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Research article

Underwater light limitation controls long-term submerged plant persistence in Lake Poyang floodplains, an important Ramsar site

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ABSTRACT

Submerged macrophytes are critical to the integrity of large river-floodplain ecosystems (RFE), yet ecological constraints on their persistence remain poorly understood. Attention has mainly focused on water level fluctuations or lateral hydrological connectivity as primary drivers. In contrast, the role of underwater light, the most widely recognized driver of submerged macrophyte dynamics in shallow lakes, has often been overlooked. This study examined whether underwater light limitation regulates long-term dynamics of *Vallisneria spinulosa,* a dominant submerged plant in numerous floodplain sub-lakes of Lake Poyang, an important Ramsar site. We integrated field vegetation surveys, long-term Landsat imagery (1986–2021), lake optics modelling, and systematic literature surveys to explore changes in underwater light during floodings, their impacts on *V. spinulosa* growth and its long-term habitat distributions, and the fundamental drivers behind these changes. Underwater light availability during the flooding period determined *V. spinulosa* biomass densities, with a minimal light threshold of SD/Dep (Secchi depth to water depth) at 0.2. Based on the threshold, derived habitat distribution in numerous sub-lakes showed strong agreement with both field observations (89 % accuracy) and satellite-classified distributions (80 % accuracy). *V. spinulosa* habitat distribution exhibited high interannual variability with no consistent long-term shrinkage, and even expansion in historically poor habitat zones. Underwater light limitation, associated with sediment dynamics influenced by rainfall, flow regimes, and sand dredging, appear to be the dominant constraint. Our findings suggest that enhancing water clarity via sediment management is essential for conserving submerged vegetation in floodplain lakes under changing hydrological and climatic conditions.

1. Introduction

Large river-floodplain ecosystems (RFE) are among the most hydrologically dynamic and biologically diverse systems (Eros et al., 2019; Petsch et al., 2023; Tockner et al., 2010). They support an extremely rich and diverse biota, including wetland plants, fish, and migratory birds (Petsch et al., 2023). These systems experience seasonal flooding pulses, which create spatial and temporal heterogeneous habitats and underpin key ecological processes such as community assembly and biodiversity maintenance (Eros et al., 2019; Petsch et al., 2023). However, RFEs are stressed synergistically and cumulatively by a mixture of factors such as hydrological alterations, land-use changes, and water pollution across their wider catchment (Petsch et al., 2023; Tockner et al., 2010). Submerged macrophytes play a foundational role in river-floodplain ecosystems. They create complex underwater habitats that provide refuge and foraging grounds for invertebrates, fish, and waterbirds (Bornette and Puijalon, 2011; Bouska et al., 2020). Submerged vegetations maintain water clarity and ecosystem stability by facilitating sediment deposition and reducing turbidity (Scheffer et al., 1993; Sokly et al., 2018). They also provide critical food resources for migratory birds

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during overwintering periods in certain occasions (Hou et al., 2020; Li et al., 2020). Thus, understanding the ecological constraints on submerged macrophytes in RFEs amid multiple stressors is central to the conservation of floodplain biodiversity and the maintenance of ecosystem services.

One of the most widely recognized drivers of submerged macrophyte distribution in shallow lakes is underwater light availability. Numerous empirical and theoretical studies have shown that water clarity thresholds strongly regulate regime shifts in macrophyte abundance and ecosystem state (Bornette and Puijalon, 2011; Chambers and Kalff, 1985; Ersoy et al., 2020; Hilt et al., 2006; Hu et al., 2019; Middelboe and Markager, 1997; Scheffer and Carpenter, 2003; van Wijk et al., 2023). In shallow lakes, the ratio of euphotic depth or Secchi depth to water depth serves as a robust predictor of macrophyte viability (Liu et al., 2016; Wang et al., 2005; Yang et al., 2022). Yet, in floodplain systems, attention has mainly focused on water level fluctuations and lateral hydrological connectivity as the primary drivers (Bouska et al., 2020; Eros et al., 2019; Van Geest et al., 2007). The role of underwater light availability has often been overlooked or merely implicated as a proximate cause that was presumably driven by fluctuating water levels (Bouska et al., 2020; Van Geest et al., 2005a, 2007). Associated with floodings, RFEs experience sediment, nutrient, and thermal pulses (Ferreira et al., 2010; Sokly et al., 2018; Tockner et al., 2000, 2010). The inflowing sediments and their hydraulically driven resuspension may reduce underwater light climate to levels that surpass physiological thresholds for submerged macrophyte growth. Alternatively, nutrient pulses fuelling algal growth may also deteriorate underwater light availability that constrains submerged vegetation. Recent studies suggest that underwater light thresholds can predict macrophyte presence in shallow lakes even under variable hydrology (Dong et al., 2021; Hu et al., 2025). Depth limits of submerged plants' penetration in lakes are arguably determined by underwater light availability, rather than water pressure and temperature (Spence, 1982). Therefore, it can be postulated that the distribution of submerged plants in large RFEs is regulated by underwater light availability, similar to shallow lakes. Yet this mechanism remains underexamined, because long-term empirical evidence from natural floodplain systems linking sediment-driven or nutrient-driven light regimes to macrophyte persistence is still rare. This knowledge gap limits our understanding of submerged plant responses to both anthropogenic and natural alterations (e.g., dam operations, catchment land-use intensification, and extreme precipitations) that could directly influence sediment- or nutrient-regimes and thus underwater light availability in floodplain lakes.

Lake Poyang, a large RFE in China and a Ramsar site, exemplifies these dynamics. It hosts approximately 0.4 million migratory bird individuals annually and is the largest overwintering site in Eastern Asia (Li et al., 2020). However, recent declines in *Vallisneria spinulosa,* the dominant species of the submerged plant community, have triggered severe food shortages for several endangered bird species (e.g., Siberian crane, whooper swan, and bean goose) (Hou et al., 2020; Li et al., 2020; Meng et al., 2023; Wang et al., 2023). Multiple factors, including hydrological changes linked to dam operations, water quality deteriorations due to catchment agricultural activities, devastating flooding events, and direct human disturbances, have been implicated (Hu and Lin, 2019; Li et al., 2020). But the specific mechanisms underlying the plant recession remain elusive, challenging its conservation. We hypothesized that underwater light limitation was the cause of the plant recession and was driven by either elevated sediment loadings or nutrient enrichment associated with flooding pulses.

In this study, we investigated whether underwater light availability through the floodings was the driver of the tempo-spatial distributions of submerged plants in floodplains of Lake Poyang. Specifically, 1) we quantified intra- and inter-annual changes in underwater light climate of the Lake Poyang floodplain area during the floodings; 2) developed an empirical model that explored the relationship between underwater light of the flooding periods and *V. spinulosa* biomass density based on field data; 3) derived the long-term (1986–2021) habitat distribution of *V. spinulosa* using remote sensing and validated it with both field observations and reported distributions of submerged macrophytes in Lake Poyang in a previous study; 4) diagnosed the critical optic component in Lake Poyang that drives underwater light variations and its dynamics associated with hydrological regime shifts and/or anthropogenic disturbances.

2. Methodology

2.1. Study site

Lake Poyang (28°4′ - 29°46′N, 115°49′ - 116°46′E) is a large RFE located at the middle-lower reaches of the Yangtze River (Fig. 1). It receives inflows from five tributaries and drains into the Yangtze (Ni et al., 2020). Forest and farmlands constitute 49.6 % and 29.7 % of its catchment area, respectively (Nixdorf and Zhou, 2018). Due to the subtropical humid monsoon climate, the lake experiences alternating wet and dry seasons. During the wet season, its water level rises rapidly from April to June (rising period) and remains high between July and September (flooding period), expanding the lake's surface area to 3000–4000 km^2 and forming the largest freshwater lake in China. Switching to dry seasons, the water level drops significantly in October, reducing the lake's area to below 1000 km^2 and exposing vast floodplains since November (Dai et al., 2015; Huang et al., 2022). On the floodplains, over 100 water bodies become isolated (while hydrologically connected to the main lake in the wet season) and are known as sub-lakes of Lake Poyang. These sub-lakes support rich aquatic plants and provide excellent habitats for over-wintering birds. To protect these critical habitats, two national nature reserves were established. They are Poyang Lake National Nature Reserve (PNR) and Nanjishan National Nature Reserve (NNR) (Fig. 1). This study focuses on floodplain sub-lakes within the two reserves (as numbered in Fig. 1).

2.2. Data collection and analysis

2.2.1. Underwater light availability dynamics

Underwater light availability was indexed by ratios of Secchi depth to water depth (SD/Dep), a widely accepted proxy in shallow lakes. Archived monthly averages of Secchi depth (SD) and water levels from April to October (2000–2008) for lake 1, lake 2, and lake 6 in PNR were compiled. SD had been determined 4 times a month with a Secchi Depth Disk at five evenly distributed sampling sites in each sub-lake (Jia et al., 2011). Averaged water depths were derived from monthly water levels (reference to the Wu-song Zero Datum) (Jia et al., 2011) adjusted to lake-bottom elevations. In total, 168 monthly averaged SD/Dep ratios from 2000 to 2008 were obtained (except for 2002 when a few months data were lacking). The SD/Dep ratios were plotted both by month (from April to October) and by year (2000-2008), then ANOVA followed by Tukey HSD tests were implemented to detect differences among the months, and among the years (JMP, SAS®, USA). Further, linear regression analysis was performed (JMP Version 16, SAS®, USA) for SD/Dep ratios against SD and water depth separately to reveal their relative influence on SD/Dep variability.

2.2.2. Relationship between underwater light availability and V. spinulosa biomass density

Fresh weight densities (FWD) of *V. spinulosa* shoots surveyed in late October or early November were archived for lakes 1, 2, and 6 between 2002 and 2008 by Wu et al. (2011), and for lakes 1, 2, 4, and 6 between 2009 and 2019 by the Bureau of Poyang Lake National Nature Reserve. The shoots of *V. spinulosa* had been collected using a standardized quadrat sampling method at 50 m intervals along two transects that cross at the lake center per sub-lake, before being dried, weighed on site, and averaged (Wu et al., 2011). Then SD/Dep averages of the flooding period (July and October) and FWD of *V. spinulosa* shoots for each

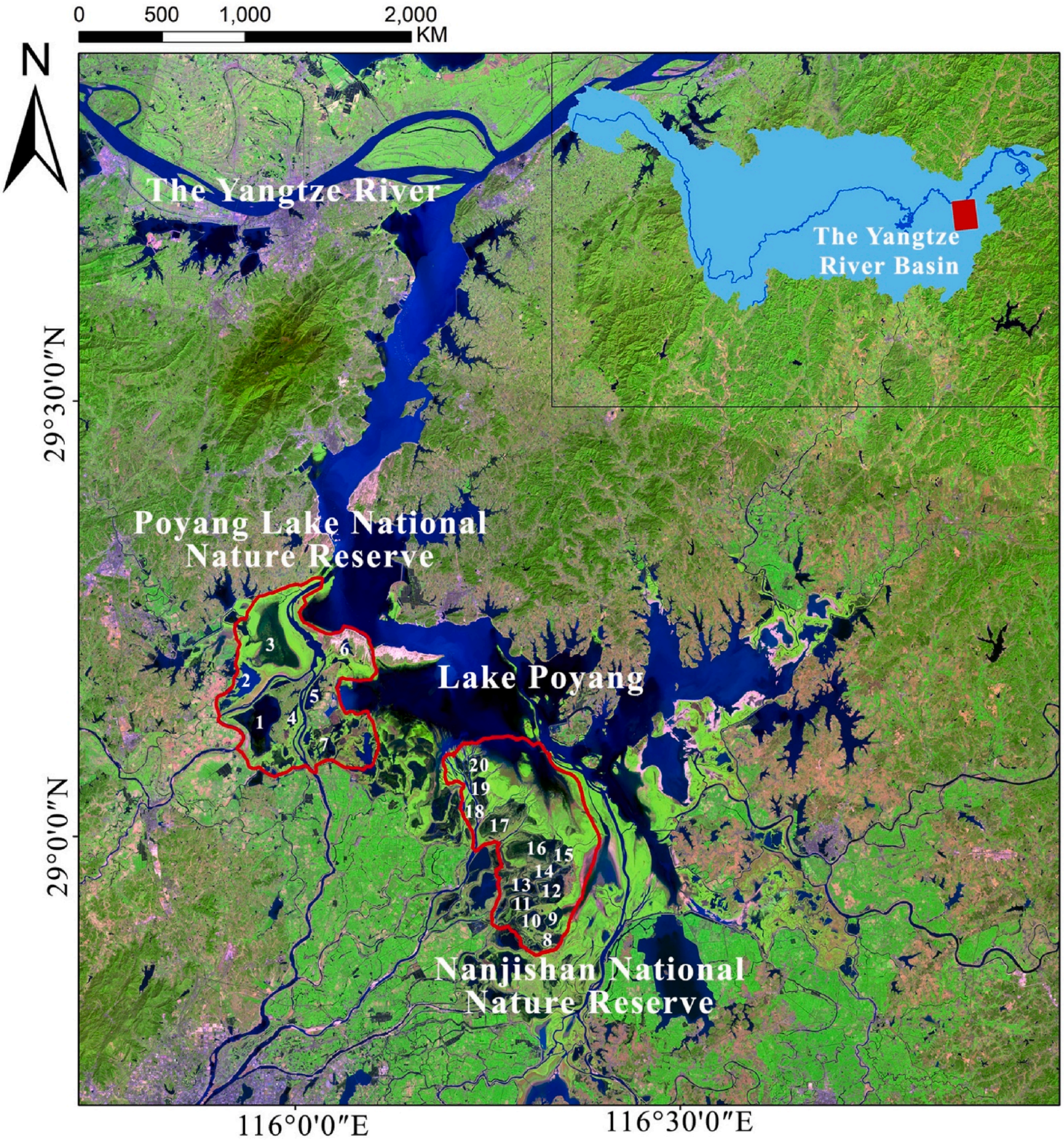

Fig. 1. An image of Lake Poyang during the dry period with numerous floodplain sub-lakes (the Poyang Lake national nature reserve and Nanjishan national nature reserve are delineated with red lines and their key floodplain sub-lakes are numbered; the map was a composite Landsat 8 image with band 2, 5, 6 and captured on October 5th, 2013; Inserted small map shows the location of Lake Poyang region as marked in red within the Yangtze River basin).

sub-lake by year (2000–2008) were linear regressed (JMP Version 16, SAS®, USA). SD/Dep ratios of the rising period (March to June) were arbitrarily excluded because they were presumably more variable than those of the flooding period. Further, a minimum SD/Dep threshold for the plant survival was obtained.

2.2.3. Underwater-light-derived *V. spinulosa* habitat distribution and long-term spatiotemporal trends

We used Landsat-5 TM, Landsat-7 ETM+, and Landsat 8 OLI imagery (1986–2021) to map long-term changes in *V. spinulosa* habitat distribution across the floodplain sub-lakes, as illustrated in Fig. 2. From the archives of the U.S. Geological Survey 251 application-ready Level-2 surface reflectance products from July to October between 1986 and 2021 were acquired for the Lake Poyang region (Table S1) (Google Earth Engine platform). By multiple reflectance comparisons between any two sensors of the three based on a pseudo-invariant feature site of the Poyang Lake region (Fig. S1), correction coefficients for the corresponding wavelength range were estimated and used to standardize reflectance among the Landsat 5/7/8 sensors. Then, water areas were selected based on the Normalized Difference Water Index (McFeeters, 1996). Water depths (Dep) were estimated by the elevation differences between the pixels of water area and their nearest water-land boundary pixels in the Digital Elevation Model of Lake Poyang (Feng et al., 2011). Secchi depth was estimated according to an empirical retrieval algorithm developed and validated exclusively for sub-lakes of Lake Poyang: $\ln(SD) = -0.4016 - 0.722\ln(B) - 0.587\ln(R)$, where B and R represent the reflectance values of the blue band and red band of the Landsat images, respectively (Wu et al., 2007). Then SD/Dep ratios were calculated for each pixel of the extracted water area.

Each year, the retrieved SD/Dep products of each month were fused to produce a monthly average product, and monthly products were fused to produce an annual product, representing underwater light availability of the flooding period of that year. Typical water areas of the floodplain sub-lakes in the dry period were delineated and selected according to their respective water/land boundaries, as illustrated in Fig. 1 (Zeng et al., 2024). Further, based on the detected minimum SD/Dep threshold (section 2.2.2), pixels were classified as habitable (SD/Dep >0.2) or inhabitable (SD/Dep≤ 0.2) for *V. spinulosa*, and marked in green

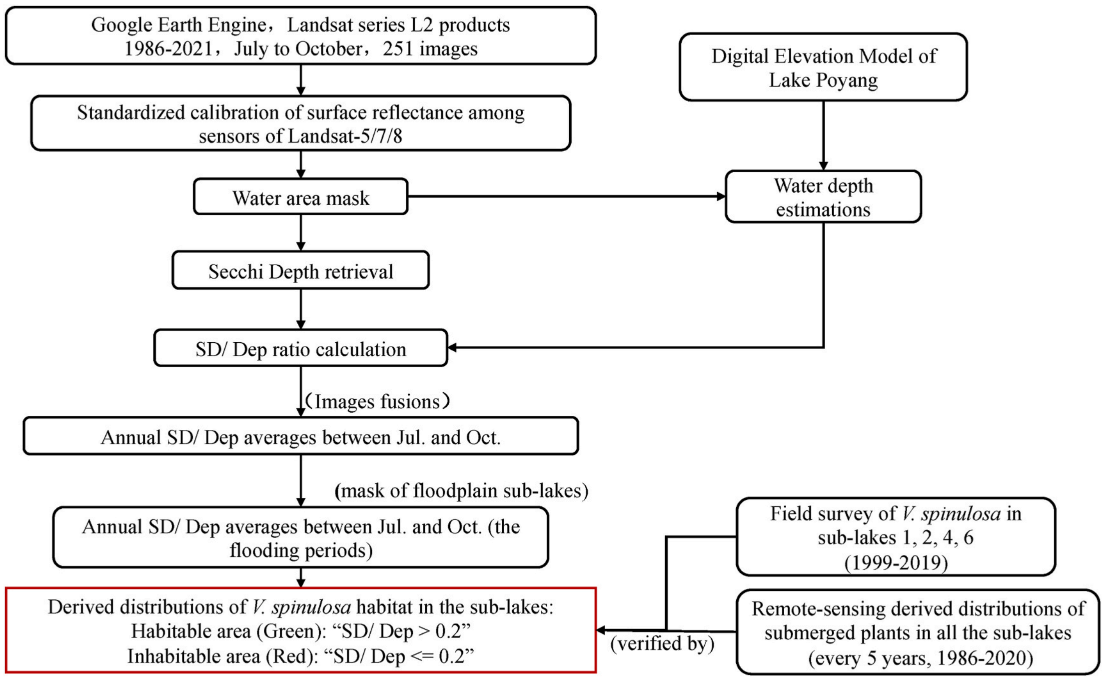

Fig. 2. A flow chart of step-by-step procedures for deriving long-term spatiotemporal distributions of *V. spinulosa* habitat in the floodplain sub-lakes and their verifications.

and red color, respectively.

To validate the derived *V. spinulosa* habitat distribution, confusion matrices were constructed by comparing predicted habitat with two independent reference datasets: *V.spinulosa* field surveys and satellite-derived distributions of submerged vegetation during the flooding period. Field surveys include FWD of *V. spinulosa* shoots and tuber densities for Lake 1, 2, 4, and 6 from 1999 to 2019 (data collection described in section 2.2.2). Distributions of submerged plants in Lake Poyang in 1986, 1990, 1995, 2000, 2005, 2010, 2015, and 2020, derived from Landsat Images with a validated machine learning method, were obtained from Cao et al. (2024) via personal communications. Then the mask of floodplain sub-lake areas (Zeng et al., 2024) was applied, visualizing the distribution of submerged macrophytes for each sub-lake by year.

For each sub-lake by year, when validation data were available, the derived classification was categorized as "Habitable" or "Inhabitable". This binary prediction was compared to observed presence or absence in the reference datasets to populate the confusion matrix: True Positives (habitable and observed), True Negatives (inhabitable and absence), False Positives (habitable but absence), and False Negatives (Inhabitable but presence). Performance metrics derived from the confusion matrix included:

Accuracy = (True Positives + True Negatives) / Total comparisons

Precision = True Positives / (True Positives + False Positives)

These metrics were calculated separately for field survey validations (n = 65) and satellite-derived validation (n = 157).

To disentangle the long-term spatial and temporal dynamics in *V. spinulosa* habitat distribution, the areal proportion of *V. spinulosa* habitat (habitable area divided by sub-lake area) was calculated for each sub-lake of each year. Then, sub-lakes were categorized into three classes of habitat suitability: "premium", "medium", and "poor" based on the grand mean of habitable areal proportions between 1986 and 2021 (premium:=> 80 %; medium:=> 50 % and <80 %; poor:≤50 %). The premium, medium, and poor sub-lake classes were marked with green, yellow, and red circles, respectively, to visualize long-term spatial differences among sub-lakes. At last, Mann-Kendall trend analysis was applied to detect long-term trends (1986–2021) in habitable areal proportions for each sub-lake class, to reveal the long-term temporal changes.

2.2.4. Potential drivers of V. spinulosa habitat distribution

To explore drivers of variations in underwater light availability, the lake optic properties were analyzed, quantifying the relative contribution of primary optically active substances, phytoplankton (chlorophyll-a) and suspended inorganic content (tripton), to the Secchi depth. Datasets of Secchi depth (SD), chlorophyll-a concentrations (Chl-a), and total suspended solids (TSS) across multiple sites of Lake Poyang between 2013 and 2018 were collected from an open-source dataset (Liu et al., 2019). Tripton was calculated as "Tripton = *TSM* – 0.07**Chl-a*" (Zhang et al., 2007). The relation of Chl-a and of Tripton to SD was analyzed by fitting datasets to a robust model ($Z_{SD} = X^b$, X is an optically active substance that is Chl-a or Tripton, *b* is a constant) (Brezonik et al., 2019; Nishijima et al., 2016) using non-linear least squares regressions. Root mean square errors (RMSE) were reported to evaluate the model fits. After identifying the critical primary light attenuator in Lake Poyang, we further searched published articles in the Web of Science that contain "tripton" or "total suspended particle" or "total suspended matter" or "suspended sediment" and "Poyang Lake" in their title and abstract, if tripton was the primary light attenuator. Or "chlorophyll-a" or "phytoplankton" or "algae" and "Poyang Lake" if Chl-a contributes more to light attenuation. We then manually excluded those that exclusively focus on remote sensing algorithm developments. Then the selected articles were systematically reviewed to address the patterns and drivers of the tripton or chlorophyll-a dynamics in Lake Poyang.

3. Results

3.1. Underwater light availability dynamics

Underwater light availability (SD/Dep) exhibited significant monthly variations (ANOVA, $p < 0.001$). SD/Dep was lowest in April, increased during the rising period (April to June), and plateaued since the start of the flooding period (July to October) (Tukey HSD test, p <

0.05) (Fig. 3A). Interannually, SD/Dep varied significantly (ANOVA, p < 0.001), with greater values in 2000 and 2001 than those from 2005 to 2007 (Tukey HSD test, p < 0.05) (Fig. 3B). Further, Secchi depth explained 70 % of the total variations in SD/Dep (Fig. 3C), while water depth explained little of the total variations, despite a significant correlation (Fig. 3D).

3.2. Relationship between underwater light availability and V. spinulosa biomass

Averaged SD/Dep of the flooding period (July to October) was linearly related to the FWD of *V. spinulosa* shoots recorded right after the floodings (late October or early November), and the former explained 74 % of the variations of the latter (Fig. 4). Further, a minimum SD/Dep threshold at 0.2 was identified, below which *V. spinulosa* shoots could not accrue biomass (Fig. 4).

3.3. Underwater-light-derived V. spinulosa habitat distribution and long-term spatiotemporal trends

Based on the minimum underwater light threshold (SD/Dep >0.2), we derived *V. spinulosa* habitat distribution in the floodplain sub-lakes each year between 1986 and 2021 (Fig. 5). Validating against the *V. spinulosa* field surveys (Table S2), the underwater-light-derived habitat successfully predicted the existence of *V. spinulosa* with a high accuracy rate at 89 % and a high precision rate at 86 % (Fig. S2). Further, in comparisons to the submerged vegetations distribution in the flooding period, our underwater-light-derived habitat predicted the submerged plants existence with an accuracy rate of 80 % and a precision rate of 89 % (Fig. S3 and S4). The underwater-light-derived

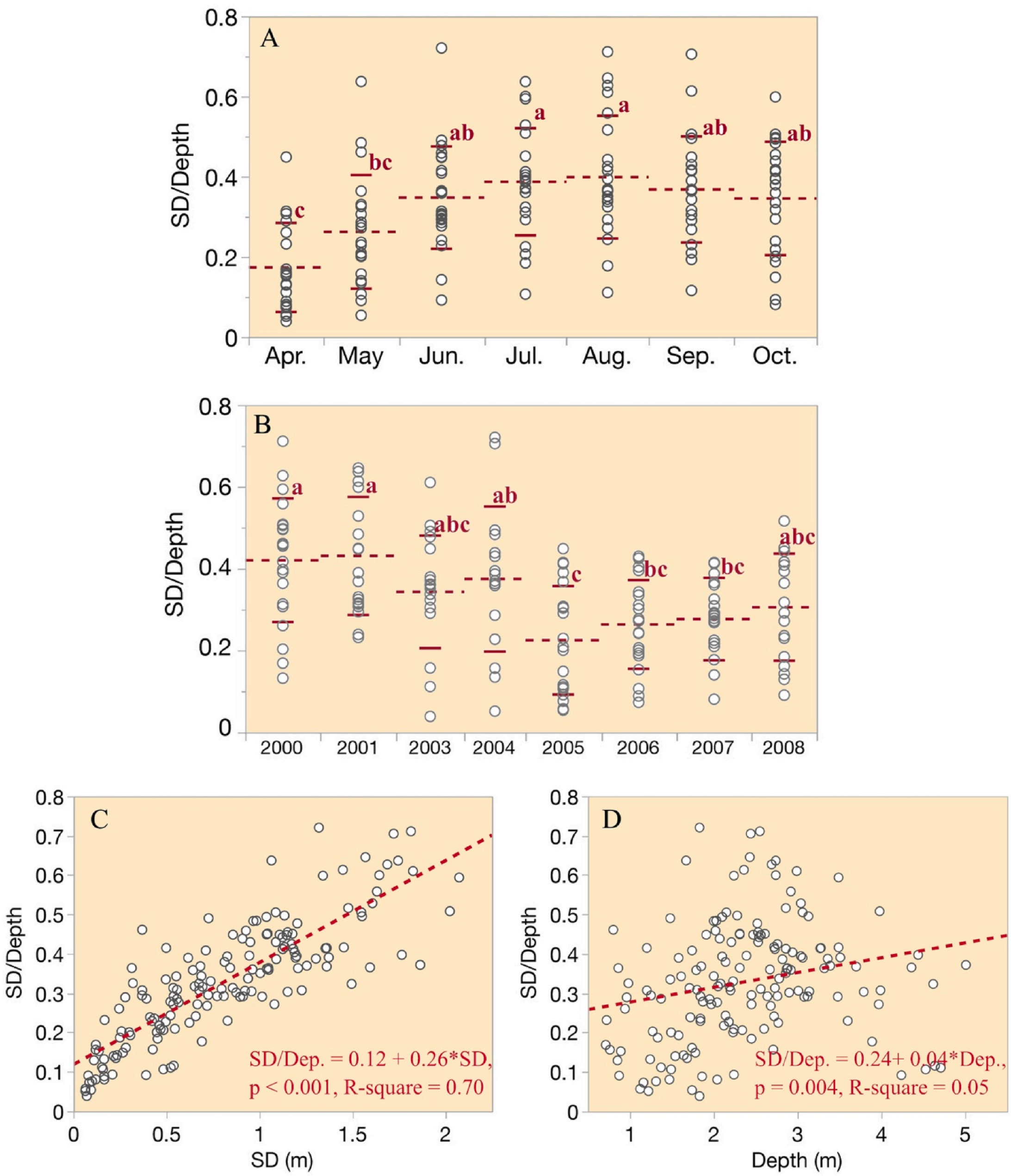

Fig. 3. A) SD/Dep ratios of the sub-lakes (Lake 1, 2, and 6) by month through the wet periods (dashed red line: monthly mean; red solid line: plus/minus one standard error of the mean; different letters indicate statistical differences among the month at p < 0.05); B) SD/Dep ratios of the sub-lakes by year from 2000 to 2008; C) Fitted linear regression (dashed red line) on SD/Dep with Secchi depth; D) Fitted linear regression (dashed red line) on SD/Dep with water depth.

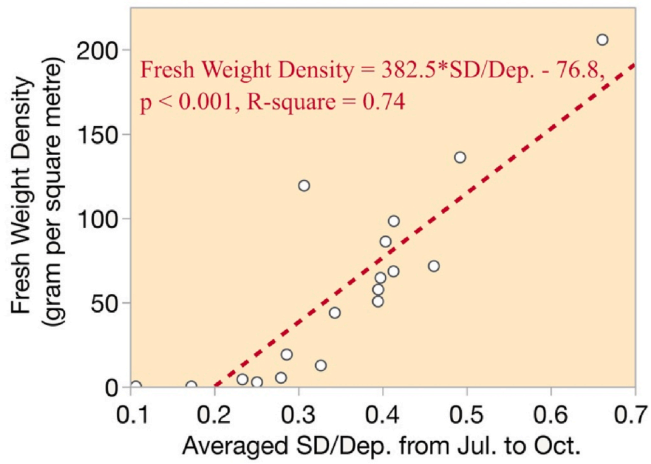

Fig. 4. Fitted linear regression (dashed red line) on fresh-weight density of *V. spinulosa* recorded after the floodings (late October or early November) with averaged SD/Dep of the flooding period (July to October) for each sub-lake per year.

V. spinulosa habitat demonstrated strong stochastic interannual fluctuations, rather than a continuous decline. Spatially, sub-lakes of the premium habitat suitability were primarily located in the south (the PNR), while sub-lakes of the medium or poor habitat suitability were located mainly in the north (the NNR) (Fig. 6). Temporally, the "premium" and "medium" sub-lake groups both demonstrate a stochastic interannual dynamic in the habitable areal proportions, instead of a monotonic shrinking trend from 1986 to 2021 as expected (Mann-Kendall test, $p > 0.05$). Surprisingly, the "poor" sub-lakes group showed an expanding trend in habitable areal proportions (Mann-Kendall test, $p < 0.01$) (Fig. 6).

3.4. *Potential drivers of V. spinulosa habitat distribution*

Changes in Secchi depth in Lake Poyang were highly related to variation in tripton, but not to that of chlorophyll-a. Tripton fitted fairly well to the empirical model that explains variations in SD, with an RMSE of 0.215 m; while chlorophyll-a fitted less well to the model, with an RMSE of 0.4 m (Fig. 7). We found 23 published studies on patterns or dynamics of suspended sediment concentration (SSC) in Lake Poyang (Table S3). Temporally, SSC in Lake Poyang was high during the wet seasons (April–October) due to intense rainfall, river inflow, and catchment runoffs, and was low in the dry seasons (November–March) due to less rainfall and inflows (Bao et al., 2014; Fu et al., 2022; Wang et al., 2013) (Table 1). There are three flow patterns through the wet seasons: the Gravity-flow pattern of the rising period, the Jacking-flow pattern of the flooding period, and the episodic Back-flow pattern (reversed flow from the Yangtze River to Poyang Lake) that occurred intermittently within the flooding period (Fig. S5) (Wang et al., 2017, 2018). The reduced velocity of the Jacking-flow pattern (flooding period) compared to that of the Gravity-flows (rising period) allows suspended particles to settle (Wang et al., 2018), whereas backflow from the Yangtze River remobilizes bottom sediments and induces short-term surges in SSC (Xu et al., 2022) (Fig. S5). Spatially, SSC is consistently higher in the northern part of the lake due to the influence of the back-flows and prevalent sand mining activities (Cui et al., 2013; Liao et al., 2024; Lu et al., 2019; Wang et al., 2018; Zhang et al., 2015). Interannually, rainfall variability drives sediment input changes (Fu et al., 2022; Zhang et al., 2015). And the operation of the Three Gorges Dam notably reduced the water level of the Yangtze River at the lake outlet and the frequency of backflows (Zhou et al., 2016). Put together, the SSC dynamics during the wet seasons were jointly driven by flow pattern, precipitation, backflows, and dredging activities.

4. Discussion

4.1. *The role of underwater light on V. spinulosa habitat persistence*

Our study demonstrates that underwater light availability during the flooding periods is the long-term controlling factor of *V. spinulosa* habitat distribution in floodplain sub-lakes of Lake Poyang (Figs. 2, 4 and 5 and Fig. S4). Although it is well recognized that underwater light is the most critical factor for distributions of submerged macrophytes in shallow lakes (Bornette and Puijalon, 2011; Chambers and Kalff, 1985; Dong et al., 2021; Ersoy et al., 2020; Hilt et al., 2006; Liu et al., 2016; Middelboe and Markager, 1997; Xu et al., 2020), its role in floodplain lakes has been not definitive. The notion that light limitation drives regime shifts or successional changes of submerged plants in floodplain lakes was either implied tentatively (Friberg et al., 2017; Loverde-Oliveira et al., 2009; Van Geest et al., 2005a, 2005b, 2007) or conceived intuitively (Bouska et al., 2020). Studies on hundreds of floodplain lakes along the Lower Rhine River show that episodes of low water levels helped maintain submerged vegetations or delayed their collapse, most likely due to temporally relieved low-light stress among years of high-water levels (Van Geest et al., 2005a, 2005b, 2007). Macrophyte dominance during high water levels and vegetation collapse during low water levels in the tropical floodplain lake Pantanal were deemed driven by seasonal water level fluctuations, rather than changes in underwater light climate (Loverde-Oliveira et al., 2009). The limiting effects of underwater light on submerged plants in floodplain lakes were definitively evidenced in Han et al. (2018), but based on mesocosm experiments rather than field observations. Our study may have provided the first long-term field evidence that underwater light availability is the primary controlling factor of submerged plant distributions in floodplain lakes, as in shallow lakes in general.

The minimal threshold for the survival of *V. spinulosa* was identified at a SD/Dep above 0.2 in the sub-lakes of Lake Poyang (Fig. 4). Wang et al. (2005) reported SD/Dep between 0.45 and 0.65 as the minimal thresholds for submerged plants (*Potamogenton crispus, P. maackianus, Najas major, Vallisneria* spp.*, Hydrilla verticillata,* and *Ceratophyllum oryzetorum*) during the spring (March to June) in four lakes in the Yangtze Plain. Dong et al. (2021) reported a SD/Dep of 0.4 as the minimal threshold in Lake Taihu during the summer. The lower minimal threshold of SD/Dep in our case may be attributed to different seasons, species, or lake optics. Firstly, plants during the flooding period (July–October) were of larger sizes compared to in the spring (March–June), such that shoot or leaf elongations allow them to reach better illuminated upper water columns and tolerate enhanced light stresses (Hu et al., 2019). Secondly, *Vallisneria* spp. have a lower light compensation point and better capabilities in utilizing low light than other submerged angiosperms (Deng et al., 2023; Yang et al., 2022). Thirdly, reported minimal underwater light thresholds were from eutrophicated lakes (Wang et al., 2005; Yang et al., 2022), where phytoplankton attenuated underwater light primarily. But in Lake Poyang, underwater light attenuation is mostly caused by suspended sediments (Fig. 7). Light attenuation by phytoplankton results in proportionally less photosynthetically useable radiation than by suspended inorganic particles (Strydom et al., 2017), that explains higher minimal light threshold in eutrophic waters.

4.2. *The patterns and drivers of the spatiotemporal dynamics of V. spinulosa habitat*

The derived *V. spinulosa* habitat distributions in floodplain sub-lakes of Lake Poyang demonstrate a stochastic dynamic pattern spatiotemporally (Fig. 5), rather than a long-term monotonic shrinking trend as expected. Li et al. (2020) reported a significant decreasing trend (1999–2017) of *V. spinulosa* biomass densities in sub-lake 1, 2, and 6. We additionally conducted time-series analysis of the *V. spinulosa* habitable areal proportion of the three sub-lakes at the same time period, and

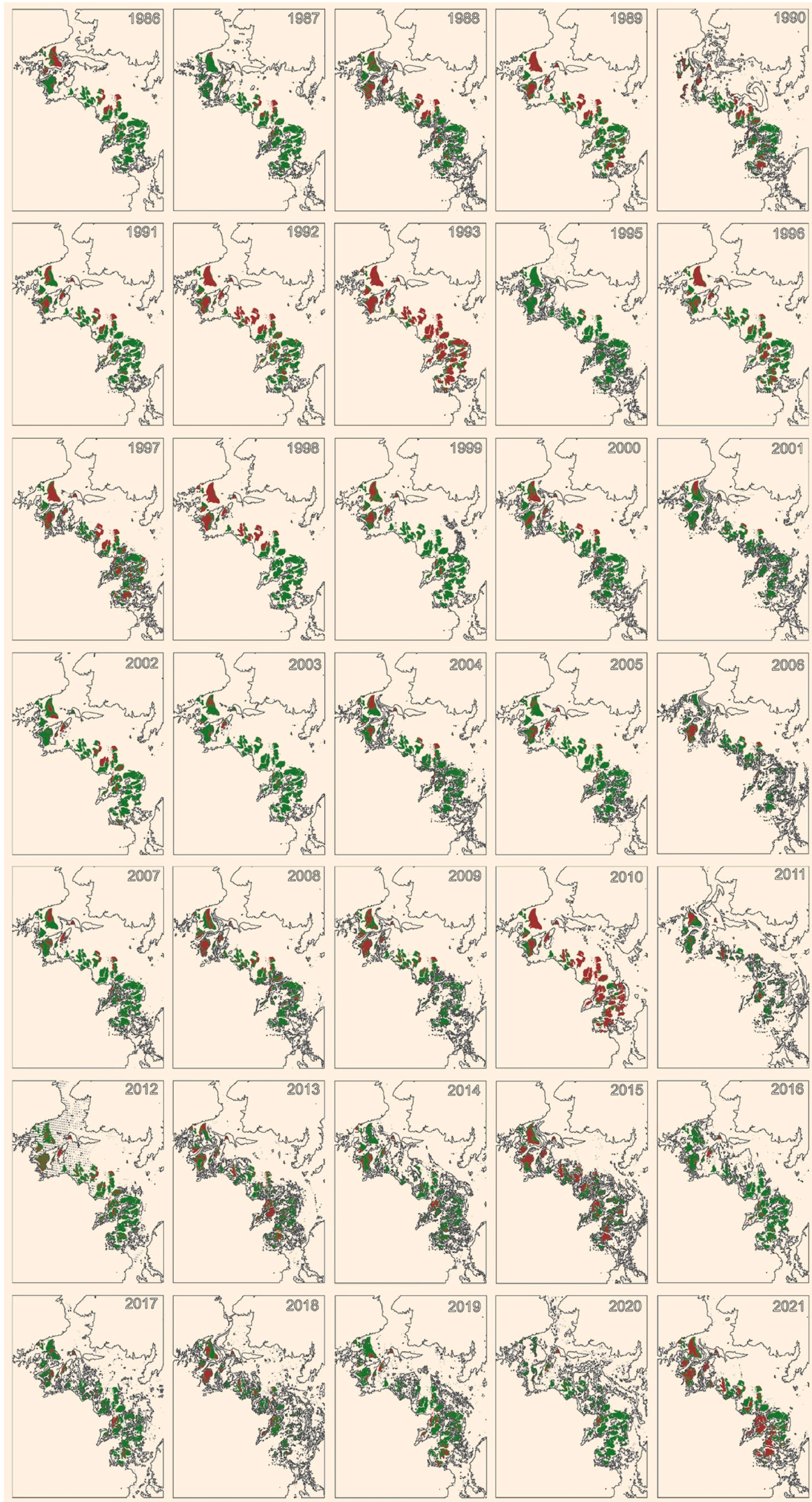

Fig. 5. Distributions of underwater-light-derived habitable (Green) and inhabitable areas (Red) for *V. spinulosa* in the floodplain sub-lakes each year between 1986 and 2021.

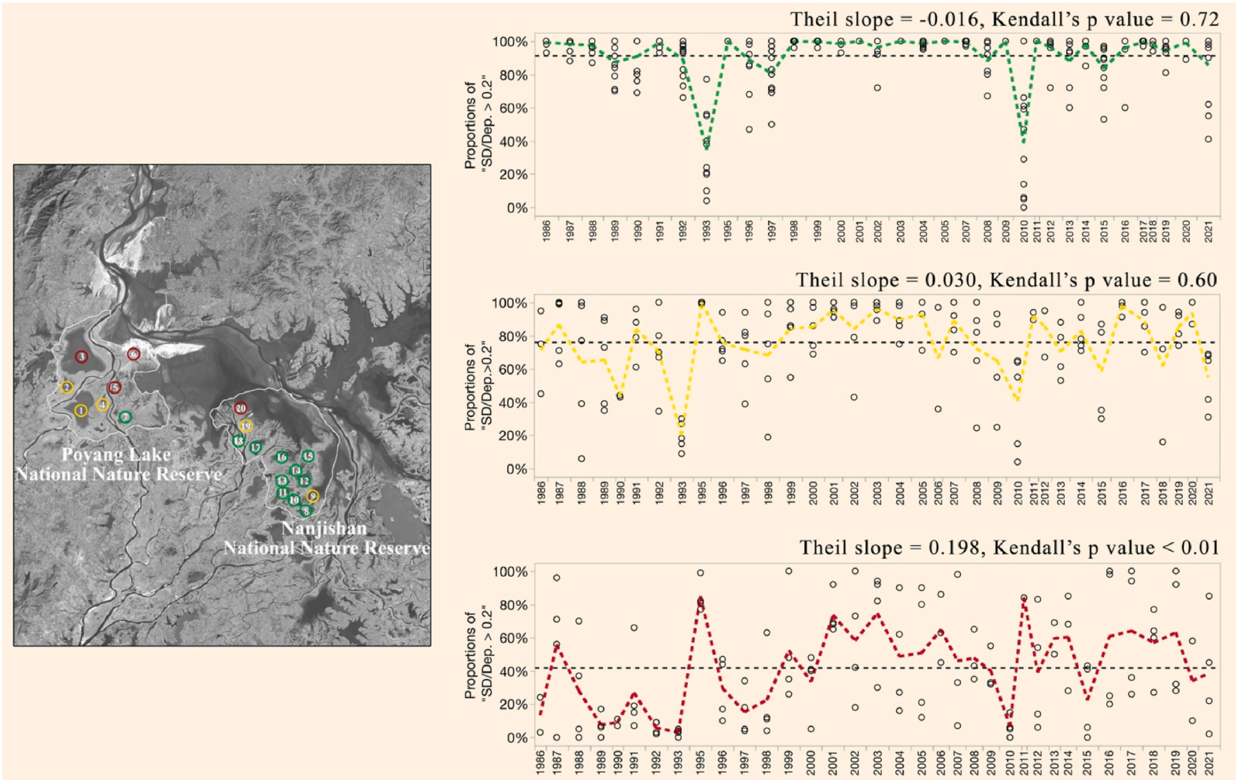

Fig. 6. (Left) The distributions of the premium (green), medium (yellow), and poor (red) habitat suitability sub-lake classes in the two nature reserves and (right) the long-term dynamic of *V. spinulosa* habitable areal proportion ("SD/Dep >0.2") for each of the classes (the dashed color line represents the moving averages of each year; the dashed black line represents the grand mean).

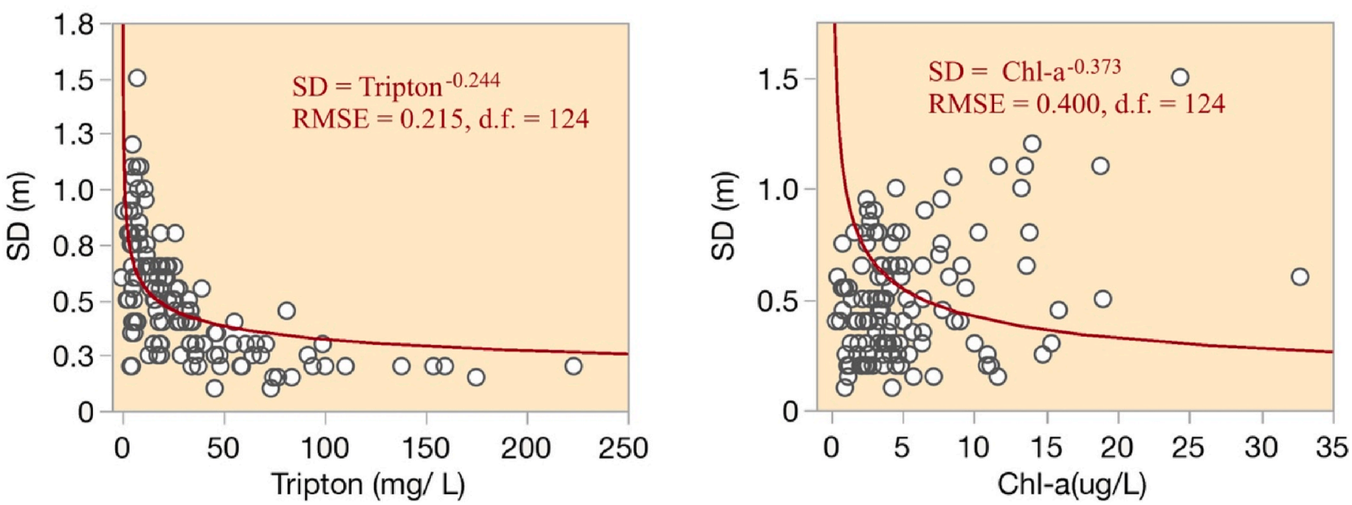

Fig. 7. Fitted non-linear regression on Secchi depth with tripton concentration (the left panel) and on Secchi depth with chlorophyll-a concentration (the right panel).

found a notable decreasing trend (Theil slope = −0.184, Kendall's p = 0.065). But on a greater spatiotemporal scale, the *V. spinulosa* habitat seemed not declining (Figs. 5 and 6). Spatially, *V. spinulosa* habitat were more extensively distributed in the southern sub-lakes than in the northern ones, as the premium sub-lake class were mainly located in the south (NNR), whereas the poor and medium sub-lake classes were primarily distributed in the north (PNR) (Fig. 6). Surprisingly, habitat distributions in the poor class even expanded over the long-term (1986–2021).

V. *spinulosa* habitat distribution was regulated by underwater light of the flooding periods that was primarily controlled by Secchi depth (Fig. 3C). Lake optic analysis revealed that inorganic particle was the primary light attenuator in Lake Poyang (Fig. 7), thus the dynamic of *V. spinulosa* habitat distribution may be associated with behaviors of suspended sediment, as advised by Friberg et al. (2017). A systematic literature review on SSC in Lake Poyang revealed that suspended sediment behaviors well explained the dynamics of *V. spinulosa* habitat distributions. Firstly, the consistent higher SSC in the northern part of Lake Poyang than the southern part explains inferior

Table 1
Key findings on drivers and patterns of suspended sediment concentration (SSC) dynamics in Lake Poyang.

Drivers	Main findings	References
Spatial & Temporal Patterns	SSC higher in northern parts due to the backflows and sand mining activities	(Cui et al., 2013; Wei et al., 2025)
	Highest SSC occurs during flood seasons with marked intra-annual fluctuations	Wang et al. (2013)
Natural Hydrodynamic Drivers	Hydrological regimes (Gravity-flow, Jacking-flow and Back-flow patterns) control SSC distribution	(Wang et al., 2017, 2018)
	Wind-induced resuspension increases turbidity in shallow zones	(Tang et al., 2023; Wang et al., 2020)
	Sediment exchange is governed by flood/dry season transitions	(Bao et al., 2014; Zhou et al., 2016)
Anthropogenic Drivers	Sand mining causes direct resuspension and alters channel morphology	(Deng et al., 2022; Tang et al., 2023)
	Agricultural land use in upstream areas leads to increased erosion and sediment yield	(Lu et al., 2019; Wang et al., 2013)
	Urbanization and dredging disturb benthic sediment layers and increase SSC	Cui et al. (2013)
Climate Change and Reservoir Impact	Climate change increases rainfall variability that contributes to significant seasonal and interannual variabilities in sediment input	(Fu et al., 2022; Wang et al., 2015; Xu et al., 2022)
	The Three Gorges Dam altered backflow patterns and reduced sediment input to Lake Poyang	Zhou et al. (2016)

habitat suitability in the northern sub-lakes than the southern ones (Fig. 6); secondly, the substantial interannual variability in SSC due to variable rainfall and runoffs in the catchment could explain the long-term stochasticity rather than a monotonic shrinking pattern in habit distributions; thirdly, the reduced frequency of back-flows may have explained the long-term expansions in habitable area for the poor sub-lake class (sub-lakes 3, 5, 6, and 20), which happen to locate in the Yangtze-river back-flows zone (Cui et al., 2009). In addition, the reduced SSC in the flooding period compared to the rising period, when the Gravity-flow pattern switches to the Jacking-flow pattern, could well explain the increase in underwater light climate (Fig. 3A and Fig. S5). In summary, suspended sediment behaviors appear to be the fundamental driver of the dynamics of *V. spinulosa* habitat distribution.

4.3. Practical implications and limitations of this study

This study highlights underwater light as a critical ecological constraint on the survival and habitat distribution of *V. spinulosa* in numerous floodplain sub-lakes of Lake Poyang. Traditional conservation approaches in floodplain lakes often focus on water-level management or hydrological reconnection (Eros et al., 2019; Havens et al., 2004; Loverde-Oliveira et al., 2009; O'Farrell et al., 2011). Our results suggest that light attenuation via suspended sediments is a more direct and limiting factor than water level fluctuations alone. Hence, ecological restoration strategies should prioritize improving water clarity, particularly during the flooding season, through targeted interventions (e.g., reducing catchment erosion via reforestation, sustainable agricultural practices, and modifying flow regimes) to stabilize sediment dynamics. *V. spinulosa* provides primary food sources for several endangered migratory birds visiting Lake Poyang. By establishing a plausible linkage between sediment dynamics and macrophyte survival, this study may have offered a causal pathway to support conservations of the world-renowned bird habitat. River-floodplain ecosystems (RFEs) worldwide experience dynamic hydrological and sediment regimes. The established methodology of this study, combining long-term remote sensing with light-threshold modeling, lake optic analysis, and exploration of the drivers and patterns of the primary light attenuator, can be adapted to other RFEs to predict submerged vegetation distributions in the context of altered hydrology and precipitation due to climate change.

Although underwater light availability was the most critical factor, other components such as fish communities or interspecific competition within aquatic plant communities may act simultaneously to redefine *V. spinulosa* habitat in sub-lakes of Lake Poyang (Poikane et al., 2024). As those sub-lakes shift between states of isolation and reconnection with the main river channel, fish communities may change significantly due to their migratory behaviours (Wang et al., 2022). Altered fish communities, particularly benthivores and zooplanktivorous fish that disturb submerged plants (Abell et al., 2022; Meijer et al., 1999; Sondergaard et al., 2007), could be another critical factor on the plant habitat but remain unexplored. Also, floating-leaf plants *Trapa* spp. becoming more dominant in aquatic plant communities in these sub-lakes has been reported recently (Liu et al., 2020). Their responses to shifts in hydrological patterns and interactions with the submerged plant *V. spinulosa* require further investigation to gain a more comprehensive understanding of the habitat suitability for *V. spinulosa*.

5. Conclusions

This study underscores the critical role of underwater light availability, rather than water level fluctuations, in driving the long-term habitat distribution of *V. spinulosa* in numerous floodplain sub-lakes of Lake Poyang. The long-term dynamic in habitat distribution reveals a stochastic pattern that were well explained by suspended sediment behaviors, which were primarily associated with shifts in flow patterns, precipitation, and sand degrading activities. These insights emphasize enhancing water transparency via catchment erosion reduction and flow regime modifications are vital for sustaining submerged vegetation and supporting biodiversity in floodplain lake ecosystems like Lake Poyang.

CRediT authorship contribution statement

Qian Hu: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Wenkai Li:** Writing – review & editing, Formal analysis, Data curation. **Aiwen Zhong:** Resources, Data curation. **Songhe Jiang:** Writing – review & editing, Resources, Data curation. **Libing Liao:** Data curation. **Lei Xu:** Investigation, Formal analysis. **Liqiao Tian:** Resources, Methodology, Formal analysis, Data curation.

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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floodplain sub-lakes of Lake Poyang.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.127615.

Data availability

Data will be made available on request.

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