Eutrophication decreases ecological resilience by reducing species diversity and altering functional traits of submerged macrophytes

Chaoyue Cheng1,2 | Jun Chen1 | Haojie Su3 | Jianfeng Chen3 | Qingyang Rao3 | Jun Yang3 | Qingchuan Chou1 | Lantian Wang1 | Xuwei Deng1 | Ping Xie1,3

1Donghu Experimental Station of Lake Ecosystems, State Key Laboratory of Freshwater Ecology and Biotechnology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China
2University of Chinese Academy of Sciences, Beijing, China
3Institute for Ecological and Pollution Control of Plateau Lakes, School of Ecology and Environmental Science, Yunnan University, Kunming, China

Correspondence
Ping Xie, Institute of Hydrobiology, Chinese Academy of Sciences, 79 Donghu South Road, Wuhan 430072, China. Email: xieping@ihb.ac.cn

Haojie Su, Institute for Ecological Research and Pollution Control of Plateau Lakes, School of Ecology and Environmental Science, Yunnan University, Kunming 650500, China. Email: suhaojie@ynu.edu.cn

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Abstract
Positive feedback is key to producing alternative stable states and largely determines ecological resilience in response to external perturbations. Understanding the positive feedback mechanisms in macrophyte-dominated lakes is crucial for resilience-based management and restoration. Based on the field investigation of submerged macrophyte communities in 35 lakes in China, we found that morphological complexity (MC) and morphological plasticity (MP) are correlated with the stoichiometric homeostasis of phosphorus (\(H_P\)) and are related to ecosystem structure, functioning, and stability. We also found that the positive feedback strength of lakes dominated by macrophytes is biomass- and diversity-dependent. Eutrophication can decrease the community biomass by decreasing community MC, MP, and \(H_P\) and the species diversity through low-light availability, ultimately decreasing the positive feedback strength and resilience of clear water states. We argue that functional traits and species diversity should be considered to build more resilient ecosystems in future changing environment scenarios.

KEYWORDS
ecosystem resilience, eutrophication, functional traits, regime shift, submerged macrophytes

1 | INTRODUCTION

Ecosystem regime shifts attract a growing concern because irreversible nonlinear, abrupt changes can significantly alter the services that the ecosystem offers to human society. Regime shifts between contrasting alternative states occur when environmental conditions cross a specific threshold, with ecological resilience decreasing as the system approaches the tipping point (Ma et al., 2021). Therefore, measuring and quantifying ecological resilience is critical to improving ecosystem management and conservation. Previous assessments of ecological resilience often focused on identifying thresholds or early warning indicators based on critical slowing down (Contamin & Ellison, 2009; Dakos et al., 2015). However, these methods do not include the specific mechanisms of regime shifts. Positive feedback is the key to understanding the pattern of ecosystem response to environmental changes, with high feedback strength creating...
bifurcations that produce alternative stable states and low feedback strength generating smooth or linear responses (Clements & Ozgul, 2018; Spanbauer et al., 2016). Positive feedbacks are self-facilitation processes during which the individuals’ growth and fitness increase with the population abundance; they allow populations to persist under disturbance by alleviating abiotic stresses (Bianchi et al., 1989). For example, in shallow lakes, the clear water state is affected by macrophytes and, in turn, influences the performance of macrophytes, in a positive feedback loop (Hilt et al., 2011). The high self-facilitation strength of macrophyte-dominated states can buffer external environmental changes and delay the transition by increasing the regime shift threshold. Thus, the ecological resilience of the macrophyte-dominated state is determined mainly by the positive feedback strength modifying water clarity. However, in an algae-dominated state, the system cannot be restored to its previous state because of the positive feedback, even if the physical and chemical factors are reduced below the collapse threshold (Möllmann et al., 2009). Therefore, enhancing the positive feedback strength dominated by submerged macrophytes and weakening the positive feedback strength dominated by algae are the key to maintaining the high resilience of the clear water state (Beisner et al., 2003). In recent years, although it became clear that positive feedback is at the core mechanism of ecosystem regime shifts, the determinants of ecological resilience remain largely unknown.

Ecological resilience can be affected by functional traits underlying plants’ performance and fitness. Morphological and physiological traits reflect the adaptability of organisms and ecological strategies of species or communities in a habitat (Cornellissen et al., 2003). They are also connected with various ecological processes of great significance for predicting global changes and revealing a species’ response and adaptation to the environment (Cornwell & Ackerly, 2009; Kraft et al., 2008). In freshwater ecosystems, submerged macrophytes with high morphological complexity (MC) can form dense mats at the bottom of the lake, release reactive oxygen from their canopy and roots, and form complex spaces (related to the plants’ surface area) to provide habitats for zooplankton, such as Daphnia (Suding et al., 2005; Thomaz & Cunha, 2010), thus inhibiting sediment phosphorus (S_p) release, enhancing mineralization, and promoting the top-down phytoplankton control, respectively (Jeppesen et al., 1998; Su, Chen, et al., 2019). Morphological plasticity (MP)—the ability of organisms to alter their morphological traits in response to changing environments—is one of the mechanisms for acquiring adaptive benefits to cope with harsh conditions. For instance, macrophytes display morphological plasticity in the differential biomass allocation to their stem when light is limited (Fu et al., 2012). Thus, plant morphological complexity and plasticity are essential in inhibiting phytoplankton growth (Jeppesen et al., 1998) and effectively obtaining light resources via enhancing the positive feedback strength (Hutchings & de Kroon, 1994), thus accumulating more biomass and maintaining community stability.

Stoichiometric homeostasis is a physiological trait used to assess the ability of plants to maintain their internal element content stable (Cooper, 2008; Sterner & Elser, 2002). The stoichiometric homeostasis of macrophytes is related to the ecosystem structure, production, and stability (Su, Wu, et al., 2019). High homeostasis plants dominate in poor-nutrient environments and consume massive energy to maintain their nutrient levels stable (Yu et al., 2010, 2011). They potentially need larger specific surface areas and higher morphological plasticity to enhance photosynthesis and nutrient absorption. Therefore, plants with high morphological complexity and plasticity may exhibit high stoichiometric homeostasis and consequently have high production and facilitation strength, which can buffer environmental stresses and increase community resilience.

Species diversity is also key to ecosystem resilience (Oliver et al., 2015). Ecosystems with high species diversity often provide higher levels of ecosystem functions and temporal invariability in controlled experiments (Kardol et al., 2018). As species may respond differently to environmental changes, species population size often varies asynchronously, providing an “insurance” effect to maintain the overall functions constant (Hummel et al., 2009; Matias et al., 2013; Wang et al., 2021). In addition, multiple species may perform higher spatial complexity and functional redundancy, which is essential in promoting coexistence, thus making them more likely to exert high positive feedback strength (Hummel et al., 2009; Naeem & Li, 1997). We assumed that ecosystems with high species diversity are resilient to environmental changes and, thus, less likely to fall into alternative states. However, although there is clear evidence of species diversity loss worldwide (Collins et al., 2002), little is known about the impacts of such loss on the ecosystem resilience of freshwater communities.

The intensification of human activities has discharged a large number of nutrients (e.g., nitrogen and phosphorus) into the lake ecosystem, resulting in eutrophication and a frequent occurrence of cyanobacteria blooms across the world (Sardans et al., 2012; Scheffer et al., 2001; Su et al., 2021). Eutrophication is considered a dominant driver of the species diversity loss and distribution area of aquatic plants (Hao et al., 2013). Under eutrophication, high species become dominant to alleviate the low light stress (Su, Chen, et al., 2019), which may ultimately weaken the positive feedback strength. Moreover, previous studies indicated that eutrophication-induced stoichiometric imbalance might destabilize the ecosystem by altering the community structure from high to low stoichiometric homeostasis species (Su, Wu, et al., 2019). As positive feedbacks allow macrophytes to persist under disturbances by mitigating the experienced stress, clarifying whether and how functional traits and species diversity influence positive feedback strength is critical to understanding the effects of eutrophication on ecological resilience.

In this study, based on the investigation of 35 subtropical lakes in China, we hypothesized that (1) morphological complexity (the plant’s specific surface area) and plasticity (the variability of the plant’s specific surface area) are correlated with stoichiometric homeostasis and are essential in community biomass, stability, and positive feedback strength; (2) positive feedback strength is dependent on biomass and species diversity; (3) eutrophication can reduce the ecological resilience by changing functional traits and reducing species diversity. We hope our work can provide new ideas...
to understand the mechanisms of regime shift further and contribute to the effective restoration and management of submerged macrophytes.

2 | MATERIALS AND METHODS

2.1 | Study sites and field sampling

Submerged macrophyte communities from 35 subtropical lakes in China were investigated between 2014 and 2021. Five hundred and thirty-four sites were sampled among those lakes distributed in the middle and lower reaches of the Yangtze Plain (2014 and 2018; an average of 16 sampling sites for each lake), Sichuan Basin (2020; an average of 11 sampling sites for each lake), and Yunnan Plateau (2021; an average of 17 sampling sites for each lake; Figure 1). The geographic information of each lake is presented in Table S2.

Water clarity was measured by a Secchi disk (Secchi depth, SD), water samples from 0.5 m depth were collected by 5 L Schindler samplers, and sediment was collected with a Peterson mud extractor. Ten species of submerged macrophytes widely distributed in subtropical lakes were studied: *Potamogeton maackianus*, *Potamogeton malayanus*, *Ceratophyllum demersum*, *Hydrilla verticillata*, *Vallisneria natans*, *Myrophyllum verticillatum*, *Potamogeton pectinatus*, *Potamogeton perfoliatus*, *Najas marina*, and *Potamogeton lucens*. The biomass of these 10 species accounted for more than 95% of the total biomass of submerged macrophytes in sampled lakes.

2.2 | Laboratory analysis

A portable leaf area meter (Yaxin 1241, Beijing Bolun Jingwei Technology Development Co., Ltd) was used to measure the surface area of plants above the sediment level. We selected healthy plants representative of the average plant size and repeated measurements to estimate the surface area accurately. The whole plant was spread on a white panel, covered with a transparent hard plastic plate matched with the leaf area meter, and flattened. Finally, the whole plant was scanned to measure its surface area. An electronic balance was used to weigh the wet biomass of the corresponding material. Plant height was defined as the length (cm) of the aboveground part. The phosphorus in plants and sediments was first digested using concentrated sulfuric acid (Taicang Hushi Reagent Co., Ltd) and hydrogen peroxide (Shanghai Wokai Biotechnology Co., Ltd), and the amount was determined using the ammonium molybdate-ascorbic acid method (Sparks et al., 1996). Total phosphorus (TP) in the water sample was digested with potassium persulfate (Sigma Aldrich) in a sterilization pot (GR85DA, Zealway instrument Inc.) at 120°C for 30 min (Huang et al., 1999).
2.3 | Calculation of community metrics

The stoichiometric homeostasis coefficient ($H$) of phosphorus in submerged macrophytes can be fitted with a regression between resources and plants (Sterner & Elser, 2002). Previous studies demonstrated that stoichiometric homeostasis reflects the limiting factors of plants (Yu et al., 2010). In lake ecosystems, phosphorus is considered a limiting factor, not nitrogen (Correll, 1999; Schindler et al., 2016). Plant phosphorus ($P_p$) displays significant relationships with sediment phosphorus ($S_p$), while $N$ presents no significant relationships (Su, Wu, et al., 2019). Therefore, only $P$ stoichiometric homeostasis was calculated in this study according to the following equation (Sterner & Elser, 2002):

$$\log (P_p) = (1/H) \times \log (S_p) + \log (c)$$  \hspace{1cm} (1)

where $P_p$ is the phosphorus content per unit dry mass (mg kg$^{-1}$) in the plant above the sediment level, $S_p$ is the phosphorus content (mg kg$^{-1}$ dry mass) in the sediment, and $c$ is the regression intercept of the equation. The stoichiometric homeostasis $H$ represents the ability of an organism to maintain a relatively stable internal element concentration regardless of changes in nutrient availability (Su, Wu, et al., 2019).

The morphological complexity (MC) of submerged macrophytes was calculated as the surface area ($cm^2$) to wet biomass (g) ratio. The plants’ morphological plasticity (MP) was represented by the coefficient of variation of MC (i.e., the standard deviation of the specific surface area to the mean value ratio). Species dominance was determined by the proportion of species biomass in the total biomass in a quadrat. Species stability was calculated as the species average biomass to standard deviation ratio (Su, Wu, et al., 2019). Community trait ($T$) is the overall mean of functional traits across all species weighted by the relative biomass (Yu et al., 2010).

$$\text{Community } T = \sum_{i=1}^{n} \text{relative biomass } \times T_i$$  \hspace{1cm} (2)

where $n$ is the number of plant species in a quadrat, $i$ is the value from 1 to $n$, and $T$ is functional traits—$H$, MC, and MP—of plants.

The community biomass of a lake is defined as the mean total biomass of all submerged macrophyte species in a quadrat, and community stability is indicated by the mean biomass to standard deviation ratio (Tilman et al., 2006). Species diversity here is affected by the H-Shannon diversity, which is calculated as the exponential of Shannon entropy, which emphasizes neither rare nor common species (Roswell et al., 2021).

$$\text{Diversity} = e^{-\sum_{i=1}^{S} p_i \ln p_i}$$  \hspace{1cm} (3)

where $p_i$ is the dominance of the $i$-th species in a quadrat, and $S$ is the number of species in a quadrat.

The positive feedback loop in which plants improve water clarity, thus promoting their growth, has been confirmed (Su, Chen, et al., 2019). Here, we define positive feedback strength as the ability of plants to improve water clarity per unit biomass.

$$\text{Feedback SD}_i = (SD_i - SD_0) / \log (\text{community biomass})$$  \hspace{1cm} (4)

where $SD_i$ is the Secchi depth (m) in the quadrant with the presence of submerged macrophytes, and $SD_0$ is the Secchi depth in the quadrant without submerged macrophytes in the same lake. To estimate the positive feedback strength of monospecific communities, those with >95% dominance by one species were selected, and an average of eight quadrats were picked for each lake. Community biomass was log-transformed to improve data normality and reduce data variations.

2.4 | Data analysis and statistics

We used the specific surface area of plants (i.e., plant surface area per unit biomass) to indicate MC. One-way ANOVA and LSD comparisons were used to analyze the differences of specific area between submerged macrophytes. To test whether MC and MP are essential in $H$, a general linear model was used to quantify the relationships between morphological traits and stoichiometric homeostasis at both the species and community levels. We also tested whether morphological traits were linked with species dominance and stability, as well as community biomass and stability. A general linear model was used to fit MC, MP, and $H$ with the positive feedback strength to explore the effect of functional traits on positive feedback strength. The paired $t$-test was used to explore whether there was a difference in positive feedback strength between monospecific and multispecies communities. Finally, a general linear model was used to test whether the positive feedback strength depended on biomass and species diversity.

The piecewise structural equation model (SEM) was constructed to explore further the cascading effect of how eutrophication affects ecosystem resilience by altering species diversity and community morphological and physiological traits. Specifically, due to the intensification of water eutrophication, low light availability is often the most limiting factor for submerged macrophytes (Sand-Jensen et al., 2008), leading to macrophytes allocating more biomass to their stem and the dominance of species with vertical growth strategy (Su, Chen, et al., 2019). As these plants often have low morphological complexity, we hypothesized that nutrient enrichment may decrease water clarity and subsequently decrease community MC and MP. Additionally, we hypothesized that MC and MP are one of the mechanisms helping plants to maintain their stoichiometric homeostasis, as plants with higher complexity and plasticity can increase photosynthesis and nutrient utilization efficiency and adjust to variations in nutrient availability. In addition, as macrophytes differ in their ability to tolerate low light stress, water clarity decline may decrease species diversity. As community biomass, stability, and species diversity are essential community properties, we tested how these community properties were affected by environmental changes and functional traits. Finally, we tested whether ecosystems
with higher species diversity, community biomass, and stability have higher ecological resilience. Here, a stronger positive submerged macrophyte/water clarity feedback strength was considered to lead to higher ecological resilience in clear water state. Following this idea, we constructed possible overall models. The insignificant pathways were sequentially deleted or changed until the final model with the lowest AIC was obtained. We classified all variables into four levels: environmental changes (changes in water TP and clarity), morphological and physiological traits (MC, MP, and H), community properties (community biomass, stability, and species diversity), and ecosystem resilience (positive feedback strength). The piecewise SEM was constructed using the R 4.0.2 (R Core Development Team, 2019) “piecewiseSEM” package. We used the “semEff” package to calculate the standardized total effects and 95% confidence intervals for each driving factor.

3 | RESULTS

3.1 Relationship between plant morphological and physiological characteristics

Each plant’s MC was obtained by calculating the average specific surface area. The relationship between the surface area and biomass (fresh weight) of each plant species is presented in Figure S1. The MC of the 10 studied species ranged from 7.29 (P. pectinatus) to 32.70 (P. maackianus), averaging 17.91. Comparing the MC average, P. maackianus, P. malaianus, V. natans, and P. lucens were classified as high MC plants, while C. demersum, M. verticillatum, H. verticillata, P. pectinatus, N. marina, and P. perfoliatus were classified as low MC plants. The variation range of the specific surface area of different plants was different, indicating different MP (Figure 2). Different letters in Figure 2 indicate differences in specific surface area. The MP of the 10 studied species ranged from 0.17 (N. marina) to 0.49 (P. maackianus), with an average of 0.31 (details in Table S1).

The stoichiometric homeostasis of each species was assessed by plotting the logarithms according to Equation (1) (Figure S2). At the species level, the H of submerged macrophytes was positively correlated with MC and MP ($R^2 = 0.80, p < 0.001; R^2 = 0.69, p = 0.003$; Figure 3a,b). At the community level, the H of submerged macrophytes was also positively correlated with MC and MP ($R^2 = 0.82, p < 0.001; R^2 = 0.81, p < 0.001$; Figure 3c,d). In addition, plant height was negatively correlated with species MC ($R^2 = 0.56, p = 0.034$; Figure S3).

3.2 Driving factors on community structure, functioning, and stability

We found that TP in water and sediment negatively affects the community biomass ($R^2 = 0.13, p = 0.031; R^2 = 0.12, p = 0.040$; Figure S4a,c) and species diversity ($R^2 = 0.17, p = 0.015; R^2 = 0.13, p = 0.030$; Figure S4b,d). SD has positive relationships with community biomass and species diversity ($R^2 = 0.12, p = 0.040; R^2 = 0.13, p = 0.031$; Figure S4e,f).

At the species level, MC and MP of submerged macrophytes are significantly correlated with species dominance ($R^2 = 0.47, p = 0.030$; $R^2 = 0.53, p = 0.017$; Figure 4a,b) and species stability ($R^2 = 0.47, p = 0.028$; $R^2 = 0.55, p = 0.014$; Figure 4c,d). At the community level, MC and MP are significantly correlated with community biomass ($R^2 = 0.21, p = 0.005$; $R^2 = 0.25, p = 0.002$; Figure 4e,f) and community stability of submerged macrophytes ($R^2 = 0.23, p = 0.004; R^2 = 0.26, p = 0.002$; Figure 4).
The dominance of high MC species was positively correlated with water clarity, while that of low MC species was negatively correlated ($R^2 = .77$, $p < 0.001$; Figure S5).

### 3.3 Factors influencing positive feedback strength

We found that community biomass ($R^2 = .21$, $p = .006$; Figure 5a) and species diversity ($R^2 = .13$, $p = .037$; Figure 5b) had significant relationships with the positive feedback strength. In addition, at the monospecific and multispecies community levels, MC ($R^2 = .21$, $p = .010$; $R^2 = .22$, $p = .009$), MP ($R^2 = .24$, $p = .005$; $R^2 = .21$, $p = .010$), and $H$ ($R^2 = .25$, $p = .004$; $R^2 = .23$, $p = .006$; Figure S6) have positive relationships with the positive feedback strength. Moreover, the positive feedback strength was higher in the multispecies than in the monospecific community (Figure S7, $p = .024$), indicating that species diversity has a positive impact on the feedback strength. As the positive feedback strength was calculated based on the Secchi depth with macrophytes (SD), the Secchi depth without macrophytes (SD$_0$), and the community wet biomass, we provided additional information on how the water total phosphorus, sediment total phosphorus, and community biomass affect SD and SD$_0$. SD and SD$_0$ were negatively correlated with total phosphorus in water ($R^2 = .31$, $p < 0.001$; $R^2 = .18$, $p = .012$; Figure S8a) and sediments ($R^2 = .29$, $p = .001$; $R^2 = .12$, $p = .039$; Figure S8b). In addition, there was a significantly positive correlation between SD and community biomass ($R^2 = .12$, $p = .040$; Figure S8c), but no significant correlation between SD$_0$ and community biomass ($p > 0.05$; Figure S8c) was observed.

### 3.4 The piecewise SEM

We initially constructed five piecewise SEM models based on assumptions (Figure S9) and ultimately selected the model with the lowest AIC to illustrate how eutrophication decreases ecological resilience via altering functional traits and species diversity (Figure 6). The model fitted the data well (Fisher’s $C = 46.91$, $p = .435$, DF = 46, AIC = 102.91, BIC = 146.46) and could explain the changes in SD, MC, MP, $H$, community biomass, species diversity, community stability, and positive feedback strength with 31%, 23%, 29%, 84%, 32%, 13%, 25%, and 44%, respectively. The standardized total effects for each driving factor of the final
FIGURE 4 The relationships between plant morphological traits and species dominance and stability (a–d) and community biomass and stability (g, h). MC and MP correlated with species dominance (a, b) and species stability (c, d). Species dominance is expressed in terms of the relative biomass of plants in the quadrat, averaging each species. Species stability was calculated by the ratio of mean value to associated standard deviation. Each point represents a species. MC and MP correlated with community biomass (e, f) and community stability (g, h). Community biomass is expressed according to the total biomass in the quadrat (kg m⁻²). Community stability was also calculated by the ratio of mean value to associated standard deviation. Each point represents a lake. MC, morphological complexity; MP, morphological plasticity.
FIGURE 5  Linking between community biomass (kg m⁻², a) and species diversity (b) on positive feedback strength. Each point represents a lake. The positive feedback strength is quantified according to the ratio of the difference in Secchi depth between sites with and without plants to the log (community biomass). Species diversity here is indicated by the H-Shannon diversity, which is calculated as the exponential of Shannon entropy.

FIGURE 6  Eutrophication affects the path of positive feedback. The numbers on the arrows indicate the path coefficients (**p < .001, *p < .01, *p < .05). In the figure, the black arrow represents a negative correlation, the red arrow represents a positive correlation, and the red dashed line indicates a nonsignificant positive correlation. R² is the variance interpretation rate for each variable. The process of decreasing Secchi depth due to the increase of total phosphorus is level 1 (environment change); the relationship between H, MC and MP is level 2 (morphological and physiological traits); Community biomass, community stability, and species diversity is level 3 (community properties). The feedback is level 4 (ecosystem resilience). Model fitting test: Fisher’s C = 46.91, DF = 46, p = .435, AIC = 102.91, BIC = 145.4. H, homeostasis coefficient; MC, morphological complexity; MP, morphological plasticity.
piecewise SEM model and its 95% confidence intervals are presented in Table S3.

4 | DISCUSSION

Positive feedbacks are self-reinforcing processes that may push the system out of a basin and shift it into another state with a substitute attractor with its own feedback when external conditions go beyond a certain threshold (Shields & Weidman, 2008). The positive feedback strength determines the response types of ecosystems to external perturbation (i.e., linear, abrupt, or catastrophic); thus, positive feedback is a necessary but insufficient condition for regime shifts. Ecological resilience reflects the ability of ecosystems to absorb disturbances and reorganize under external perturbation to maintain their original function and structure (Walker et al., 2004), which is highly related to positive feedback strength in a specific state (Carpenter et al., 2001; Thrush et al., 2012). However, human activities can cause the loss of resilience by removing functional groups of species and decreasing the response diversity (Folke et al., 2004). Therefore, clarifying the source of positive feedback strength is critical for maintaining an ecosystem within a desired state in the face of changing environment. In this study, we first quantified the MC and MP of macrophytes and revealed that they had a positive correlation with $H$, community structure, functioning, and stability. In addition, we found that positive feedback strength was related to community biomass and species diversity, suggesting that ecosystem resilience is biomass- and diversity-dependent. Thus, eutrophication, as the initial driver of the chain reaction, could decrease ecological resilience by altering functioning traits and decreasing species diversity, causing the ecosystem to tip more readily into a non-macrophyte turbid water regime.

4.1 | Linking functional traits with community structure, functioning, and stability

Functional traits can be defined as different morphological, physiological, and other traits affecting the fitness of individuals by influencing their growth, reproduction, and survival (Viole et al., 2007). In the past decades, functional traits of species have received increasing attention as a way to link niche-based approaches to community patterns and ecosystem resilience (Cadotte et al., 2015). However, most studies focused on the effects of functional traits on the adaptive strategy in a stressful environment (Li et al., 2018; Stefanidis & Papastergiadou, 2019) and ignored the potential links of functional traits with community structure, functioning, and ecological resilience. Our study found that morphological complexity and plasticity were linked with stoichiometric homeostasis, essential in determining the ecosystem structure, functioning, and stability (Su, Wu et al., 2019; Yu et al., 2010). In addition, we found positive relationships between morphological complexity and plasticity. Complex plant morphologies often have a higher ability to acquire resources and tolerate physical stresses, meaning that plants with high morphological complexity may be more adaptable to changing environments and have more opportunities for plasticity in response to environmental heterogeneity (Suzuki & Stuefer, 1999). For instance, submerged macrophytes with a large specific surface area probably perform higher photosynthesis, can better inhibit sediment suspension, better absorb nutrients from the water column, and provide more refuge space for large Daphnia. (Jeppesen et al., 1998), thus facilitating their growth environment and creating conditions for a species to adopt a more plastic survival strategy (Suzuki & Stuefer, 1999). In return, the plastic growth of plants can easily form complex spatial structures (Brito et al., 2021; McCrea & Carpenter, 1987), increasing morphological complexity and promoting species coexistence.

Morphological complexity and plasticity might be essential mechanisms helping plants to maintain their stoichiometric homeostasis. In our study, morphological complexity refers to the specific surface area of plants, which is essential in determining how efficiently plants acquire resources, such as light and nutrients. Greater complexity in plant morphology is associated with increased nutrient utilization and higher photosynthetic ability, enabling the plant to fix and accumulate resources to maintain stoichiometric homeostasis under varying environmental conditions (Hessen et al., 2013). Previous studies demonstrated that phenotypic plasticity in plants is related to the environment they live in (Gianoli, 2001; Matesanz et al., 2010; Schlichting, 1989; Valladares et al., 2007; Wood & Brodie, 2015). Plants with greater morphological plasticity can better adjust to variations in nutrient availability and maintain stoichiometric homeostasis. As most lakes are P-limited (Correll, 1999; Schindler et al., 2016), high-MP plants can flexibly change their morphology, facilitating the adoption of more conservative nutrient utilization strategies (Hermans et al., 2006; Hutchings & de Kron, 1994; Li et al., 2022; Stuefer et al., 1996; Yu et al., 2011) to maintain high stoichiometric homeostasis. However, eutrophication-induced imbalance in nutrient supply would decrease the dominance of high homeostasis species, ultimately leading to decreased community biomass and stability (Su, Wu et al., 2019). In addition, high morphological plasticity means that plants may have a higher ability to adjust the resource allocation among organs to maintain internal homeostasis at an individual level, which may help them overcome harsh conditions (Hutchings & de Kron, 1994; Roff, 1999; Scheiner, 1993). In short, our results suggest that morphological complexity, plasticity, and stoichiometric homeostasis are all inter-connected and critical to the ecosystem’s structure, functioning, and stability. Specifically, macrophyte communities with high morphological complexity, plasticity, and stoichiometric homeostasis may have higher biomass, stability, and positive feedback strength, which could consequently buffer strong environmental stresses and increase community resilience toward disturbances.

In the piecewise-SEM, we found that the relationship between the changes in $H$ driven by MP was not significant ($p=0.64$), probably because MC plays a more important role on $H$. Additionally,
this study only focused on MC, MP, and H, while ignoring other important traits, such as maximum growth rates and root:shoot ratio. Plants with low H adopting the luxury-absorbing nutrient strategy tend to have a higher maximum growth rate, while plants with high H often have conservative nutrient utilization strategies (Yu et al., 2011). Our previous results found that plants with high H and MC tend to dominate in a more oligotrophic condition (Su, Wu, et al., 2019), which may lead to macrophytes allocating more biomass in the root to more efficiently absorb nutrients from sediment, such as P. maackianus and V. natans (Hao et al., 2013; Xiao et al., 2006; Xie et al., 2005). Therefore, macrophytes with high H and MC probably have a lower maximum growth rate and higher root:shoot ratio. Future works should include more plant traits to validate if correlations observed in this study might be side effects of other more important functional traits. Overall, our results can provide a theoretical basis for further understanding how functional traits affect community functions, stability, and ecosystem resilience (Dakos et al., 2019; Fu et al., 2018).

4.2 Roles of species diversity on ecosystem resilience

Our results suggest that communities with high species diversity tend to have higher positive feedback strength and, consequently, higher ecosystem resilience. Communities with multiple species of submerged macrophytes often have a higher ability to improve water clarity than those with a single species (Liu et al., 2020), which is beneficial for establishing a submerged macrophyte-dominated clear water state (Zhao et al., 2022). Firstly, the species response variability to environmental changes within functional groups (i.e., response diversity) is critical for ecosystem resilience (Chapin III et al., 1997; Elmqvist et al., 2003; Norberg et al., 2001). For example, when adapting to the underwater low-light environment in eutrophic lakes, rosette plants increase their leaf chlorophyll content, while canopy plants increase their leaf area and stem height through rapid growth (Chen et al., 2016; Hao et al., 2020; Su, Chen, et al., 2019; Zervas et al., 2019; Zhu et al., 2018). This adaptation diversity expands the ecological niche of submerged plants, thus improving their ability to adapt to changing environments (Cardinale, 2011). Secondly, species diversity is considered to have a positive relationship with functional diversity and redundancy. Under harsh conditions, the disappearance of one species could be filled by another functionally similar species, ensuring the functional maintenance of the rangeland under various environmental conditions (Walker et al., 1999). The insurance hypothesis states that lake ecosystems with high species diversity are more likely to have redundant stable species, thus enhancing the lake ecosystem resilience (Hummel et al., 2009; Matias et al., 2013). In addition, the complex spatial structure of different species can promote the coexistence of the whole community. Thus, species diversity can maintain ecosystem structure and functions and the response diversity and functional redundancy of plant traits, thereby enhancing ecosystem resilience. Overall, maintaining ecosystem resilience through species diversity helps to buffer the adverse effects of environmental stress and maintain the desired state of ecosystems under external random disturbances.

4.3 Eutrophication reduces ecosystem resilience by altering community metrics

Eutrophication is often thought to increase light competition between submerged plants and algae and lead to macrophyte species diversity loss (Sand-Jensen et al., 2008; Suding et al., 2005; Figure S4), which has been the focus of studies on global changes in aquatic ecosystems (Ho et al., 2019). Our results suggest that eutrophication affected community structure, functioning, and ecosystem resilience via altering community functional traits and species diversity loss to weaken the positive feedback strength under a clear water regime (Figure 6). As macrophytes differ in their ability to tolerate low light stress, interspecific competition for light among macrophyte species at local scales (Fu et al., 2014) may lead to the decrease of species diversity and a change in community composition. Macrophyte communities with high surrounding water clarity had more biomass and were rich with high MC plants, while communities in low water clarity had less biomass and were enriched in low MC plants (Figures S4 and S5). Thus, eutrophication may weaken the functioning of plant communities by inhibiting the dominance of high MC plants. In addition, plants with high MC probably had a higher investment in leaves and a lower one in height, while plants with low MC had a higher investment in stems and height (Figure S3). Eutrophication will facilitate higher plants (low MC) and inhibit the growth of smaller ones (high MC) by shading (Su, Chen, et al., 2019). In addition, highly complex plants could provide a habitat for attached algae, resulting in shading and transport barriers for dissolved inorganic carbon for macrophytes (Brenner et al., 2006; House & Donaldson, 1986; Wang et al., 2022). In addition, environmental filtering caused by eutrophication could limit the range and variation of some key functional traits in macrophyte communities (Fu et al., 2014), explaining why eutrophication weakens MP. In previous studies, ecological management often focused on the restoration of abiotic environmental factors, such as nutrient reduction, while ignoring the role of morphological and physiological traits and species diversity (Maxwell et al., 2017). Functional traits and species diversity should be involved in ecosystem management to improve ecological resilience in future environmental change scenarios.

5 Conclusion

Our study showed that morphological complexity and plasticity had positive relationships with the stoichiometric homeostasis of submerged macrophytes, suggesting that morphological traits can
significantly affect the balance of essential elements in plant tissues. In addition, morphological and physiological traits were positively correlated with species dominance, biomass, and stability at the species and community levels. As the feedbacks are often biomass-dependent, communities with high morphological complexity, plasticity, and stoichiometric homeostasis tend to have stronger positive feedback strength. Moreover, species diversity had positive relationships with positive feedback strength and, thus, ecological resilience. Eutrophication can decrease ecological resilience by reducing species diversity and altering morphological and physiological traits. Our results revealed the role of functional traits and species diversity in determining community structure, functioning, and ecosystem resilience under the pressure of eutrophication, deepening our understanding of regime shifts. These results are significant for ecological restoration and lake management in light of future environmental change scenarios.

AUTHOR CONTRIBUTIONS

All persons who meet authorship criteria are listed as authors, and all authors certify that they have participated sufficiently in the work to take public responsibility for the content, including participation in the design, analysis, writing, or revision of the manuscript. Furthermore, each author certifies that this material or similar material has not been and will not be submitted to or published in any other publication before its appearance in the Global Change Biology. Haojie Su and Ping Xie planned and designed the research. Haojie Su, Jianfeng Chen, Qingchuan Chou, Jun Yang, and Chaoyue Cheng participated in field sampling. Haojie Su and Chaoyue Cheng analyzed data and wrote the manuscript. Haojie Su, Qingyang Rao, Chaoyue Cheng, Lantian Wang, Jun Chen, Xuwei Deng, and Ping Xie revised the manuscript and gave important and critical input.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in dryad digital repository at: https://datadryad.org/stash/share/T1O8DEFSwJJBkYbdjuqYKDFr4bqUckQn0kd_jnTtk8, reference number: 10.5061/dryad.mkwh715f.

ORCID

Chaoyue Cheng https://orcid.org/0000-0002-6878-3908
Xuwei Deng https://orcid.org/0000-0002-7816-2136

REFERENCES


SUPPORTING INFORMATION
Additional supporting information can be found online in the Supporting Information section at the end of this article.