Environmental Science & Technology

pubs.acs.org/est

Article

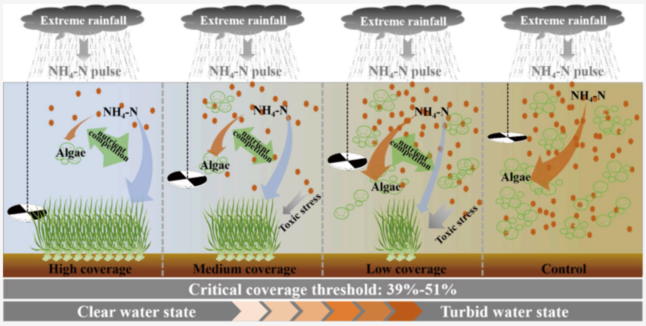
Quantifying Critical Thresholds of Submerged Macrophyte Coverage to Buffer Climate-Amplified Ammonium Pulses and Stabilize Clear-water States

Chaochao Lv, Lei Shi, Yuqing Tian, Hang Shan, Qingchuan Chou,* Wei Liu, Kuanyi Li, and Te Cao*

Cite This: https://doi.org/10.1021/acs.est.5c04237

Read Online

ABSTRACT: Climate change intensifies nutrient pulses through extreme rainfall and agricultural runoff, yet the buffering capacity of submerged macrophytes against such disturbances remains unquantified. Through a large-scale enclosure experiment simulating ammonium pulses (1.24 mg/L NH_4−N), we tested how submerged macrophytes coverage (SMC, 0−100%) modulates water quality, ecosystem resilience, and regime shifts (from clear to turbid). The system's buffering capacity and resilience stability increased significantly with SMC, whereas its recovery stability decreased. High SMC (>50%) accelerated NH_4−N removal (96 h vs 168 h in controls), suppressed phytoplankton blooms (Chl-*a* increase: 102.5% vs 237.4%), and sustained clear water. Conversely, low and medium SMC (<50%) did not prevent transitions to algal-dominated states. Furthermore, NH_4−N stress was inversely correlated with SMC, and persistently high NH_4−N at low SMC increased macrophyte degradation risk. Structural equation modeling revealed that macrophytes-mediated nutrient competition and light stabilization underpinned these effects. Additionally, we identify a critical SMC threshold (39−51%) to mitigate pulse impacts—a finding urgently needed to guide lake restoration in a changing climate. This work bridges the gap between pulse ecology and adaptive management, offering actionable strategies for SDG 6 (Clean Water) and 13 (Climate Action).



KEYWORDS: *NH_4−N pulse, submerged macrophyte coverage, phytoplankton bloom, buffering capacity, clear-water state*

1. INTRODUCTION

As global warming intensifies, the frequency of rare heavy precipitation events will increase nonlinearly, with 10 and 50 year events likely doubling and tripling in frequency at 4 °C warming,[1] exacerbating nutrient pulses via runoff and sewer overflows.[2,3] These pulses threaten freshwater resilience, yet aquatic studies lag behind terrestrial systems in quantifying biotic buffers. The period since the Industrial Revolution has witnessed a noticeable rise in the use of chemical fertilizers, urbanization, industrial emissions, deforestation, and land development. These human activities, characterized by inefficient resource utilization, are major factors contributing to the intensification of resource pulses,[4−7] and have had detrimental impacts on the ecosystem. Resource surges can cause widespread ecosystem impacts such as habitat destruction, water and air pollution, and biodiversity loss. However, current research predominantly focuses on terrestrial ecosystems when examining the effects of resource pulses,[8−10] with relatively less emphasis placed on their impact on aquatic ecosystems.[11] Nowlin et al.[12] indicated that, due to shorter generation times and faster growth rates of aquatic biota, aquatic ecosystems respond more rapidly and sensitively to resource pulses than terrestrial ones. For example, phytoplankton's quick response to nutrients can rapidly boost primary productivity,[13] thereby swiftly altering the trophic structure and biotic community composition of aquatic ecosystems and affecting their overall function and stability.[12,14] Moreover, the impacts of pulse versus press perturbations on aquatic systems diverge sharply: press perturbations—such as chronic nutrient enrichment—may gradually erode the system's tolerance or latent resilience without causing significant visible changes, as internal feedbacks sustain the current state; only when these feedbacks are sufficiently weakened can even minor further perturbations trigger an abrupt shift to an alternative stable state.[15] In contrast, pulse perturbations may immediately exceed the adaptive capacity of species and ecosystems,[13,16] potentially pushing ecosystems past tipping points more abruptly.[17] As one study indicates, both press and pulse

Received: April 2, 2025
Revised: July 24, 2025
Accepted: July 25, 2025
Published: August 4, 2025

phosphorus inputs can increase algal density, but biotic and abiotic indicators tend to be less stable in systems experiencing phosphorus pulse inputs than in those experiencing press inputs.[16] Therefore, it is essential to broaden research endeavors to gain deeper insights into the consequences of resource pulses on aquatic ecosystems and formulate comprehensive strategies for mitigating their negative impacts.

The influx of resources generated by human activities can be introduced into aquatic ecosystems as a result of precipitation or flooding driven by climate change, which frequently acts as triggers for resource pulses in aquatic ecosystems. Nitrogen and phosphorus, key nutrients for aquatic primary producers, deserve attention for their potential to stimulate algal blooms through pulse inputs.[13] In shallow lakes, phosphorus is commonly regarded as the limiting nutrient,[18] while nitrogen's role remains debated.[19,20] Yet, nitrogen's role might be particularly high in shallow lakes[21,22] due to high denitrification rates and sequestration of nutrients in biomass.[20] A study shows that from 2005 to 2018, only 9% of annual external nitrogen input was retained in Lake Taihu, with denitrification removing 54% of the external nitrogen load and nitrogen leaving the lake faster than phosphorus, thereby creating persistent nitrogen limitation.[23] Nitrate and ammonium, being directly utilizable by algae and submerged plants, play a crucial role in nitrogen cycling and serve as a vital intermediate product within the material and energy cycle of aquatic ecosystems.[24−26] Ammonium, however, has ambiguous effects.[11] A sufficient supply of ammonia promotes plant growth by supplying essential nutrients, but its excess can cause algal blooms,[24] eutrophication,[27] and toxicity to aquatic organisms,[28−30] threatening aquatic ecosystem stability and sustainable development. In addition, high ammonium loading can promote sediment phosphorus release,[31] further intensifying the nutrient stress on the lake ecosystem and the risk of regime shifts. These findings highlight the particular concern for nitrogen pulses. In severe cases, the abundance of ammonia nitrogen can even cause failure in ecological restoration projects. For instance, during the 2013−2023 water environment treatment of the GuXiang River, issues like rain-sewage mixing often caused high ammonium nitrogen concentrations and widespread aquatic plant deaths. After ten years of restoration, the water quality was still classified as poor Class V.[32] Moreover, many studies have shown that excessive ammonium nitrogen can cause death or decline of submerged plants,[25,33,34] and during ecological restoration, the newly transplanted and unstable plant communities may be more vulnerable to the toxic stress of strong ammonium nitrogen pulses, leading to restoration failures. Therefore, it is vital to take measures aimed at reducing the level of influx of ammonia nitrogen into aquatic ecosystems. Managing phosphorus inputs is equally important, since simultaneous control of both nutrients is often necessary to prevent phytoplankton overgrowth, particularly in systems with nitrogen-fixing cyanobacteria. If reducing external sources is not feasible, enhancing the aquatic ecosystem's resilience by improving its ability to withstand sudden nutrient spikes is essential.

Submerged macrophytes, serving as the primary producers in aquatic ecosystems, have a vital function in preserving the well-being of aquatic environments. According to regime shift theory, shallow lakes may exist in two distinct states under the same environmental conditions: a clear-water state dominated by submerged macrophytes and a turbid-water state dominated by phytoplankton.[35] These states can switch under external disturbances, with submerged macrophytes being crucial for establishing and maintaining the clear-water state.[36−38] An essential role of submerged macrophytes lies in their capacity to uptake nitrogen and phosphorus via their roots and leaves, effectively regulating nutrient levels in the water column.[39−43] Additionally, they can inhibit algal proliferation by competing for nutrients and carbon sources, creating shade, and producing allelochemicals.[44−46] Furthermore, submerged macrophytes provide shelter and refuge for zooplankton, contributing to enhanced control of phytoplankton by grazers.[47] The extensive growth of submerged macrophytes also aids in stabilizing sediment by reducing suspended particle accumulation[48] while restricting nutrient release from sediment.[49,41,50] In summary, submerged macrophytes play a critical and irreplaceable role in maintaining the ecological balance of shallow aquatic ecosystems. Their preservation is essential for the overall health of the system. Consequently, it is anticipated that the coverage or biomass of submerged macrophytes will be closely linked to the ecosystem's ability to mitigate ammonia pulses.

Previous studies have documented submerged macrophyte responses to NH_4−N stress,[33] such that intermittent NH_4−N surges may enhance trait connectivity in plant trait networks, particularly those linked to biomass allocation, thereby improving plant adaptability.[11] However, their capacity to buffer acute pulses—a hallmark of climate-driven disturbances—remains unquantified. Moreover, no study has yet determined the coverage thresholds necessary to prevent regime shifts. Even though some studies have determined the optimal submerged macrophytes coverage (SMC) for water quality improvement, such as 20% as suggested by Dai et al. and 50% by Zhang et al.,[51,52] significant differences remain between them. Moreover, nutrient pulses may further increase the uncertainty in the coverage thresholds. This gap impedes adaptive management in shallow lakes facing intensified nutrient pulses.[2,3] Ruggiero et al.[53] and Søndergaard et al.[54] have reported an inverse link between coverage of submerged macrophytes and nutrient levels in the water column. But further investigation is needed to gain a comprehensive understanding of the role played by submerged macrophytes in mitigating external ammonia fluctuations. Therefore, in this study, we conducted a large-scale macrocosm control experiment to explore how changes in the coverage of submerged macrophytes influence the ecosystem's ability to buffer against external ammonia pulses and maintain ecological resilience. We hypothesize that (1) the system's buffering capacity and resilience to NH_4−N pulses positively correlate with the coverage of submerged macrophytes; (2) threshold effects exist, where a coverage of ≥50% prevents regime shifts; (3) macrophytes-mediated nutrient competition with phytoplankton underpins stability.

2. MATERIALS AND METHODS

2.1. Experimental Design. The experiment was conducted at the aquatic plant cultivation base of Erhai Lake in Dali city (25.951022°N, 100.147358°E), China. The research period stretched from September 23, 2020, to September 30, 2020. Initially, a large pond, with a depth of 1.4 m and a surface area of 2241 m^2, was partitioned into 12 similar-sized enclosures using light-transmitting PVC boards (height: 1.2 m, inserted 20 cm into the mud). The mean area of the enclosures was 148.6 ± 1.7 m^2 (mean ± SE). One enclosure was excluded from this study due to uncontrollable factors, making it

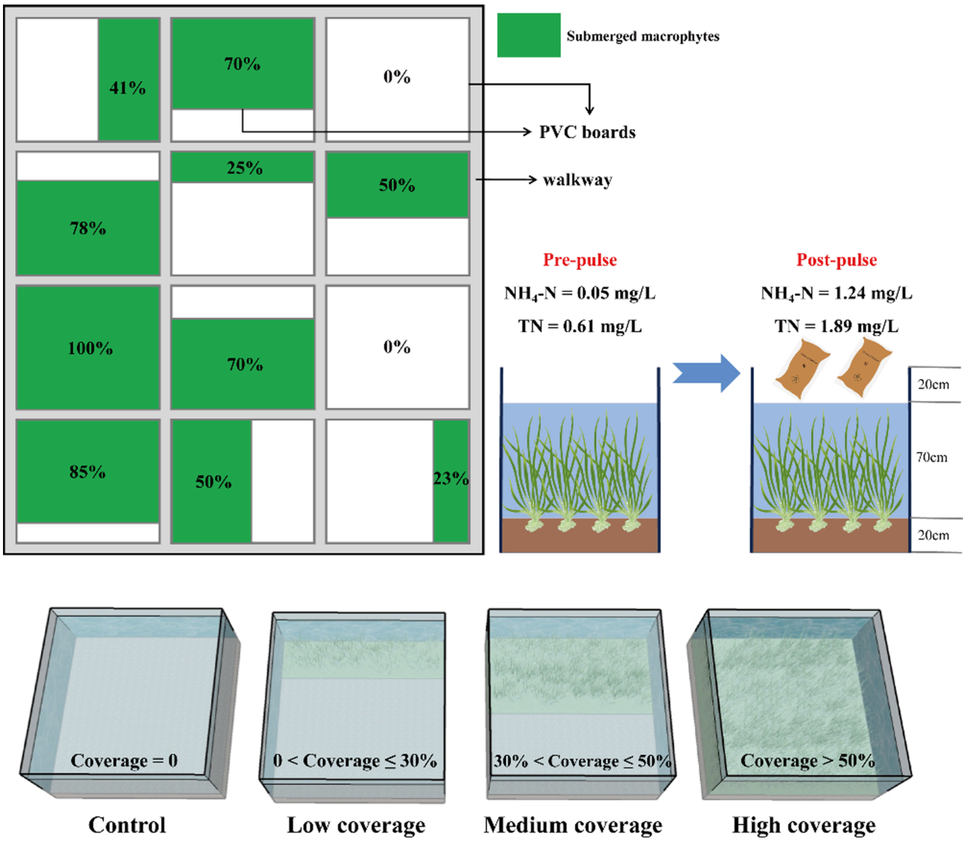


Figure 1. Drawing showing experimental design.

unsuitable. Subsequently, a random number generator was used to determine plant coverage for each enclosure. Yet, to guarantee uniformity, we carried out many random generations of coverage, screened for, and selected the relatively uniform designs among them, so as to improve the representativeness and generalizability of the experimental results. This process yielded coverages of 0, 0, 23, 25, 41, 50, 50, 70, 70, 78, and 100% for the respective enclosures. According to the difference in coverage, each enclosure was divided into four coverage levels, as shown in Figure 1. We selected *Vallisneria spinulosa*, a representative submerged macrophyte in the middle and lower reaches of the Yangtze River,[55] as the experimental material. Known for its strong adaptability to diverse aquatic environments (from oligotrophic to eutrophic waters)[56] and its ability to inhibit algae via allelopathic substances (phenolic acids),[57] it is widely used in water purification and ecological restoration.[55] However, its population may decline if ammonium nitrogen concentration exceeds 0.56 mg/L.[33] Uniform *V. spinulosa* seedlings from the nursery were selected and planted based on the predetermined coverage in each enclosure. Furthermore, to guarantee the applicability of this research to the Erhai Lake ecological restoration project, we have conducted a cross-reference of the biomass (3.7 ± 0.1 kg/m^2) of communities dominated by *V. spinulosa* at the corresponding water depth within the concurrent time frame. PVC boards (height: 30 cm, inserted 15 cm into the sediment) were set up at the boundary between the vegetated and unvegetated areas to prevent changes in coverage. Thereafter, water from Erhai Lake was added until all PVC boards were immersed by more than 30 cm and left for 1 week to guarantee complete and uniform water exchange within each enclosure. Following this, an external ammonia pulse was introduced, and the water level was reduced to 10 cm below the PVC boards, marking the establishment of each enclosure as an independent system and the official start of the experiment.

2.2. Ammonium Pulse Simulation and Sampling.

To investigate how submerged macrophytes with various coverage impacts the ability of aquatic ecosystems to mitigate ammonia influx and maintain ecological resilience, ammonium sulfate was introduced into enclosure systems to simulate external ammonia pulses. Before the simulation, water quality parameters were measured at 10 randomly chosen sites across the pond to assess the consistency of the conditions across all enclosures. After confirming the consistency of water quality in each enclosure, ammonium sulfate was added to simulate an NH_4−N pulse. Given that extreme precipitation can cause waterbody NH_4−N concentrations to surge several-fold,[13,58] with potentially even greater increases in agricultural areas,[4] and considering that the surface water-quality standard (GB3838−2002) in China specifies Class III water (with an NH_4−N concentration below 1.0 mg/L) as good quality while Class IV water (with NH_4−N between 1.0 and 1.5 mg/L) signifies poor quality,[59] we opted to spike the NH_4−N concentration to 1.24 mg/L (approximately the midpoint of Class IV water) in this study to simulate a strong NH_4−N pulse. Such concentrations occur in nature. For instance, the annual NH_4−N concentration of water in the Wuxi Port was 1.09−1.72 mg/L from 2010 to 2015.[60] The average concentrations of other water quality parameters before and after the ammonium pulse are detailed in Table S1. Finally, the water level of the entire pond was lowered to ensure that the PVC boards of all enclosures remained above the water, effectively isolating them from each other. The water depth was kept at 70 cm until the conclusion of the experiment.

https://doi.org/10.1021/acs.est.5c04237
Environ. Sci. Technol. XXXX, XXX, XXX−XXX

Throughout the study, water samples were gathered at various time intervals: 0 (on the same day as the ammonium pulse), 1, 2, 3, 4, 5, 6, and 7 days. Detailed methods for water sample collection and the determination of related water quality parameters are provided in the Supporting Information.

2.3. Calculation of Submerged Macrophytes and Aquatic Ecosystem Indicators.

Before and after the experiment, we assessed the changes in wet biomass per unit area of plants in each enclosure by quadrant sampling, collecting plants from a 0.2 m^2 area.[61] Two quadrants were randomly established in the plant area of each enclosure, and the average of the results represented the wet biomass per unit area of the corresponding enclosure's plants.[13] During the experimental phase, the relative growth rate (RGR) of submerged macrophytes in each enclosure system was calculated using the equation:

$$\mathrm{RGR} = {}^{(\mathrm{FB} - \mathrm{IB})}\Big/_{t}$$

where FB represents the final plant biomass per unit area, IB denotes the initial plant biomass per unit area, and t signifies the duration of the experiment in days.

To assess the buffering capacity of systems with varying SMC, we determined buffering capacity as the discrepancies in total nitrogen (TN), total dissolved nitrogen (TDN), total phosphorus (TP), total dissolved phosphorus (TDP), nitrate nitrogen (NO_3−N), ammonium nitrogen (NH_4−N), orthophosphate (PO_4−P), dissolved organic phosphorus (DOP), chlorophyll a (Chl-*a*), total suspended solids (TSS), turbidity, and light extinction coefficient (K) between enclosures with different SMCs and enclosures lacking plants.[13] We calculated the buffering capacity (BC) using the following formula:

$$\mathrm{BC} = {}^{(X_{\mathrm{control}} - X_{\mathrm{SMC}})}\Big/_{d}$$

where X represents TN, TDN, NH_4−N, TP, TDP, Chl-*a*, TSS, turbidity or K, X_{control} refers to the mean value of all replicates in treatments without plants, X_{SMC} denotes the mean value of all replicates in treatments with different coverages, and d represents the days.

In order to quantitatively evaluate the state of the lake ecosystem in the alternative stable state theory, we defined the ratio of the dry weight of submersed macrophytes to the dry weight of plankton algae as the conversion index (CI) based on the research of Bachmann et al.[62] and Lv et al.[13] We calculated the CI using the following formula:

$$\mathrm{CI} = {}^{\mathrm{DW}_{\mathrm{macrophytes}}}\Big/_{\mathrm{DW}_{\mathrm{plankton\ algae}}}$$

where $\mathrm{DW}_{\mathrm{macrophytes}}$ represents the dry weight of submerged macrophytes, $\mathrm{DW}_{\mathrm{plankton\ algae}}$ represents the dry weight of plankton algae. $\mathrm{DW}_{\mathrm{plankton\ algae}}$ was calculated by multiplying Chl-*a* values by 70, a factor that has been used in other studies.[63] The dry weight of the plants was determined by drying the collected plant samples to a constant weight, yielding the dry biomass per unit area. The total dry weight for each enclosure's plants was then calculated by multiplying this value by the corresponding plant area of the enclosure. The mean total dry weight of the plants before and after the experiment represented the $\mathrm{DW}_{\mathrm{macrophytes}}$. The conversion index divides all states of shallow lakes into three types, which are clear-water state, transition state, and turbid-water state. Clear-water states dominated by macrophytes were those where the conversion index was 100 or greater, transition states were those where the conversion indices were >1 and <100, and turbid-water states dominated by phytoplankton were those where the conversion index was 1 or less.

Based on the research of Xu et al.,[64] we calculated the resilience and recovery stability of various water quality parameters using the following formula:

$$\text{resilience stability} = -\ln(X_{\text{post-pulse}}/X_{\text{pulse}})$$

$$\text{recovery stability} = \ln(X_{\text{post-pulse}}/X_{\text{pre-pulse}})$$

where $X_{\text{pre-pulse}}$, X_{pulse}, and $X_{\text{post-pulse}}$ represents the values of water quality parameters in pre-pulse, pulse, and post-pulse, respectively (Figure S1). $X_{\text{post-pulse}}$ refers to the mean values of water quality parameters from days 1 to 7 post-ammonium addition, and X_{pulse} refers to these parameters measured immediately following ammonium addition, corresponding to the data on day 0. More positive values of resilience stability indicate a faster recovery from perturbations and thus greater resilience (0 = no resilience). More positive values of recovery stability indicate a larger deviation from the predisturbance state after recovery from a perturbation and thus lower recovery capacity.

2.4. Statistical Analysis.

In order to investigate the influence of submerged macrophytes coverage on water quality parameters, we utilized Mantel tests to measure the correlation patterns between water quality parameters and SMC,[65] based on significant Pearson correlation coefficients ($P < 0.05$). To compare water quality parameters across different coverage systems, we divided all enclosures into four coverage gradients based on SMC levels: control treatment (SMC = 0%), low coverage treatment (0% < SMC ≤ 30%), medium coverage treatment (30% < SMC ≤ 50%), and high coverage treatment (50% < SMC ≤ 100%). We then applied repeated measures analysis of variance (rANOVA) to determine differences in water quality parameters among the various coverage gradients.

The RGR was employed to evaluate the effect of ammonium stress on the submerged plant growth. The biomass per unit area was assessed prior to and after the experiment for the purpose of the RGR calculation. Subsequently, a linear regression analysis was performed to explore the correlation between the RGR and SMC.

The buffer capacity is an essential measure for evaluating the buffering ability of the system. We performed an assessment of the buffer capacity for each enclosure over a 7 day period after the pulse. Later, we used linear regression to explore the correlation between buffer capacity and coverage, thus obtaining an understanding of the fluctuating buffer capabilities of the system.

The magnitude of changes in some important parameters of a system when disturbed reflects its stability. Systems with high stability exhibit smaller changes in state when they are faced with disturbances. Therefore, we performed an assessment of the stability of water quality parameters for each enclosure over a 7 day period after the pulse. Then, we used linear regression to explore the correlation between the stability and coverage.

Structural equation modeling (SEM) was utilized to examine the direct and indirect effects of low, medium, and high SMC on water quality after the pulse event. The assessment included the computation of R^2, path coefficients, and model fit parameters using Amos 25.0 software created by Amos Development Corporation, Chicago, USA.

https://doi.org/10.1021/acs.est.5c04237
Environ. Sci. Technol. XXXX, XXX, XXX−XXX

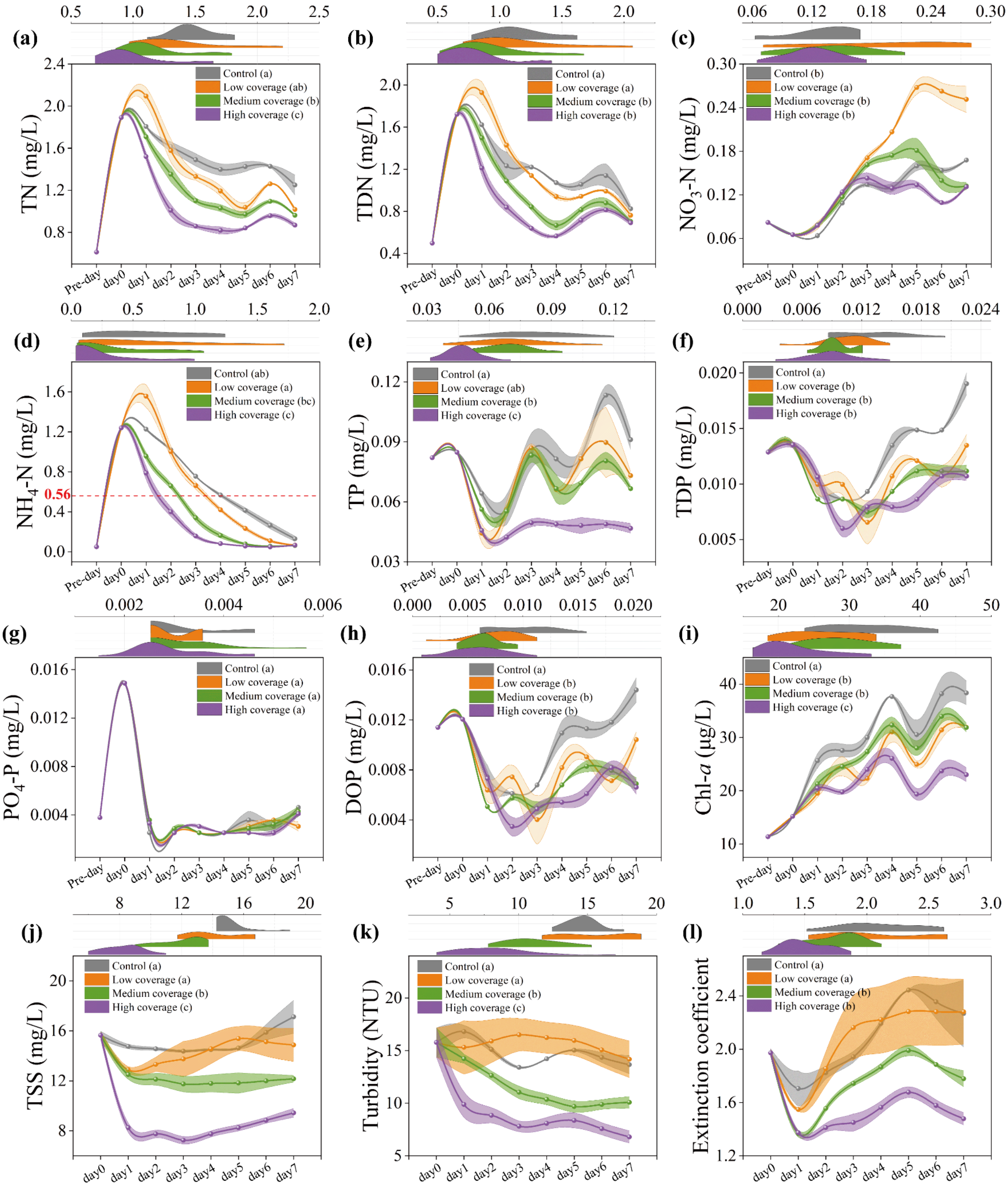


Figure 2. Temporal variations in water physicochemical parameters across experimental treatments. Ridgeline plots illustrate the distribution of these parameters across treatments during the experiment. The red dashed line in subfigure d represents the ammonium nitrogen toxicity threshold for the decline of *Vallisneria natans*.[33] Shading represents standard errors. Different lowercase letters in the legend indicate significant differences.

3. RESULTS

3.1. Effects of SMC on Water Physicochemical Parameters after Ammonium Pulse. As a whole, SMC strongly modulated water quality responses to NH_4−N pulse (Figure S2). During the experiment, SMC was significantly correlated with TN, TDN, TP, TDP, NH_4−N, DOP, Chl-*a*, TSS, turbidity, and the extinction coefficient. Chl-*a*, TSS, turbidity, and the extinction coefficient were significantly positively correlated with the phosphorus nutrients (TP, TDP, and DOP). Yet, Chl-*a* and NO_3−N were significantly negatively correlated with NH_4−N during the experiment (Figure S2).

Before the experiment, water quality parameters did not differ significantly among treatments. However, during the experiment, significant differences in these parameters emerged among different SMC treatments (Figure 2). During the experiment, the mean concentrations of TN, TDN, and NH_4−N in each treatment followed the order: high-coverage < medium-coverage < low-coverage < control (Figure 2a,b,d). Higher SMC (>50%) accelerated NH_4−N removal, restoring pre-pulse concentrations in approximately 96 h—2.3 times faster than controls (168 h; Figure 2d). High SMC increased TN by 41.7% post-pulse, contrasting sharply with controls (103.9% increase), while medium and low SMC showed intermediate effects (57.0 and 66.1% increase). TDN followed

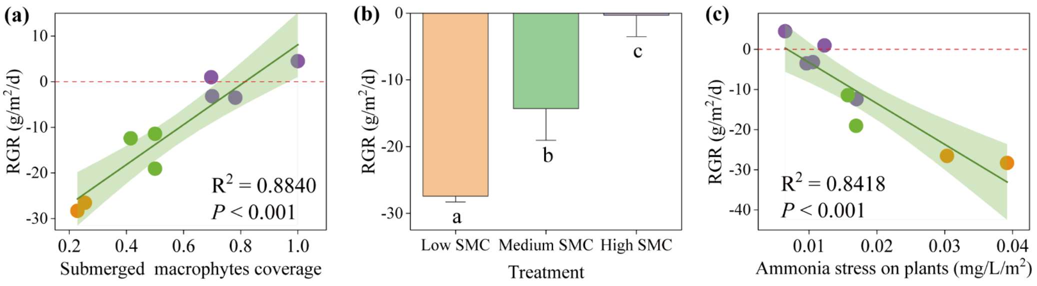


Figure 3. Relationships between relative growth rate (RGR) and coverage of submerged macrophytes, and the ammonium stress on plants. Green shading represents 95% point-wise confidence bands. Different lowercase letters indicate significant differences.

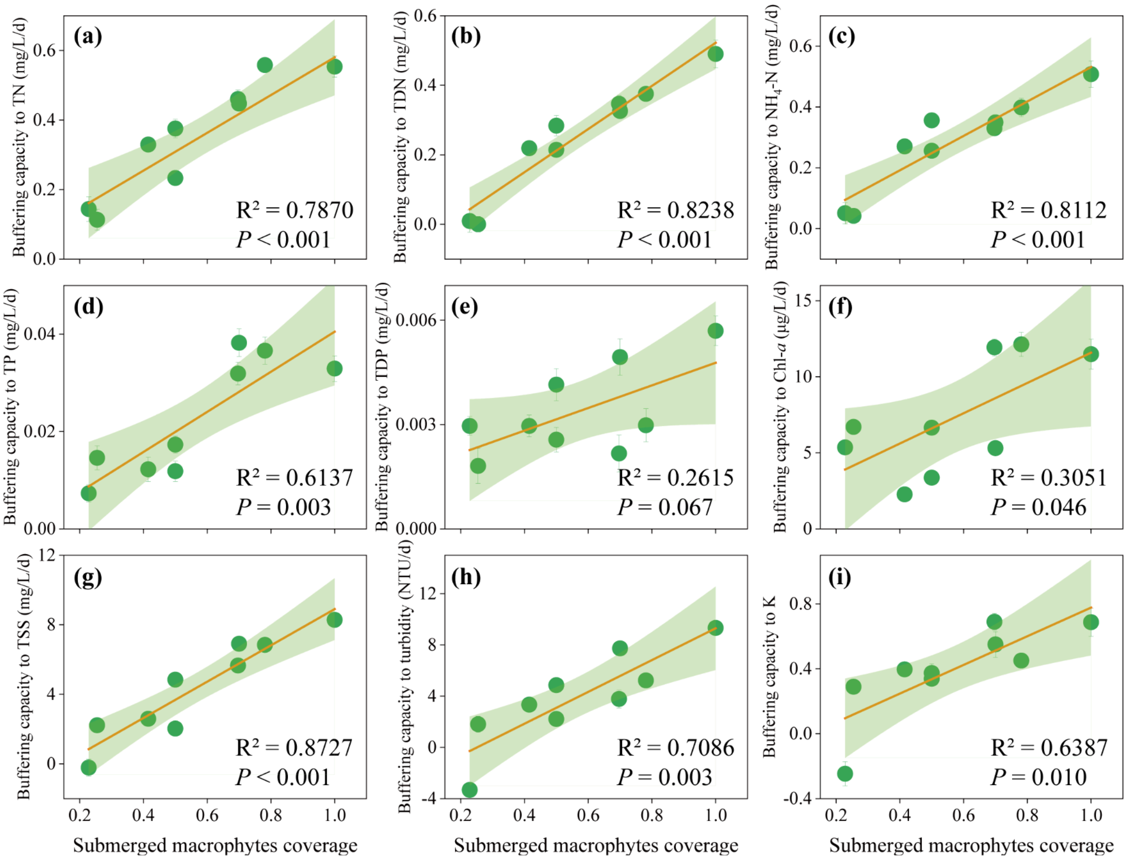


Figure 4. Correlation between the coverage of submerged macrophytes and their buffering capacity. Green shading represents 95% point-wise confidence bands.

similar trends, with no significant differences between medium and high SMC, but both showed significant decreases compared with control and low SMC, which did not differ significantly from each other. $NO_3{-}N$ showed a different pattern, with its accumulation peaking in low SMC treatments, being 1.4, 1.6, and 1.5 times higher than in medium SMC, high SMC, and controls, respectively ($P < 0.05$; Figure 2c), reflecting nitrification dominance. Additionally, the ridgeline plot showed that all nitrogen components peaked in low SMC treatments, reflecting the instability of low SMC (Figure 2a–d).

Phosphorus dynamics diverged from the nitrogen patterns. Compared to pre-pulse levels, TP decreased by 35.1 and 7.6% in the high and medium SMC, respectively, but increased by 1.4 and 26.4% in the low SMC and control, respectively (Figure 2e). During the experiment, TP was highest in the high SMC treatment and significantly higher in the medium SMC treatment than in the control, with no significant differences among other treatments (Figure 2e). TDP in the control treatment was significantly higher than that in other treatments, while there was no significant difference among the other treatments (Figure 2f). $PO_4{-}P$ levels remained low (<5 μg/L) across all treatments, with no significant differences among them (Figure 2g). The trends and differences in DOP among treatments were consistent with those of TDP. (Figure 2h).

Chl-*a* responses highlighted SMC-driven phytoplankton suppression: controls surged by 237.4% versus 102.5% in high SMC ($P < 0.05$; Figure 2i). Medium and low SMC treatments exhibited intermediate increases (180.2 and 180.7%). Physical parameters further underscored SMC benefits—high coverage reduced TSS (47.5%), turbidity (48.1%), and light extinction (K; 23.7%) versus initial levels (Figure 2j–l), while medium SMC achieved moderate

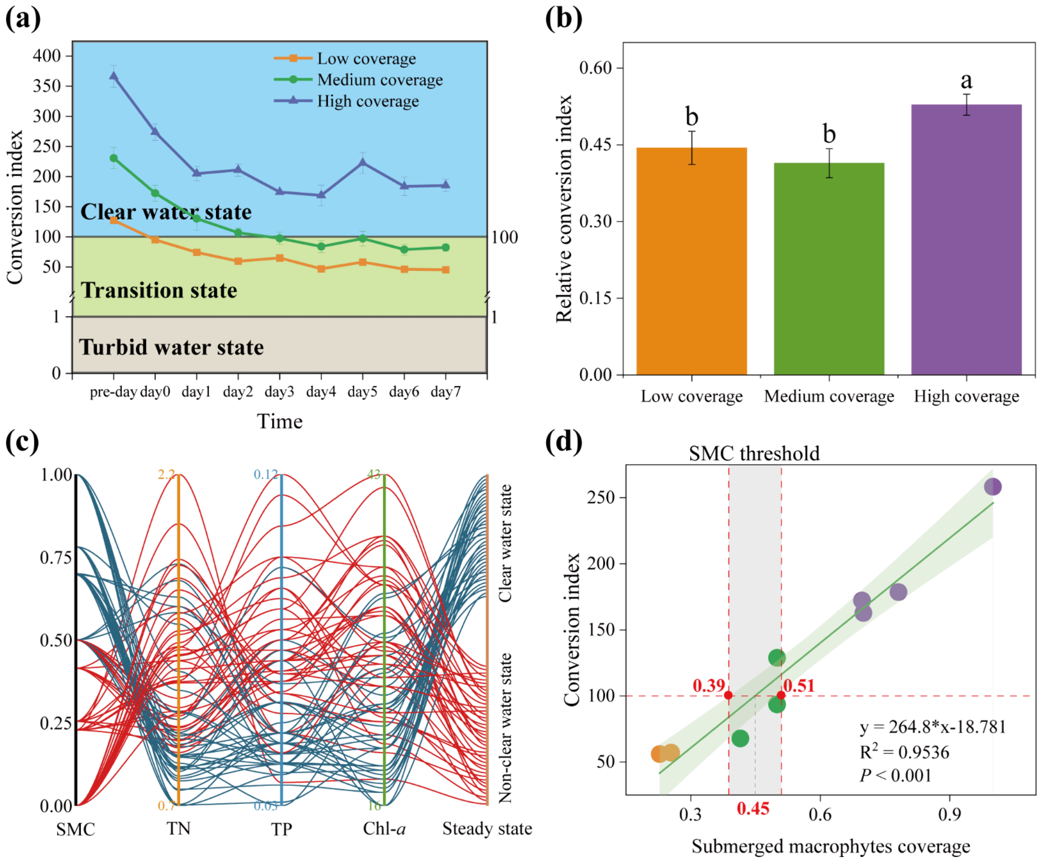


Figure 5. Comparison of conversion index among different coverage treatments during the experiment. (a) Changes in the conversion coefficients of low, medium, and high coverage treatments over time, (b) differences in the relative conversion coefficients of low, medium, and high coverage treatments, (c) parallel set diagram of the relationships among SMC, TN, TP, Chl-*a*, and steady-state during the experiment, (d) linear fitting of conversion coefficients with SMC. Relative conversion index: ratio of conversion index to initial conversion index. Different lowercase letters indicate significant differences. Green shading in subfigure c represents 95% point-wise confidence bands.

improvements (23.2% reductions in TSS; 29.5% reductions in turbidity; 11.7% reductions in K). In contrast, low SMC and the control treatment showed reductions of less than 9% in TSS and turbidity, and both led to an average increase of at least 5% in K (Figure 2j−l). Overall, TSS, turbidity, and K values were significantly lower in the high SMC treatment than in other treatments. The medium SMC treatment had significantly lower values than the low SMC and control treatments, which did not differ significantly from each other (Figure 2j−l).

3.2. Impact of Ammonium Stress on Submerged Macrophyte Growth. Ammonium stress significantly reduced submerged macrophyte biomass, but higher SMC mitigated these effects. Over 7 days, low SMC (≤30%) systems exhibited the steepest biomass decline (27.4 $g/m^2/day$), while medium (30−50%) and high SMC (>50%) showed progressively smaller losses (14.3 and 0.3 $g/m^2/day$, respectively; Figure 3b). Notably, the relative growth rate (RGR) of macrophytes with low/medium SMC was significantly lower compared to those with high SMC, and the RGR of submerged macrophytes with low SMC was significantly lower than that with medium SMC (Figure 3b). RGR was strongly correlated with SMC ($R^2 = 0.88$, $P < 0.001$; Figure 3a), indicating that denser stands diluted ammonium toxicity per unit biomass. This ″dilution effect″ was quantified via negative correlations between ammonium load per unit area and RGR ($R^2 = -0.84$, $P < 0.001$; Figure 3c). This underscores SMC as a key lever for enhancing the macrophyte resilience in pulse-disturbed ecosystems.

3.3. Buffering Capacity of Submerged Macrophytes. SMC exhibited dose-dependent enhancements in buffering capacity across the most water quality parameters ($P < 0.05$; Figure 4a−i). For instance, compared to the control treatment, the highest SMC enclosure (D4) buffered an additional 0.51 mg of NH_4−N/L/day, while B1 (plant coverage = 23%) buffered only an additional 0.05 mg of NH_4−N/L/day (Figure 4c). Despite having only 4 to 5 times the plant coverage of B1, D4 had about 10 times the NH_4−N buffering capacity. The results showed that the enclosure system's buffering capacity for TN, TDN, NH_4−N, TP, Chl-*a*, TSS, turbidity, and K was significantly positively correlated with SMC (Figure 4). Notably, B1 (the lowest coverage) exhibited negative buffering for TSS, turbidity, and K, with values exceeding those of enclosures without plants by 12−18% (Figure 4g−i).

The conversion index (CI) revealed stark contrasts in ecosystem stability: high SMC (>50%) maintained clear-water states (CI > 100) throughout the experiment, despite NH_4−N-induced CI declines (366 to 210; Figure 5a). However, medium and low SMC systems gradually transition to an algal-dominated state (CI < 100) after the pulse (Figure 5a). In high SMC systems, the relative CI was significantly higher than those in low and medium SMC systems, with no significant difference between low and medium SMC systems (Figure 5b). The parallel set diagram illustrated the distribution and

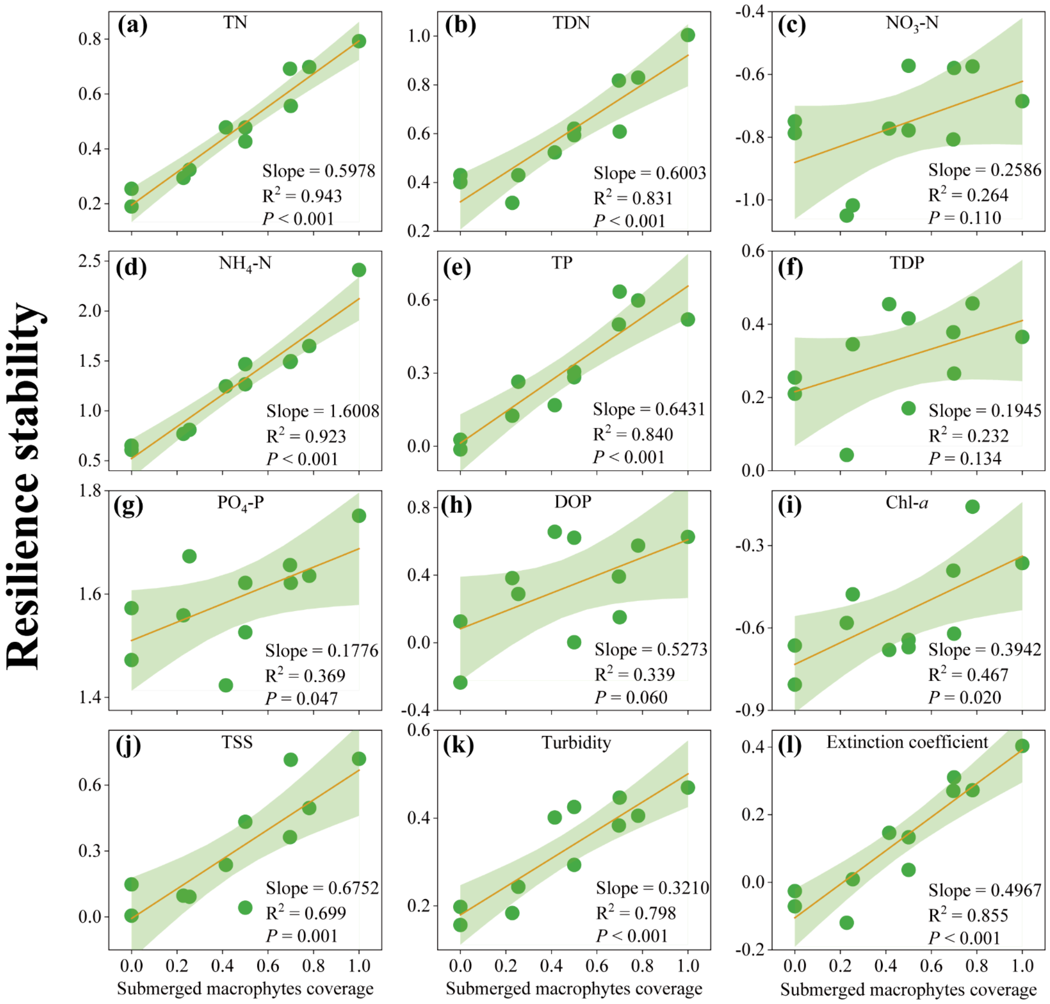


Figure 6. Effects of submerged macrophytes coverage on the resilience stability of various water quality parameters. Green shading represents 95% point-wise confidence bands.

trends of nutrients, Chl-*a*, and the conversion index in each enclosure. It revealed that the threshold of SMC for maintaining the clear-water state was between approximately 40 and 50% (Figure 5c). Logistic regression revealed a significant positive correlation between the conversion coefficient and the SMC (Figure 5d). Notably, the intersection of the boundary distinguishing clear-water from nonclear-water states (CI = 100) with the fitted line identified 45% SMC as the critical threshold (Figure 5d). Moreover, the 95% confidence interval further defined the threshold range as 39−51% (Figure 5d).

3.4. Influence of Submerged Macrophyte Coverage on System Stability. SMC exerted contrasting effects on two stability dimensions: resilience (resistance to perturbation) and recovery (return to predisturbance states). Resilience increased with SMC, while recovery stability decreased (Figures 6 and 7). TN resilience in high SMC was significantly higher than in others (1.5× higher than medium SMC, 2.2× higher than low SMC, and 3.1× higher than controls). TDN resilience followed a similar pattern, with high SMC treatments showing 1.4, 2.2, and 2.0× higher resilience than medium, low SMC, and controls, respectively (Figure 6 and Figure S3). Conversely, NO_3-N resilience was negative across all treatments, with low SMC showing significantly lower resilience than other treatments (Figure S3). NH_4-N resilience in high SMC was significantly higher than that in low SMC and controls, with increases of 25.3, 110.6, and 179.7% in low, medium, and high SMC treatments, respectively, compared to controls (Figure 6 and Figure S3). High SMC treatments showed significantly higher resilience for TP (1.2, 1.9, and 78.3× higher than medium SMC, low SMC, and controls, respectively; Figure 6 and Figure S3), but no significant differences were observed for TDP, PO_4-P, and DOP resilience among treatments. After the NH_4-N pulse, Chl-*a* concentrations increased across all treatments (Figure 2), resulting in negative resilience values. Despite this, a high SMC had at least 27.6% higher Chl-*a* resilience than other treatments (Figure 6 and Figure S3). Similarly, high SMC exhibited higher resilience for TSS, turbidity, and K (Figure S3).

TN recovery stability was highest in the controls, decreasing by 13.1, 28.8, and 49.0% in low, medium, and high SMC, respectively (Figure 7 and Figure S4). TDN recovery stability in high SMC decreased significantly by 27.1% vs medium SMC, 42.3% vs low SMC, and 39.8% vs controls, with no significant differences among medium, low SMC, and controls (Figure 7 and Figure S4). NO_3-N recovery stability was highest in low SMC, with no significant differences among other treatments. NH_4-N recovery stability followed a similar pattern to that of TN, decreasing by 6.0, 27.8, and 42.2% in low, medium, and high SMC, respectively. TP recovery

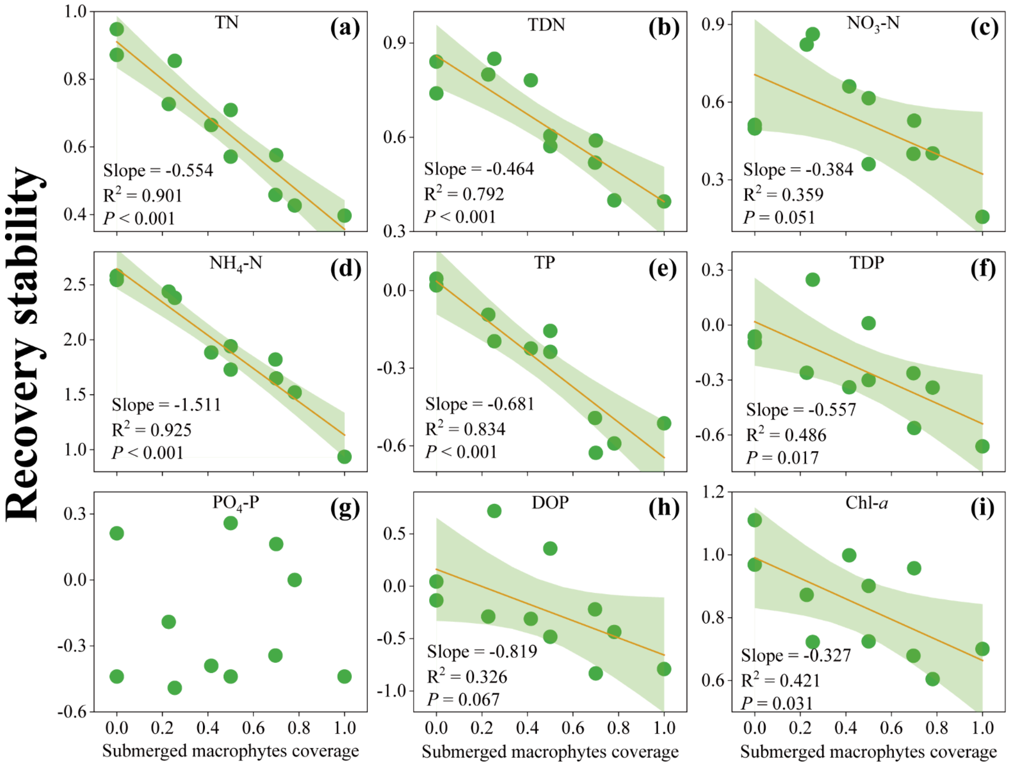


Figure 7. Effects of submerged macrophytes coverage on the recovery stability of various water quality parameters. Green shading represents 95% point-wise confidence bands.

stability decreased significantly in all SMC treatments compared to controls (536.4, 720.8, and 1778.5% in low, medium, and high SMC, respectively). TDP recovery stability differed significantly only between high and low SMC treatments, while no significant differences were observed for PO_4−P and DOP. In addition, Chl-*a* recovery stability decreased significantly by 29.3% in high SMC compared to controls, with nonsignificant decreases of 15.9 and 23.3% in low and medium SMC, respectively (Figure 7 and Figure S4).

3.5. Differences in NH_4−N Pulse Responses among Various Cover Systems.

Structural equation modeling (SEM) elucidated divergent NH_4−N pulse responses across SMC gradients, revealing three interconnected mechanisms (SRMR < 0.08, CFI > 0.90; Figure 8). First, SMC universally suppressed phytoplankton biomass (path coefficient = −0.56 to −0.81, $P < 0.01$), yet phytoplankton proliferation elevated light extinction coefficients (path coefficient = 0.54−0.83, $P < 0.001$). Second, NH_4−N removal exhibited coverage dependency: low SMC (≤30%) showed an insignificant removal (path coefficient = 0.06; $P > 0.05$), while medium (30−50%) and high SMC (>50%) achieved 0.27 and 0.29 mg/L/day removal, respectively (path coefficient = 0.64−0.70; $P < 0.001$). Crucially, enhanced NH_4−N removal under medium/low SMC promoted phytoplankton growth (path coefficient = 0.61/0.51, $P < 0.05$), whereas high SMC decoupled this relationship ($P > 0.05$). Third, SMC differentially modulated light regimes—low coverage systems increased extinction coefficients (path coefficient = 0.49, $P < 0.05$), likely via macrophyte decay under NH_4−N stress, while medium/high coverage stabilized light through particulate reduction (path coefficient = −0.31/−0.43, $P < 0.05$). These pathways highlight SMC thresholds governing trade-offs between nutrient removal and ecosystem stability.

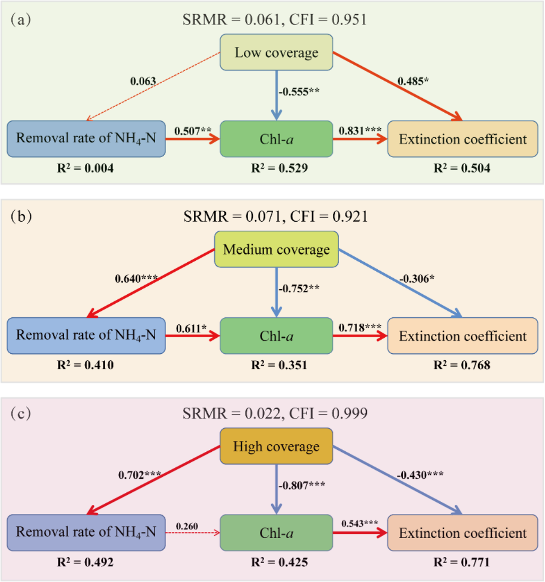


Figure 8. Structural equation model (SEM) showing the effects of submerged macrophytes on NH_4−N removal rate, Chl-*a*, and extinction coefficient, as well as their interactions, under low coverage (a), medium coverage (b), and high coverage (c). Numbers adjacent to the arrows are standardized path coefficients (*$P < 0.05$,**$P < 0.01$,***$P < 0.001$). Significant positive and negative effects and insignificant interactions among variables are depicted in red and blue solid and dashed arrows, respectively. The proportion of variance explained (R^2) is shown below each response variable in the model.

4. DISCUSSION

SMC is a linchpin for maintaining ecological stability in shallow lakes,[52,66] particularly as climate change amplifies the

https://doi.org/10.1021/acs.est.5c04237
Environ. Sci. Technol. XXXX, XXX, XXX−XXX

frequency and intensity of nutrient pulses.[13] Our study quantifies a critical threshold of 39−51% SMC to buffer NH_4−N pulses and prevent regime shifts—a finding that bridges theoretical ecology and practical lake management.

In this study, high SMC systems achieved rapid NH_4−N removal (0.29 mg/L/day), completing recovery within about 4 days—1.73 times faster than the controls (which did not recover to the initial state even after 7 days)—while suppressing phytoplankton blooms (Chl-*a* increase: 102.5% vs 237.4% in controls). These outcomes arise from three synergistic mechanisms. First, high coverage (biomass) shows a superior NH_4−N removal capacity. After an NH_4−N pulse, plants directly absorb NH_4−N,[21,67,68] and nitrate (NO_3−N) levels rise, indicating enhanced nitrification. However, the abundant submerged macrophytes promote rhizosphere denitrification, accelerating nitrogen cycling and improving nitrogen removal.[69] Second, high biomass dilutes NH_4−N toxicity, reducing exposure durations above the 0.56 mg/L threshold for *V. natans* mortality[33] from 4 days (the controls) to less than 2 days. Third, high SMC stabilizes light regimes by reducing suspended solids (TSS: −39.7%) and turbidity (−56.9%), which suppresses phytoplankton through nutrient competition and enhanced zooplankton grazing.[45,63,70] These mechanisms form a self-reinforcing loop where nutrient removal and light availability sustain macrophyte dominance—a feedback absent in low-coverage systems. Therefore, lakes with abundant submerged macrophytes typically have low nutrient levels, low algae density, and high transparency,[54,71] while those with insufficient submerged macrophytes are often characterized by high nutrient levels, high algal density, and low transparency.[72,73]

Furthermore, low SMC (≤30%) systems exhibited paradoxical degradation, with NH_4−N concentrations exceeding toxicity thresholds (0.56 mg/L)[33] for more than 3 days after the pulse (Figure 2d). This triggered a stress cascade: prolonged NH_4−N exposure induced macrophyte decay (27.4 g/m^2/day biomass loss—nearly 90× higher than high SMC),[74,75] releasing nutrients and elevating suspended solids (TSS + 18% vs controls).[76−78] Concurrently, sediment resuspension from reduced root stabilization increased turbidity,[54] favoring phytoplankton that thrived on residual NH_4−N.[24,79] Structural equation modeling quantified these dynamics, revealing that low SMC amplified phytoplankton responses to NH_4−N (path coefficient = 0.51, $P < 0.05$), while high SMC decoupled this relationship (path coefficient = 0.26, $P > 0.05$). Remarkably, sometimes low-coverage systems even surpassed controls in TN, NH_4−N, TSS, and turbidity—a counterintuitive finding challenging the assumption that minimal SMC is preferable to none. This aligns with observations in eutrophic lakes where partial macrophyte loss may accelerate eutrophication through similar feedbacks.[20,54,80] Therefore, understanding feedback loops' role in ecosystem stability and instability is crucial for lake management;[81] otherwise, improvement efforts may fail.[82]

Nevertheless, it should be emphasized that in some aspects, low SMC still outperforms the no-plant condition. For instance, low SMC still resulted in some phytoplankton bloom suppression and nutrient removal relative to the control (Figures 2 and 8). We posit that whether low SMC is better than the no-plant condition hinges on the plants' ability to adapt to such pulse events and maintain stability. If the plants fail to adapt, as evidenced by their remarkable negative growth trend under low SMC in this study (Figure 3), and considering that such pulse events may become more frequent in the future,[7] the degradation of plants under low SMC would be further aggravated.[13] Such degradation could trigger secondary pollution,[83] leading to the paradoxical conclusion that low SMC might be worse than the no-plant condition. Conversely, if the plants can adapt, then a low SMC will be superior to the no-plant condition. As depicted in Figure 8a, under NH_4−N pulses, compared to the control treatment, low SMC could both suppress algal growth, which was beneficial to the system, and worsen the underwater light conditions, thereby being unfavorable to the system.

Another notable phenomenon was that following the NH_4−N pulse, the NO_3−N levels rose in all treatments. Notably, the low-coverage treatment showed the highest NO_3−N levels during the experiment, while the medium-coverage, high-coverage, and control treatments had similar average concentrations. This might be attributed to the combined effects of several mechanisms: First, nitrification was stimulated by high NH_4−N concentrations from the pulse but declines as NH_4−N levels drop. Second, submerged macrophytes can directly absorb NH_4−N and NO_3−N, with preferential absorption of ammonium nitrogen.[68,84] Third, these plants enhance nitrification by increasing water-column dissolved oxygen and offering more attachment sites for nitrifying bacteria with their complex structures.[85] In the low-coverage treatment, weaker NH_4−N and NO_3−N uptake meant high NH_4−N levels persisted (Figure 2d), prolonging nitrification stimulation, hence the high NO_3−N levels (Figure 2c). Along with the structural support that plants provide for nitrifying bacteria to boost nitrification,[85] the limited nutrient absorption due to insufficient vegetation and plants' preference for NH_4−N uptake caused the low-coverage treatment to have higher NO_3−N levels than the control. However, the medium- and high-coverage treatments had stronger nutrient-absorption abilities. They rapidly reduced NH_4−N concentrations (Figure 2d), lessening high NH_4−N-driven nitrification stimulation and thereby stabilizing NO_3−N levels faster (Figure 2c). Despite also promoting nitrification through their structures, their strong nutrient-absorption capacity may offset this effect, leading to no significant difference in the NO_3−N levels between these treatments and the control.

The above discussion confirmed that macrophytes with high coverage contribute to improved water quality, thereby mitigating the impact of nutrient pulses.[13] Moreover, the buffering capacity and resilience were further strengthened as the SMC increased (Figures 4 and 8). These tight relationships largely dictate the direction of regime shifts in aquatic ecosystems: high SMC endows aquatic ecosystems with greater resilience, enabling a swift return to a clear water state postdisturbance.[86,87] In contrast, in plant-sparse systems, resource pulses may facilitate exponential algal population growth, which can overwhelm top-down control and cause dramatic ecosystem shifts.[88,89] Moreover, other impacts of pulsed-events, such as the high NH_4−N induced plant stress observed in this study, may further exacerbate the system's shift toward a phytoplankton-dominated turbid water state. Underpinning these differences in resilience and buffering capacity may be chiefly attributed to the stability of plant communities under disturbance. In nature lakes, plant communities with high coverage (biomass), typically characterized by complex structures and strong ecological functions, possess high species diversity and functional redundancy.[63,90,91] This complexity and redundancy allow the plant community to maintain overall functional stability through interspecific interactions and compensatory effects when facing environmental changes.[92,93]

Additionally, it is worth noting that although many studies have explored the relationship between environmental variables and SMC,[86,94,39] research on quantifying the coverage threshold of submerged macrophytes is relatively limited and yields significantly varied results.[51,52] For instance, Dai et al.[51] identified 20% *Ceratophyllum demersum* coverage as optimal for restoring eutrophic water bodies, while Zhang et al.[52] found 50% to be best. Both agreed that exceeding the threshold did not further improve water quality, differing from our study's view that higher coverage leads to better water quality. The differences in experimental scales and climatic conditions could be the reason for the divergent conclusions. More importantly, the external disturbance—the NH_4−N pulse simulated in this study—was an important factor not considered in the two aforementioned studies. Also, the SEM results revealed that medium SMC (30−50%) significantly promoted NH_4−N removal like high SMC, yet it could not effectively decouple the relationship between nutrients and algae and maintain a stable clear-water state as high SMC did (Figure 8). Its conversion index fluctuated around 100 (the critical value for a clear-water state). Further analysis identified 45% as the SMC threshold for effectively mitigating NH_4−N pulses, with a 95% confidence interval of 39%−51% (Figure 5d), consistent with our prior nutrient-pulse experiments.[13] Interestingly, this parallels findings in terrestrial ecosystems, where Arroyo-Rodríguez et al. indicated that at least 40% forest cover is needed to sustain ecosystem services and biodiversity across appropriately sized landscapes,[95] and Macchi et al. also emphasized the importance of maintaining woody cover levels above about 40%.[96] Based on ecological threshold theory, evaluating an ecosystem's resource and environmental carrying capacity enables effective management and safety monitoring, ensuring early restoration or repair before irreversible changes happen.[97,98] The convergence of thresholds at around 40% in both aquatic and terrestrial systems implies that maintaining vegetation cover at this level is crucial for ecosystem stability.

However, critical knowledge gaps remain. Although our 7 day experiment elucidated the acute response to a single NH_4−N pulse, the long-term effects of repeated pulses remain unquantified. Theory suggests that resource pulses may induce stability or disrupt the stability of food webs, depending on the pulse amplitude and/or frequency,[13,99] and may be an important driving factor for the system to move between different stable states,[88,89,100] so pulse intensity and frequency may greatly alter the results. For instance, under weak nutrient pulses, low-SMC treatments in our study might maintain a stable clear-water state by promptly reducing nutrients and curbing algae. But climate change is increasing the frequency of such pulse events.[2,7] We speculate that if multiple high-intensity nutrient pulses occur in a short period, the system may be unable to recover to its initial state before the next pulse. In other words, the system's self-purification capacity would be surpassed. The accumulation of nutrients, particularly NH_4−N, could lead to the progressive dominance of algae and sustained NH_4−N stress, thereby aggravating the risk of a regime shift. However, it should be pointed out that plant adaptability[11] and the role of microbial communities also need to be taken into account. Trait-based differences among macrophyte species (e.g., canopy-forming *Myriophyllum spicatum* vs rosette *Vallisneria* sp.) in pulse resilience, and the link between submerged macrophytes community composition/functional diversity and ecosystem stability, deserve in-depth exploration. Additionally, high-concentration NH_4−N can be highly toxic to aquatic animals,[101] even causing mass fish mortality. The decomposition of dead fish may trigger a new resource-pulse event,[14] which deserves attention. Addressing these gaps will refine restoration protocols and enhance predictive capacity in a changing climate.

In conclusion, this study redefines SMC not merely as an ecological asset but also as a quantifiable safeguard against climate-driven instability. The proliferation of algae and the intensification of high NH_4−N stress may increase the risk of regime shifts in systems with insufficient SMC against the backdrop of climate change-induced frequent nutrient pulse events. By anchoring lake restoration in empirically derived SMC thresholds (39−51%), we provide a reference for achieving water security (SDG 6) in an era of escalating disturbances. This work underscores the urgency of translating ecological resilience into actionable preservation—a vital step toward climate-adaptive freshwater stewardship.

■ ASSOCIATED CONTENT

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.est.5c04237.

Additional experimental details, methods, and results, including four figures and one table (PDF)

■ AUTHOR INFORMATION

Corresponding Authors

Qingchuan Chou − *Erhai Plateau lake ecosystem research station, Institute of Hydrobiology and State Key Laboratory of Breeding Biotechnology and Sustainable Aquaculture, Institute of Hydrobiology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China*; Email: chouqc@ihb.ac.cn

Te Cao − *Erhai Plateau lake ecosystem research station, Institute of Hydrobiology and State Key Laboratory of Breeding Biotechnology and Sustainable Aquaculture, Institute of Hydrobiology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China*; Email: caote@ihb.ac.cn

Authors

Chaochao Lv − *Erhai Plateau lake ecosystem research station, Institute of Hydrobiology and State Key Laboratory of Breeding Biotechnology and Sustainable Aquaculture, Institute of Hydrobiology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China*; orcid.org/0000-0002-3275-155X

Lei Shi − *Erhai Plateau lake ecosystem research station, Institute of Hydrobiology and State Key Laboratory of Breeding Biotechnology and Sustainable Aquaculture, Institute of Hydrobiology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China; University of Chinese Academy of Sciences, Beijing 100049, China*

Yuqing Tian − *Faculty of Resources and Environmental Science, Hubei University, Wuhan 430062, China*

Hang Shan − *College of Life Sciences, Zhejiang University, Hangzhou 310050, China*

Wei Liu − *State Environmental Protection Key Laboratory of Drinking Water Source Management and Technology,* *Shenzhen Research Academy of Environmental Sciences, Shenzhen 518001, China*

Kuanyi Li − *State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, Nanjing 210008, China*

Complete contact information is available at: https://pubs.acs.org/10.1021/acs.est.5c04237

Author Contributions

T.C., K.L., and W.L. planned and designed the research. C.L., L.S., H.S., and Y.T. performed the experiment. C.L. analyzed data and wrote the manuscript. C.L. and Q.C. revised the manuscript and gave important and critical input. All authors revised and approved the final manuscript

Notes

The authors declare no competing financial interest.

■ ACKNOWLEDGMENTS

This work was supported by the National Natural Science Foundation of China (32330068 and 32101319).

■ REFERENCES

(1) IPCC *AR6 Synthesis Report: Climate Change 2023*. 2023.

(2) Ockenden, M. C.; Hollaway, M. J.; Beven, K. J.; Collins, A. L.; Evans, R.; Falloon, P. D.; Forber, K. J.; Hiscock, K. M.; Kahana, R.; Macleod, C. J. A.; Tych, W.; Villamizar, M. L.; Wearing, C.; Withers, P. J. A.; Zhou, J. G.; Barker, P. A.; Burke, S.; Freer, J. E.; Johnes, P. J.; Snell, M. A.; Surridge, B. W. J.; Haygarth, P. M. Major agricultural changes required to mitigate phosphorus losses under climate change. *Nat. Commun.* **2017**, *8* (1), 161.

(3) Chang, D.; Li, S.; Lai, Z. Effects of extreme precipitation intensity and duration on the runoff and nutrient yields. *Journal of Hydrology* **2023**, *626*, No. 130281.

(4) Guo, H. Y.; Zhu, J. G.; Wang, X. R.; Wu, Z. H.; Zhang, Z. Case Study on Nitrogen and Phosphorus Emissions from Paddy Field in Taihu Region. *Environmental Geochemistry and Health* **2004**, *26* (2), 209−219.

(5) Heathwaite, A. L. Multiple stressors on water availability at global to catchment scales: understanding human impact on nutrient cycles to protect water quality and water availability in the long term. *Freshwater Biology* **2010**, *55* (s1), 241−257.

(6) Reidsma, P.; Feng, S.; van Loon, M.; Luo, X.; Kang, C.; Lubbers, M.; Kanellopoulos, A.; Wolf, J.; van Ittersum, M. K.; Qu, F. Integrated assessment of agricultural land use policies on nutrient pollution and sustainable development in Taihu Basin, China. *Environmental Science & Policy* **2012**, *18*, 66−76.

(7) Ockenden, M. C.; Deasy, C. E.; Benskin, C. M. W.; Beven, K. J.; Burke, S.; Collins, A. L.; Evans, R.; Falloon, P. D.; Forber, K. J.; Hiscock, K. M.; Hollaway, M. J.; Kahana, R.; Macleod, C. J. A.; Reaney, S. M.; Snell, M. A.; Villamizar, M. L.; Wearing, C.; Withers, P. J. A.; Zhou, J. G.; Haygarth, P. M. Changing climate and nutrient transfers: evidence from high temporal resolution concentration-flow dynamics in headwater catchments. *Sci. Total Environ.* **2016**, *548*−*549*, 325−339.

(8) Inglima, I.; Alberti, G.; Bertolini, T.; Vaccari, F. P.; Gioli, B.; Miglietta, F.; Cotrufo, M. F.; Peressotti, A. Precipitation pulses enhance respiration of Mediterranean ecosystems: the balance between organic and inorganic components of increased soil CO2 efflux. *Global change biology* **2009**, *15* (5), 1289−1301.

(9) Miller, T. E.; Buhler, M. L.; Cuellar-Gempeler, C. Species-specific differences determine responses to a resource pulse and predation. *Oecologia* **2019**, *190* (1), 169−178.

(10) Tao, Z.; Shen, C.; Qin, W.; Gui, Y.; Wang, Y.; Siemann, E.; Huang, W. Magnitude and timing of resource pulses interact to affect plant invasion. *Oikos* **2021**, *130* (11), 1967−1975.

(11) Yuan, G.; Tan, X.; Guo, P.; Xing, K.; Chen, Z.; Li, D.; Yu, S.; Peng, H.; Li, W.; Fu, H.; Jeppesen, E. Linking trait network to growth performance of submerged macrophytes in response to ammonium pulse. *Water Res.* **2023**, *229*, No. 119403.

(12) Nowlin, W. H.; Vanni, M. J.; Yang, L. H. Comparing resource pulses in aquatic and terrestrial ecosystems. *Ecology* **2008**, *89*, 647−659.

(13) Lv, C.; Tian, Y.; Huang, L.; Shan, H.; Chou, Q.; Zhang, W.; Su, H.; Li, K.; Zhang, X.; Ni, L.; Cao, T.; Jeppesen, E. Buffering capacity of submerged macrophytes against nutrient pulses increase with its coverage in shallow lakes. *Chemosphere* **2023**, *332*, No. 138899.

(14) Weber, M. J.; Brown, M. L. Effects of resource pulses on nutrient availability, ecosystem productivity, and temporal variability following a stochastic disturbance in eutrophic glacial lakes. *Hydrobiologia* **2016**, *771* (1), 165−177.

(15) Van Meerbeek, K.; Jucker, T.; Svenning, J.-C. Unifying the concepts of stability and resilience in ecology. *Journal of Ecology* **2021**, *109* (9), 3114−3132.

(16) Zhao, Y.; Wang, R.; Zhang, E.; Guan, B.; Xu, M. Aquatic ecosystem responds differently to press and pulse nutrient disturbances as revealed by a microcosm experiment. *Ecology and Evolution* **2022**, *12* (10), No. e9438.

(17) Yang, L. H.; Bastow, J. L.; Spence, K. O.; Wright, A. N. What can we learn from resource pulses? *Ecology* **2008**, *89*, 621−634.

(18) Schindler, D. W.; Hecky, R. E.; Findlay, D. L.; Stainton, M. P.; Parker, B. R.; Paterson, M. J.; Beaty, K. G.; Lyng, M.; Kasian, S. E. M. Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37-year whole-ecosystem experiment. *Proc. Natl. Acad. Sci. U. S. A.* **2008**, *105* (32), 11254−11258.

(19) Scott, J. T.; McCarthy, M. J. Nitrogen fixation may not balance the nitrogen pool in lakes over timescales relevant to eutrophication management. *Limnology and Oceanography* **2010**, *55* (3), 1265−1270.

(20) Jeppesen, E.; He, H.; Søndergaard, M.; Lauridsen, T. L.; Davidson, T. A.; Levi, E. E.; McCarthy, M. J. Experimental evidence of the role of nitrogen for eutrophication in shallow lakes: A long-term climate effect mesocosm study. *Innovation* **2025**, *6* (4), No. 100756.

(21) Søndergaard, M.; Lauridsen, T. L.; Johansson, L. S.; Jeppesen, E. Nitrogen or phosphorus limitation in lakes and its impact on phytoplankton biomass and submerged macrophyte cover. *Hydrobiologia* **2017**, *795* (1), 35−48.

(22) Qin, B.; Zhou, J.; Elser, J. J.; Gardner, W. S.; Deng, J.; Brookes, J. D. Water Depth Underpins the Relative Roles and Fates of Nitrogen and Phosphorus in Lakes. *Environ. Sci. Technol.* **2020**, *54* (6), 3191−3198.

(23) Xu, H.; McCarthy, M. J.; Paerl, H. W.; Brookes, J. D.; Zhu, G.; Hall, N. S.; Qin, B.; Zhang, Y.; Zhu, M.; Hampel, J. J.; Newell, S. E.; Gardner, W. S. Contributions of external nutrient loading and internal cycling to cyanobacterial bloom dynamics in Lake Taihu, China: Implications for nutrient management. *Limnology and Oceanography* **2021**, *66* (4), 1492−1509.

(24) Dugdale, R. C.; Wilkerson, F. P.; Hogue, V. E.; Marchi, A. The role of ammonium and nitrate in spring bloom development in san francisco bay. *Estuarine Coastal & Shelf Science* **2007**, *73* (1−2), 17−29.

(25) Zhu, Z.; Yuan, H.; Wei, Y.; Li, P.; Zhang, P.; Xie, D. Effects of Ammonia Nitrogen and Sediment Nutrient on Growth of the Submerged Plant *Vallisneria natans*. *CLEAN-Soil, Air, Water* **2015**, *43* (12), 1653−1659.

(26) Zeng, Q.; Qin, L.; Bao, L.; Li, Y.; Li, X. Critical nutrient thresholds needed to control eutrophication and synergistic interactions between phosphorus and different nitrogen sources. *Environmental Science and Pollution Research* **2016**, *23* (20), 21008−21019.

(27) Domingues, R. B.; Barbosa, A. B.; Sommer, U.; Galvão, H. M. Ammonium, nitrate and phytoplankton interactions in a freshwater tidal estuarine zone: potential effects of cultural eutrophication. *Aquatic Sciences* **2011**, *73* (3), 331−343.

(28) Zhao, M.; Yao, D.; Li, S.; Zhang, Y.; Aweya, J. J. Effects of ammonia on shrimp physiology and immunity: a review. *Reviews in Aquaculture* **2020**, *12* (4), 2194−2211.

(29) Lin, W.; Luo, H.; Wu, J.; Hung, T.-C.; Cao, B.; Liu, X.; Yang, J.; Yang, P. A Review of the Emerging Risks of Acute Ammonia Nitrogen Toxicity to Aquatic Decapod Crustaceans. *Water* **2023**, *15* (1), 27.

(30) Yuan, G.; Fu, H.; Zhong, J.; Cao, T.; Ni, L.; Zhu, T.; Li, W.; Song, X. Nitrogen/carbon metabolism in response to NH4+ pulse for two submersed macrophytes. *Aquatic Botany* **2015**, *121*, 76−82.

(31) Ma, S. N.; Wang, H. J.; Wang, H. Z.; Li, Y.; Liu, M.; Liang, X. M.; Yu, Q.; Jeppesen, E.; Søndergaard, M. High ammonium loading can increase alkaline phosphatase activity and promote sediment phosphorus release: a two-month mesocosm experiment. *Water Res.* **2018**, *145*, 388−397.

(32) The Anhui Provincial Ecological and Environmental Department of China *Anhui Ecological Environment Protection Inspection Case Four: Ineffective and Lingering Water Environment Treatment of GuXiang River in Quanjiao*. 2023, (in Chinese).

(33) Cao, T.; Xie, P.; ni, L.; Wu, A.-p.; Zhang, M.; Wu, S.; Smolders, A. The role of NH_4^+ toxicity in the decline of the submersed macrophyte Vallisneria natans in lakes of the Yangtze River basin, China. *Marine and Freshwater Research* **2007**, *58*, 581−587.

(34) Yu, Q.; Wang, H.; Wang, H.; Xu, C.; Liu, M.; Ma, Y.; Li, Y.; Ma, S.; Hamilton, D. P.; Jeppesen, E. Effects of High Ammonium Loading on Two Submersed Macrophytes of Different Growth Form Based on an 18-Month Pond Experiment. *Front. Plant Sci.* **2022**, *13*, No. 939589.

(35) Scheffer, M.; Carpenter, S. R. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology and Evolution* **2003**, *18*, 648−656.

(36) Scheffer, M. Multiplicity of stable states in freshwater systems. *Hydrobiologia* **1990**, *200-201*, 475−486.

(37) Bal, K.; Struyf, E.; Vereecken, H.; Viaene, P.; Doncker, L. D.; Deckere, E. D.; Mostaert, F.; Meire, P. How do macrophyte distribution patterns affect hydraulic resistances? *Ecol. Eng.* **2011**, *37* (3), 529−533.

(38) Bornette, G.; Puijalon, S. Response of aquatic plants to abiotic factors: a review. *Aquatic Sciences* **2011**, *73* (1), 1−14.

(39) Dhote, S.; Dixit, S. Water quality improvement through macrophytes-a review. *Environmental Monitoring and Assessment* **2009**, *152* (1−4), 149−153.

(40) Cao, T. E.; Ni, L.; Xie, P.; Xu, J. U. N.; Zhang, M. Effects of moderate ammonium enrichment on three submersed macrophytes under contrasting light availability. *Freshwater Biology* **2011**, *56* (8), 1620−1629.

(41) Christiansen, N. H.; Andersen, F. Ø.; Jensen, H. S. Phosphate uptake kinetics for four species of submerged freshwater macrophytes measured by a ^{33}p phosphate radioisotope technique. *Aquatic Botany* **2016**, *128*, 58−67.

(42) Zeng, L.; He, F.; Dai, Z.; Xu, D.; Liu, B.; Zhou, Q.; Wu, Z. Effect of submerged macrophyte restoration on improving aquatic ecosystem in a subtropical, shallow lake. *Ecological Engineering* **2017**, *106*, 578−587.

(43) Chen, Z. Q.; Zhao, D.; Li, M. L.; Tu, W. G.; Luo, X. M.; Liu, X. A field study on the effects of combined biomanipulation on the water quality of a eutrophic lake. *Environ. Pollut.* **2020**, *265*, No. 115091.

(44) Kosten, S.; Kamarainen, A.; Jeppesen, E.; van Nes, E. H.; Peeters, E. T. H. M.; Mazzeo, N.; Hauxwell, J.; Hansel-Welch, N.; Lauridsen, T. L.; Søndergaard, M.; Bachmann, R. W.; Lacerot, G.; Scheffer, M. Climate-related differences in the dominance of submerged macrophytes in shallow lakes. *Global Change Biol.* **2009**, *15* (10), 2503−2517.

(45) Vanderstukken, M.; Mazzeo, N.; Van Colen, W.; Declerck, S.; Muylaert, K. Biological control of phytoplankton by the subtropical submerged macrophytes *Egeria densa* and *Potamogeton illinoensis*: A mesocosm study. *Freshwater Biology* **2011**, *56*, 1837−1849.

(46) Jeppesen, E.; Søndergaard, M.; Søndergaard, M.; Christofferson, K. *The structuring role of submerged macrophytes in lakes*; Springer, 1998.

(47) Lauridsen, T. L.; Pedersen, L. J.; Jeppesen, E.; Søndergaard, M. J. The importance of macrophyte bed size for cladoceran composition and horizontal migration in a shallow lake. *J. Plankton Res.* **1996**, *18* (12), 2283−2294.

(48) Horppila, J.; Nurminen, L. Effects of submerged macrophytes on sediment resuspension and internal phosphorus loading in Lake Hiidenvesi (southern Finland). *Water Res.* **2003**, *37* (18), 4468−4474.

(49) Moss, B.; Jeppesen, E.; Søndergaard, M.; Lauridsen, T. L.; Liu, Z. W. Nitrogen, macrophytes, shallow lakes and nutrient limitation: resolution of a current controversy? *Hydrobiologia* **2013**, *710*, 3−21.

(50) Xu, X. G.; Zhou, Y. W.; Han, R. M.; Song, K.; Zhou, X. H.; Wang, G. X.; Wang, Q. L. Eutrophication triggers the shift of nutrient absorption pathway of submerged macrophytes: implications for the phytoremediation of eutrophic waters. *Journal of Environmental Management* **2019**, *239*, 376−384.

(51) Dai, Y.; Jia, C.; Liang, W.; Hu, S.; Wu, Z. Effects of the submerged macrophyte Ceratophyllum demersum L. on restoration of a eutrophic waterbody and its optimal coverage. *Ecological Engineering* **2012**, *40*, 113−116.

(52) Zhang, X.; Zhang, J.; Li, Z.; Wang, G.; Liu, Y.; Wang, H.; Xie, J. Optimal submerged macrophyte coverage for improving water quality in a temperate lake in China. *Ecological Engineering* **2021**, *162*, No. 106177.

(53) Ruggiero, A.; Solimini, A. G.; Carchini, G. Nutrient and chlorophyll *a* temporal patterns in eutrophic mountain ponds with contrasting macrophyte coverage. *Hydrobiologia* **2003**, *506−509* (1−3), 657−663.

(54) Søndergaard, M.; Johansson, L. S.; Lauridsen, T. L.; Jørgensen, T. B.; Liboriussen, L.; Jeppesen, E. Submerged macrophytes as indicators of the ecological quality of lakes. *Freshwater Biol.* **2010**, *55* (4), 893−908.

(55) Lv, C.; Shan, H.; Tian, Y.; Zhao, X.; Wen, Z.; Yin, C.; Li, Z.; Su, H.; Wang, W.; Chou, Q.; Li, K.; Zhang, X.; Cao, T. The dual role of benthic fish: Effects on water quality in the presence and absence of submerged macrophytes. *Water Res.* **2024**, *267*, No. 122466.

(56) Rui, W.; Liang, H.; Meng, Z.; Te, C.; Xiaolin, Z.; Ying, L.; Leyi, N.; Gang, G. Factors on seed germination, tuber sprout and plant growth of Vallisneria species in China. *Journal of Lake Sciences* **2021**, *33* (5), 1315−1333.

(57) Xian, Q.; Chen, H.; Qu, L.; Zou, H.; Yin, D. Allelopathic potential of aqueous extracts of submerged macrophytes against algal growth. *Allelopathy J.* **2005**, *15*, 95−104.

(58) Skidmore, M.; Andarge, T.; Foltz, J. The impact of extreme precipitation on nutrient runoff. *Journal of the Agricultural and Applied Economics Association* **2023**, *2* (4), 769−785.

(59) Su, J.; Ji, D.; Lin, M.; Chen, Y.; Sun, Y.; Huo, S.; Zhu, J.; Xi, B. Developing surface water quality standards in China. *Resources, Conservation and Recycling* **2017**, *117*, 294−303.

(60) Huishu, L.; Hongbin, L.; Xudong, L.; Ting, S.; Shen, L.; Qiuliang, L.; Tianzhi, R.; Shuxia, W.; Ying, L. Characteristics of nitrogen variation and its response to rainfall: a case study in Wuxi Port at Taihu Lake Basin. *Environ. Sci.* **2017**, *38* (12), 5047−5055.

(61) Chou, Q.; Zhang, W.; Chen, J.; Ren, W.; Yuan, C.; Wen, Z.; Zhang, X.; Cao, T.; Ni, L.; Jeppesen, E. Phenotypic responses of a submerged macrophyte (Vallisneria natans) to low light combined with water depth. *Aquatic Botany* **2022**, *176*, No. 103462.

(62) Bachmann, R. W.; Horsburgh, C. A.; Hoyer, M. V.; Mataraza, L. K.; Canfield, D. E. Relations between trophic state indicators and plant biomass in Florida lakes. *Hydrobiologia* **2002**, *470* (1), 219−234.

(63) Scheffer, M. *Ecology of Shallow Lakes*; Chapman and Hall, 1998.

(64) Xu, Q.; Yang, X.; Song, J.; Ru, J.; Xia, J.; Wang, S.; Wan, S.; Jiang, L. Nitrogen enrichment alters multiple dimensions of grassland functional stability via changing compositional stability. *Ecology letters* **2022**, *25* (12), 2713−2725.

(65) Borcard, D.; Legendre, P. Is the Mantel correlogram powerful enough to be useful in ecological analysis? *A simulation study. Ecology* **2012**, *93* (6), 1473−1481.

(66) Peng, X.; Lin, Q. W.; Liu, B. Y.; Huang, S. Z.; Yan, W. H.; Zhang, L.; Ge, F. J.; Zhang, Y.; Wu, Z. B. Effect of submerged plant coverage on phytoplankton community dynamics and photosynthetic activity in situ. *Journal of Environmental Management* **2022**, *301*, No. 113822.

(67) Cao, T.; Xie, P.; Li, Z.; ni, L.; Zhang, M.; Xu, J. Physiological Stress of High NH 4 + Concentration in Water Column on the Submersed Macrophyte Vallisneria Natans L. *Bulletin of environmental contamination and toxicology* **2009**, *82*, 296−299.

(68) Xian, L.; Ochieng, W. A.; Muthui, S. W.; Otieno, D. O.; Yu, S.; Li, W.; Yan, X.; Yu, Q.; Liu, F. The Above-Ground Part of Submerged Macrophytes Plays an Important Role in Ammonium Utilization. *Front. Plant Sci.* **2022**, *13*, No. 865578.

(69) Wang, S.; Li, J.; Wang, R.; Hu, Y.; Li, W.; Cui, L. Specific root length regulated the rhizosphere effect on denitrification across distinct macrophytes. *Geoderma* **2024**, *449*, No. 117002.

(70) Mulderij, G.; Van Nes, E. H.; Van Donk, E. Macrophyte−phytoplankton interactions: The relative importance of allelopathy versus other factors. *Ecological Modelling* **2007**, *204* (1), 85−92.

(71) Scheffer, M.; Hosper, S. H.; Meijer, M. L.; Moss, B.; Jeppesen, E. Alternative equilibria in shallow lakes. *Trends in ecology & evolution* **1993**, *8* (8), 275−279.

(72) Norlin, J. I.; Bayley, S.; Ross, L. C. M. Submerged macrophytes, zooplankton and the predominance of low-over high-chlorophyll states in western boreal, shallow-water wetlands. *Freshwater Biology* **2005**, *50* (5), 868−881.

(73) Hilt, S.; Henschke, I.; Rücker, J.; Nixdorf, B. Can submerged macrophytes influence turbidity and trophic state in deep lakes? suggestions from a case study. *Journal of Environmental Quality* **2010**, *39* (2), 725−733.

(74) Zhong, A.; Cao, T.; ni, L.; Xie, P. Growth and membrane permeability of two submersed macrophytes in response to ammonium enrichment. *Aquatic Biology* **2013**, *19*, 55−64.

(75) Tan, X.; Yuan, G.; Hui, F.; Peng, H.; Ge, D.; Lou, Q.; Zhong, J. Effects of ammonium pulse on the growth of three submerged macrophytes. *PLoS One* **2019**, *14*, No. e0219161.

(76) Shilla, D.; Asaeda, T.; Fujino, T.; Sanderson, B. Decomposition of dominant submerged macrophytes: implications for nutrient release in Myall Lake, NSW. *Australia. Wetlands Ecology and Management* **2006**, *14* (5), 427−433.

(77) Zhang, L.; Zhang, S.; Lv, X.; Qiu, Z.; Zhang, Z.; Yan, L. Dissolved organic matter release in overlying water and bacterial community shifts in biofilm during the decomposition of Myriophyllum verticillatum. *Science of The Total Environment* **2018**, *633*, 929−937.

(78) Zhang, F.; Li, Z.; Lei, T.; Wang, J.; Shen, C.; He, X.; Li, R.; Feng, J.; Li, N. Effects of Submerged Macrophyte Decomposition on Water Quality. *Nat. Environ. Pollut. Technol.* **2022**, *21*, 1049−1058.

(79) Herndon, J.; Cochlan, W. P. Nitrogen utilization by the raphidophyte heterosigma akashiwo: growth and uptake kinetics in laboratory cultures. *Harmful Algae* **2007**, *6* (2), 260−270.

(80) Wang, L.; Liu, Q.; Hu, C.; Liang, R.; Qiu, J.; Wang, Y. Phosphorus release during decomposition of the submerged macrophyte Potamogeton crispus. *Limnology* **2018**, *19* (3), 355−366.

(81) Su, H.; Chen, J.; Wu, Y.; Chen, J.; Guo, X.; Yan, Z.; Tian, D.; Fang, J.; Xie, P. Morphological traits of submerged macrophytes reveal specific positive feedbacks to water clarity in freshwater ecosystems. *Science of The Total Environment* **2019**, *684*, 578−586.

(82) Bicudo, D. D. C.; Fonseca, B. M.; Bini, L. M.; Crossetti, L. O.; Bicudo, C. E. D. M.; AraÚJo-Jesus, T. Undesirable side-effects of water hyacinth control in a shallow tropical reservoir. *Freshwater Biology* **2007**, *52* (6), 1120−1133.

(83) Zhang, X.; Wan, A.; Wang, H.; Zhu, L.; Yin, J.; Liu, Z.; Yu, D. The overgrowth of Zizania latifolia in a subtropical floodplain lake: Changes in its distribution and possible water level control measures. *Ecological Engineering* **2016**, *89*, 114−120.

(84) Wen-bin, Y.; Yang, L.; Gong-xian, S. Effects of Two Submerged Macrophytes on Dissolved Inorganic Nitrogen in Overlying Water and Interstitial Water. *Environ. Sci.* **2014**, *35* (6), 2156−2163.

(85) Eriksson, P. G.; Weisner, S. E. B. An experimental study on effects of submersed macrophytes on nitrification and denitrification in ammonium-rich aquatic systems. *Limnology and Oceanography* **1999**, *44* (8), 1993−1999.

(86) Jeppesen, E.; Jensen, J. P.; Kristensen, P.; Søndergaard, M.; Olrik, K. Fish manipulation as a lake restoration tool in shallow, eutrophic, temperate lakes 2: threshold levels, long-term stability and conclusions. *Hydrobiologia* **1990**, *200-201* (1), 219−227.

(87) Chen, K. N.; Bao, C. H.; Zhou, W. P. Ecological restoration in eutrophic lake wuli: a large enclosure experiment. *Ecological Engineering* **2009**, *35* (11), 1646−1655.

(88) Holt, R. D. Theoretical perspectives on resource pulses. *Ecology* **2008**, *89* (3), 671−681.

(89) Scheffer, M.; van Nes, E. H.; Holmgren, M.; Hughes, T. Pulse-Driven Loss of Top-Down Control: The Critical-Rate Hypothesis. *Ecosystems* **2008**, *11* (2), 226−237.

(90) Wang, H.; Zhang, X.; Shan, H.; Chaochao, l.; Ren, W.; Wen, Z.; Tian, Y.; Weigel, B.; Ni, L.; Cao, T. Biodiversity buffers the impact of eutrophication on ecosystem functioning of submerged macrophytes on the Yunnan-Guizhou Plateau, Southwest China. *Environ. Pollut.* **2022**, *314*, No. 120210.

(91) Li, X.; Gao, X.; Tang, N.; Wang, L.; Xing, W. Functional traits of exotic submerged macrophytes mediate diversity-invasibility relationship in freshwater communities under eutrophication. *Science of The Total Environment* **2024**, *949*, No. 175060.

(92) Pillar, V. D.; Blanco, C. C.; Müller, S. C.; Sosinski, E. E.; Joner, F.; Duarte, L. D. S. Functional redundancy and stability in plant communities. *Journal of Vegetation Science* **2013**, *24* (5), 963−974.

(93) Benkwitt, C. E.; Wilson, S. K.; Graham, N. A. J. Biodiversity increases ecosystem functions despite multiple stressors on coral reefs. *Nature Ecology & Evolution* **2020**, *4* (7), 919−926.

(94) Meijer, M. L.; de Boois, I.; Scheffer, M.; Portielje, R.; Hosper, H. Biomanipulation in shallow lakes in the Netherlands: an evaluation of 18 case studies. *Hydrobiologia* **1999**, *408*, 13−30.

(95) Arroyo-Rodríguez, V.; Fahrig, L.; Tabarelli, M.; Watling, J. I.; Tischendorf, L.; Benchimol, M.; Cazetta, E.; Faria, D.; Leal, I. R.; Melo, F. P. L.; Morante-Filho, J. C.; Santos, B. A.; Arasa-Gisbert, R.; Arce-Peña, N.; Cervantes-López, M. J.; Cudney-Valenzuela, S.; Galán-Acedo, C.; San-José, M.; Vieira, I. C. G.; Slik, J. W. F.; Nowakowski, A. J.; Tscharntke, T. Designing optimal human-modified landscapes for forest biodiversity conservation. *Ecology letters* **2020**, *23* (9), 1404−1420.

(96) Macchi, L.; Baumann, M.; Bluhm, H.; Baker, M.; Levers, C.; Grau, H. R.; Kuemmerle, T. Thresholds in forest bird communities along woody vegetation gradients in the South American Dry Chaco. *Journal of Applied Ecology* **2019**, *56* (3), 629−639.

(97) Hilderbrand, R. H.; Utz, R. M.; Stranko, S. A.; Raesly, R. L. Applying thresholds to forecast potential biodiversity loss from human development. *J. North Am. Benthological Soc.* **2010**, *29* (3), 1009−1016.

(98) de Oliveira Roque, F.; Menezes, J. F. S.; Northfield, T.; Ochoa-Quintero, J. M.; Campbell, M. J.; Laurance, W. F. Warning signals of biodiversity collapse across gradients of tropical forest loss. *Sci. Rep.* **2018**, *8* (1), 1622.

(99) Huxel, G. R.; McCann, K. Food web stability: the influence of trophic flows across habitats. *American Naturalist* **1998**, *152* (3), 460−469.

(100) Hughes, T. P. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **1994**, *265* (5178), 1547−1551.

(101) Randall, D. J.; Tsui, T. K. N. Ammonia toxicity in fish. *Mar. Pollut. Bull.* **2002**, *45* (1), 17−23.

NOTE ADDED AFTER ASAP PUBLICATION

Due to a production error, the version of this article that was published ASAP August 4, 2025, contained an error in the resilience stability formula in section 2.3. The corrected version was posted August 4, 2025.