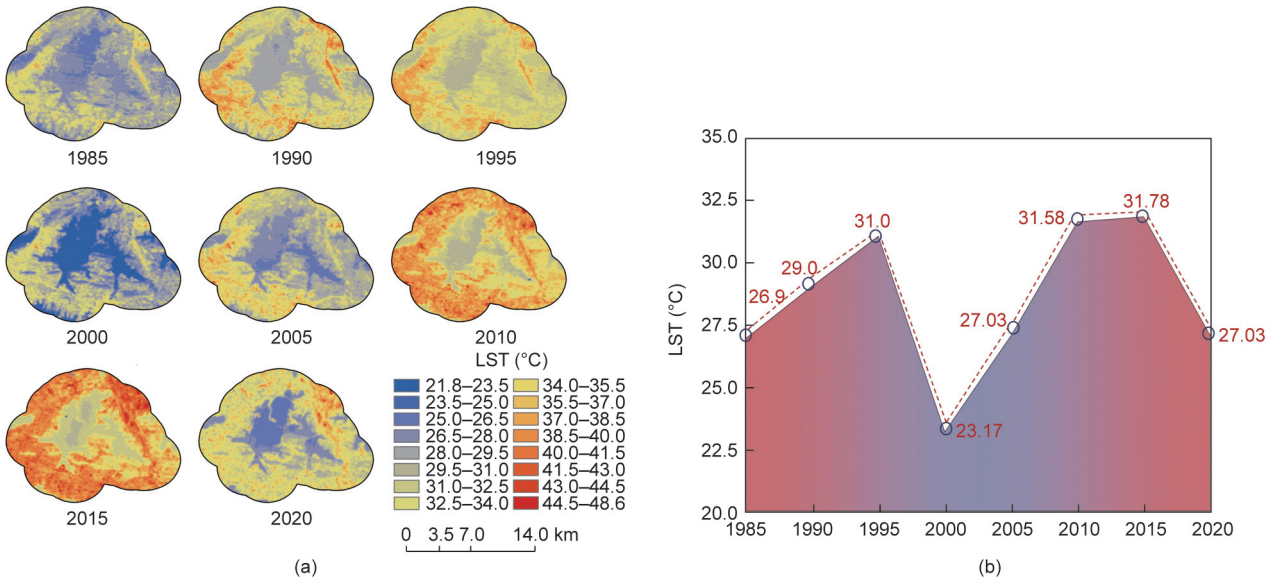


**Fig. 6.** (a) Spatiotemporal patterns in LST and (b) mean temperature in Donghu Lake from 1985 to 2020.

between the urban heat island effect and land use in Wuhan city over the past decade and demonstrated that the increase in the total developed area significantly contributed to the intensification of the heat island effect [95]. Changes in land cover can result in alterations in land surface temperature, and this relationship can be attributed to the role of vegetative cover in shading the Earth's surface and reducing direct solar radiation [96].

Eutrophication and climate warming are recognized as important factors driving outbreaks of cyanobacterial blooms. For example, studies on lakes worldwide have revealed that the synergistic effects of eutrophication and climate warming are related to the nutrient level and algal community structure associated with cyanobacterial blooms [97]. For example, increased temperatures have led to more frequent and extensive cyanobacterial blooms in Lake Taihu [98]. The experience modeling method was used to establish a dataset of 1000 lakes in the United States, and multiple linear regression revealed that temperature is directly correlated with the formation of Cyanobacteria [99]. Appropriate or excessive temperatures and nutrients can affect the growth, species succession, proliferation, and aggregation of planktonic plants. In this study, urbanization led to changes in land surface temperatures, which can impact the community structure of cyanobacterial communities (Fig. 6 and Fig. S4 in Appendix A). Climate change increases the occurrence, frequency, and scale of harmful algal blooms [100]. Researchers have also utilized Bayesian modeling and revealed that, compared with residence time, temperature is a more important factor driving the variation in Cyanobacteria abundance in regulated rivers [101].

Eutrophication has been recognized as a key factor driving the decline in aquatic organisms in shallow lakes [102] and an important driver of multiple stable state transitions in lake ecosystems [42]. Our results revealed that as the intensity of disturbance increased, the lake ecosystem underwent phase changes: ① changes in water quality that ultimately affected habitat quality at the local scale; ② succession of dominant species, as well as a decrease in biodiversity; and ③ changes in the structure and stability of the lake ecosystem (Fig. 7). Changes in intraspecific and interspecific interactions within biomes affect structural composition and stability [42,103]. As the state of a lake ecosystem changes, the symbiotic and competitive relationships between species shift, leading to the turnover of dominant species. Currently, engineering methods such as sediment dredging and vegetation restoration are often employed to restore damaged aquatic ecosystems [104]. These engineering measures can impact biodiversity and ecosystem health, including species composition and primary productivity [105]. In this study, it was found that ecological succession has already occurred between Cyanobacteria and aquatic plants in Donghu Lake, so in future engineering measures, establishing a rational biological population structure, species protection, and establishing a long-term ecological maintenance mechanism should be the priorities.

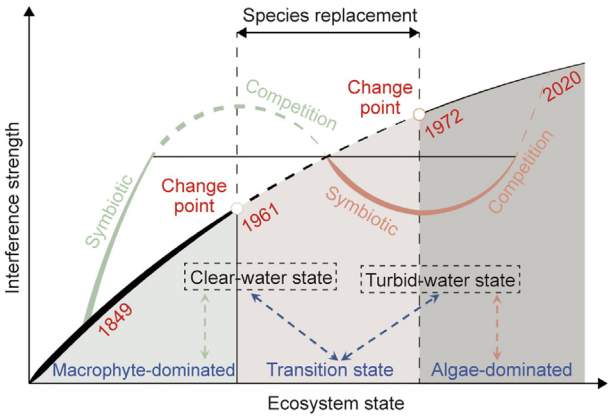


**Fig. 7.** Conceptual diagram of state transitions and change points in the Donghu Lake ecosystems.

## 4. Conclusions

Nutrient imbalance leads to significant disruptions in lake ecosystems, which also places substantial demands on lake conservation and management efforts. By analyzing paleoenvironmental variables and the correlation between the abundance of Cyanobacteria and aquatic plant genes, we revealed that the TN and TP contents in the sediment of Donghu Lake significantly influenced the richness and coverage of cyanobacterial and aquatic plant communities. The TOC content in the sediment significantly affected the richness, evenness, and coverage of cyanobacterial species. The inflection point analysis results indicate that the community structure of aquatic organisms in Donghu Lake has undergone dynamic changes. Rapid urbanization in the area surrounding Donghu Lake is also an important factor leading to changes in the structure of the lake's aquatic ecosystem. However, in this study, we analyzed only key environmental factors influencing biological succession on the basis of eDNA sequencing results. In future studies, researchers should combine diverse biological monitoring techniques for a more comprehensive study.

## CRediT authorship contribution statement

**Hongwei Yu:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Formal analysis, Data curation. **He Ji:** Formal analysis, Data curation. **Yang Li:** Investigation, Funding acquisition. **Jing Qi:** Methodology, Investigation, Funding acquisition. **Baiwen Ma:** Supervision, Software. **Chengzhi Hu:** Visualization, Validation, Supervision, Software, Resources. **Jiuhui Qu:** Visualization, Validation, Supervision, Software, Resources, Project administration.

## Declaration of competing interest

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

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.eng.2025.04.012.

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