


ORIGINAL ARTICLE

Density-driven facilitations increase ecological resilience under eutrophic stress

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Abstract

1. Eutrophication has been observed to decrease the ecological resilience of macrophyte-dominated freshwater ecosystems, thereby resulting in more vulnerability to external perturbations and easily tipping into an algae-dominated state. The stress-gradient hypothesis (SGH) posits that plants exhibit positive plant-plant interaction (facilitation) in response to stress, potentially buffering the detrimental impacts of eutrophication. However, few studies attempted to link plant density with species-species interactions and ecological resilience in the context of eutrophic stress.
2. Here, we investigated how the density of neighbour plant species (*Potamogeton lucens*) affects the change rate of nutrients or Chl a (chlorophyll-a) and target plant species (*Potamogeton maackianus*) along a gradient of nutrient levels (oligotrophic, mesotrophic, eutrophic) via a 42 days mesocosm experiment. Our objective was to corroborate: (1) species interactions may shift from competition to facilitation with the increased eutrophic stress. (2) High plant density is indispensable to generate facilitation and thereby augment ecological resilience under high eutrophic stress.
3. Results showed that eutrophic scenarios significantly augmented chlorophyll-a concentration and inhibited plant height, number of branches and leaves, showing that submerged macrophytes in eutrophic states are exposed to stressful conditions. However, the increasing density of neighbouring vegetation reduced nutrient and Chl a concentrations and enhanced the performance of *Potamogeton maackianus* in eutrophic conditions, but not in mesotrophic and oligotrophic conditions. Our results indicated that density-dependent facilitation is more prevalent in eutrophic circumstances, and species interactions are likely transformed from competition to facilitation with increasing nutrient concentrations.
4. Our research demonstrated that plant density could alter the relationship between facilitation and competition; high plant density is indispensable for the operation of the stress-gradient hypothesis. Density-dependent facilitation under severe conditions could mitigate the adverse influence of eutrophication. With freshwater ecosystems progressively subjected to eutrophication, harnessing the

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density-dependent facilitation of submerged macrophytes in resilience-driven management is crucial to inhibiting the transition to an algae-dominated turbid state, which further broadens our understanding of the theory of alternative stable states in shallow lakes.

KEYWORDS

ecological resilience, eutrophic stress, facilitation, regime shifts, submerged macrophytes

1 | INTRODUCTION

Industrial and agricultural activities discharge vast quantities of macronutrients (e.g. nitrogen and phosphorus) into the lakes, which ultimately results in eutrophication and curtails the growth and reproduction of aquatic macrophytes by diminishing light availability (Dodds et al., 2009; Smith, 2003; Tilman et al., 2001). Concurrently, eutrophication heightens the risk of regime shifts from macrophyte-dominated clear-water states to algae-dominated turbid states (Scheffer et al., 1993, 2001; Scheffer & Carpenter, 2003), propelling the system towards a scenario that is difficult to shift back to macrophyte-dominated and undermines the utility functions of ecosystems for human well-beings (Chambers & Kalff, 1987; Sand-Jensen et al., 2008). Submerged macrophytes, as key components in shallow lakes, can suppress sediment resuspension (Horppila & Nurminen, 2003; Madsen et al., 2001) and compete with phytoplankton for nutrients (Jeppesen et al., 1997; Scheffer et al., 1993), potentially maintaining a clear-water state even under eutrophic conditions.

Positive plant–plant interactions (facilitation) are key factors affecting ecosystem structure and functioning that may increase the buffering capacity of lakes to eutrophication (Kéfi et al., 2016). The stress-gradient hypothesis (SGH) postulates that facilitation among plants will occur under stressful environments, potentially mitigating the adverse impacts of stress (Bertness & Callaway, 1994). In oligotrophic shallow lakes, submerged macrophytes with conservative nutrient absorption strategies predominate (i.e. in nutrient-depleted environments) (Su, Wu, et al., 2019) and interspecific competition is intensified (Gopal & Goel, 1993). However, eutrophication will favour fast-growing species, resulting in competition for light between submerged macrophytes and phytoplankton (Sand-Jensen et al., 2008) rather than for nutrients among submerged macrophytes. Thus, plant–plant interactions may shift from competition to facilitation with the intensification of eutrophic stress, which helps enhance macrophyte-dominated resilience and maintain a clear-water state under eutrophic stress (Hillebrand et al., 2007; Sand-Jensen et al., 2008). Positive interactions can expand species' realized niches and hence are expected to broaden the distribution area and geographic range by ameliorating unfavourable conditions (Bulleri et al., 2016; Stephan et al., 2021; Zheng, Babst, et al., 2024).

Moreover, it is widely acknowledged that submerged macrophytes with diverse morphology contribute to the efficient use of space and resources (Engelhardt & Richie, 2002). Submerged macrophyte vegetation forms positive feedback with water clarity: the more vegetation, the higher the water clarity, which can be mediated by plant diversity and morphological traits (Cheng et al., 2023; Su et al., 2024).

Plant communities with higher morphological complexity may be easier to generate positive plant–plant interactions in harsh conditions, which consequently have higher positive feedback strength and ecological resilience. Morphological plasticity of submerged macrophytes is essential for adaptation to low-light environments caused by eutrophication. For example, in nutrient-rich environments, plants will allocate more biomass to the stem to enhance the competition with phytoplankton (Goulder, 1969; Ozimek et al., 1990) for light, which will inhibit the proliferation of phytoplankton and subsequently in turn provide conducive conditions for their own development.

Plant density is associated with multiple ecological rules such as species competition, species coexistence and self-thinning (Levine et al., 2017; Weiner & Freckleton, 2010). Abundant macrophytes are suggested to ameliorate the harmful effects of eutrophication and improve the resilience of clear-water state. Density-dependent facilitation among submerged macrophytes is projected to mitigate the severe low-light availability (Cheng et al., 2023; Scheffer et al., 1993). That is, neighbours are needed under higher stress of eutrophication to maintain a given level of habitat improvement (Le Bagousse-Pinguet et al., 2012). However, to our knowledge, there is scarce experimental evidence substantiating the role of density-dependent facilitation in promoting the resilience of macrophyte-dominated states under eutrophication.

Here, we tested how neighbour density influenced the growth of central species with intensification of eutrophication. Our objective is to underscore the significance of plant density as a crucial regulator for plant–plant facilitation under eutrophic stress. We propose that (1) plant–plant interactions may shift from competition to facilitation with the intensification of eutrophication. That is, facilitation among plants (positive indirect interaction) occurs in nutrient-rich environments (eutrophic stress) but not in the nutrient-poor state (Figure 1a–c). (2) A higher plant density is paramount to instigate facilitation and thereby improve ecological resilience and thus buffer adverse effects caused by eutrophication (Figure 1d).

2 | MATERIALS AND METHODS

2.1 | Experimental design

Potamogeton maackianus and *Potamogeton lucens* are widely distributed around the world and in China (Cao et al., 2017). *Potamogeton maackianus*, erstwhile the predominant species in Yangtze shallow lakes (Chambers & Kalff, 1987; Qiu et al., 2001), has been significantly suppressed by eutrophication and manifests difficulty restoring its

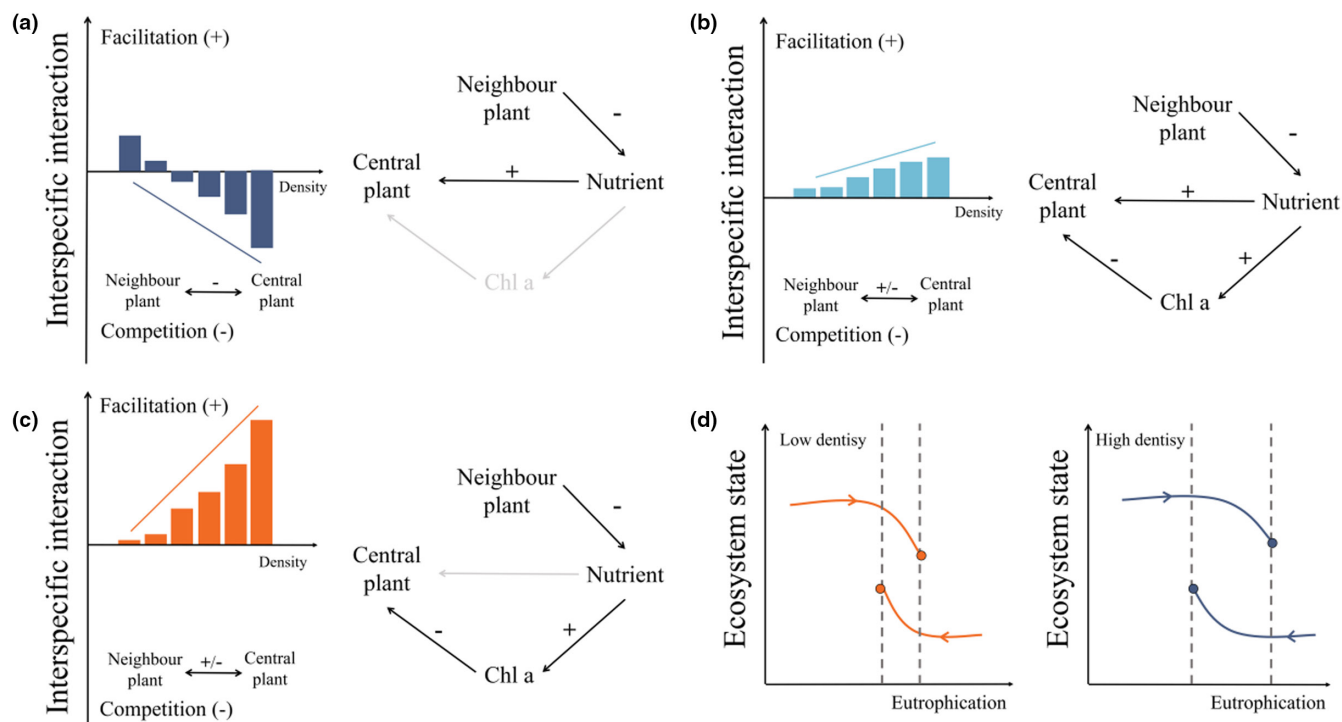


FIGURE 1 Relationships between plant density and species interaction with increasing pressure of eutrophication. (a–c) show the relationship between plant interactions and plant density in oligotrophic, mesotrophic and eutrophic conditions (shown by dark blue, sky blue and orange, respectively), and the possible pathways leading to the relationships. Positive values indicate facilitation, while negative values indicate competition. (d) shows the relationship between plant interactions and plant density and the effect of plant density on macrophyte-dominated ecological resilience under eutrophic pressure. The overlapping area indicates ecological resilience.

population, despite its capacity to withstand a broad range of fluctuations in environmental nutrient concentrations (Fu et al., 2013; Ni, 2001). Moreover, *P. lucens* is also sensitive to eutrophication, showing inhibited growth and expansion (Litav & Lehrer, 1978; Uehara et al., 2006). Thus, we opted for *P. maackianus* and *P. lucens* in our experiment given their sensitivity to eutrophic stress.

Our experiment was conducted at the Donghu Ecosystem Experimental Station, Institute of Hydrobiology, Chinese Academy of Sciences (114.36 E, 30.55 N) for 42 days. *Potamogeton maackianus* and *P. lucens* were collected from Erhai (100.1902 E, 25.7582 N) in Yunnan Province, China. Submerged plants with a shorter main axis (such as *Potamogeton maackianus*) can form a dense mat at the bottom of lakes and have an advantage in inhibiting sediment resuspension (Barko & James, 1998; Li et al., 2008). Compared with *P. maackianus*, *P. lucens* could tolerate low light to compete with phytoplankton because of its greater height. Thus, the system in which species of different plant heights co-occur may be more likely to exhibit stronger positive interactions. We emulated the methodology of prior research (Le Bagousse-Pinguet et al., 2012) where *P. maackianus* was selected as the central species and *P. lucens* was chosen as the neighbour species (n), with the planting layout depicted in Figure 2. Three nutrient levels (oligotrophic, mesotrophic and eutrophic) were established and 3 *P. maackianus* and 0, 3, 6, 9, 12, or 16 *P. lucens* were planted in each nutrient level (50 cm × 50 cm × 80 cm). We set up one control group ($n=0$) and five treatment groups ($n=3, 6, 9, 12, 16$, respectively) in each nutrient level. For each species, plants with similar height

(length of main axis, cm) and number of leaves were chosen, and surplus branches were pruned. Subsequently, plants were transplanted into plastic containers (7 cm in diameter and 10 cm in height) bearing sediment harvested from East Lake of Wuhan using a Peterson sediment harvester. There were three replicates per treatment or control, yielding an aggregate of 18 tanks per nutrient level, with a total of 54 tanks. The entire experiment was draped with cloth to prevent excessive solar radiation from damaging the plants.

All plants were thoroughly acclimatized to the aquatic environment for 2 weeks. After that, based on the evaluation of the possible nutrient thresholds of lakes (Cheng & Li, 2006; Richardson et al., 2007; Yang et al., 2008), the concentrations of total nitrogen and total phosphorus were adjusted by adding NaNO_3 and K_2HPO_4 (Oligotrophic: + 1 mg L⁻¹ N, + 0.1 mg L⁻¹ P; Mesotrophic: + 0.5 mg L⁻¹ N, + 0.05 mg L⁻¹ P; Eutrophic: + 0.1 mg L⁻¹ N, + 0.01 mg L⁻¹ P). Then, TN and TP (total nitrogen and phosphorus of surface water, mg L⁻¹, including the content in particulate matter) in the tank were measured immediately after the addition of nitrogen and phosphorus, while Chl a was measured on 2 days later, at which juncture the concentrations of TN, TP and Chl a were denoted as the results of the first week. One week later, TN, TP, and Chl a in the water were measured again, at which juncture the concentrations of TN, TP and Chl a were denoted as the results of the second week. Subsequently, all *P. maackianus* were gently removed from tanks along with their respective cups to measure plant height (cm), number of branches and leaves as the result for the second week of morphological traits. Then, *P. maackianus* plants were placed back into the tanks. After

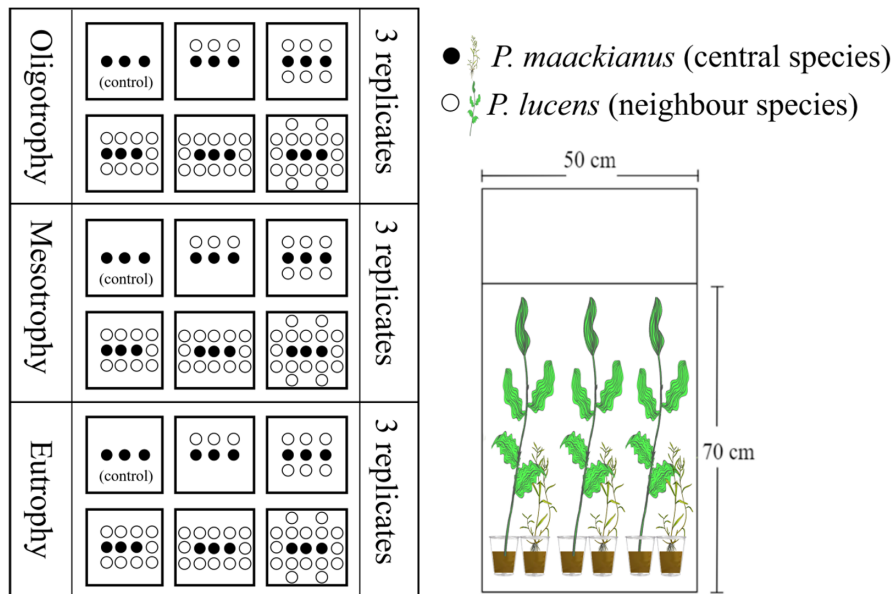


FIGURE 2 Detailed experimental design. We set three nutrient levels. In each nutrient level, we set up one control group (neighbour species=0) and five treatment groups (neighbour species=3,6,9,12,16, respectively). Three replicates were set for each control and treatment group. The black circle represents *P. maackianus* (central species) and the white circle represents *P. lucens* (neighbour species).

the sediment settled, the above steps were repeated, and the measured results were recorded as TN, TP, Chl a in the third and fourth weeks, and as morphological traits at the fourth week. During the experiment, nutrients were added twice to achieve a significant nutrient gradient (Figure 3a,b and Figure S5a,b). TN, TP and Chl a were measured four times, and morphological traits were measured twice and each replicate was sampled on a different day. Each time, 80mL of surface raw water was taken to measure TN and TP concentrations in water, and 1L of surface water was filtered through a GFC membrane, and then used to measure Chl a. At the end of the experiment, the central species and the neighbour species were taken out to measure dry weight (g).

2.2 | Laboratory analysis

Total nitrogen (TN, mg L⁻¹) and total phosphorus (TP, mg L⁻¹) in the water column were measured by standard methods (Huang et al., 1999). In particular, the water TN and TP were digested with potassium persulfate (Sigma Aldrich, Sigma Aldrich Trading Co., LTD) in a sterilized pot (GR85DA, Zealway instrument Inc.) at 120°C for 30min in advance. In addition, the water (filter 1L per measurement) is first filtered through the Whatman GF/C fibre glass filter (GF/C, Whatman, GE Healthcare UK Limited) and subsequently extracted from the residue on the fibre glass filter with 90% ethanol (GoldWallReagent Co. LTD) at 4°C for 24h, and finally Chl a (µg L⁻¹) was determined by spectrophotometer (UV-2550, Shimadzu Instrument Co., LTD). The neighbour species and the central species were dried to a constant mass in an oven (101-1AB, Tianjin Test Instrument Co., LTD) at 60°C and the dry weight was weighed (g).

2.3 | Data analysis

The log-response ratio (LRR) (Hedges et al., 1999) of nutrient decrease could be used to quantify the rate of change of the

treatment (neighbour=3, 6, 9, 12 and 16) relative to the control group (neighbour=0) and indirectly reflect the interactions among plants (Le Bagousse-Pinguet et al., 2012), as specified in Equation (1):

$$\text{LRR} = \log \left(\frac{T_2 - T_1}{C_2 - C_1} \right) \quad (1)$$

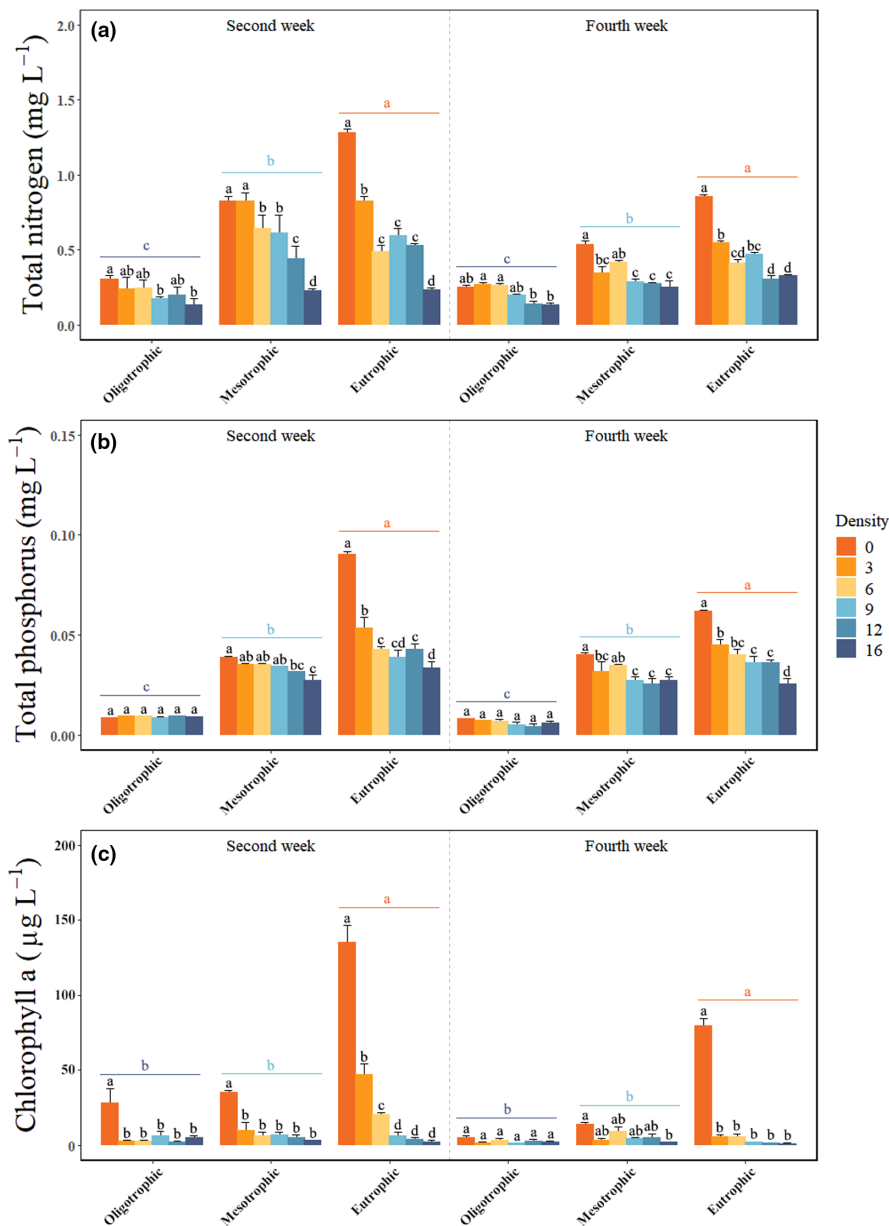
Where, T_1 and T_2 are TN, TP and Chl a of the water in the first (third) and second (fourth) measurement results in treatment groups of each nutrient level. C_1 and C_2 are TN, TP and Chl a of the water in the first (third) and second (fourth) measurement results in control groups, respectively. The LRR calculated using TN, TP, and Chl a of the first (third) and second (fourth) weeks is recorded as the LRR of second (fourth) week. Positive interactions triggered by neighbour plants under eutrophic stress increased with the TN, TP, and Chl a rate of change (Le Bagousse-Pinguet et al., 2012). Conversely, if nutrient change in the treatment group was lower than that in the control group, there may be negative plant-plant interactions (competition) in the system.

To further explore the interactions between central and neighbour species, especially for morphological traits, we quantified the effects of neighbours on central species using a neighbour-effect intensity index with additive symmetry (NInt_A, Equation 2), because NInt_A exhibits additive symmetry, avoiding underestimation of facilitation (Danet et al., 2024; Díaz-Sierra et al., 2017). NInt_A <0 indicates competing interactions, and >0 indicates facilitating interactions.

$$\text{NInt}_A = 2 \frac{\Delta P}{P_{-N} + |\Delta P|} \quad (2)$$

Where, ΔP is the total neighbour effect ($P_{+N} - P_{-N}$). P_{-N} is the performance (number of branches, height and number of leaves) of central species without neighbours. P_{+N} is the performance of central species with neighbours. Measurements of morphological traits in second and fourth week were used to quantify the effects of neighbouring species

FIGURE 3 Differences in total nitrogen, phosphorus and chlorophyll-a concentrations (mean \pm se) in neighbour density \times nutrient treatments in the second and fourth week of the experiment. Significant differences ($P < 0.05$) are indicated by different letters. Dark blue, sky blue and orange letters show the difference between oligotrophic, mesotrophic and eutrophic levels, respectively. Black letters indicate the difference caused by neighbour density within the nutrient level.



on morphological traits of central species ($NInt_A$) in the second and the fourth week, respectively.

2.4 | Data analysis

Firstly, we used two-way repeated measures ANOVA to compare the differences in TN, TP, and Chl a among three nutrient levels in the first and third week of the experiment to determine the existence of a nutrient gradient. Subsequently, repeated measures ANOVA (for groups without neighbour) and linear mixed models were used to explore the effect of eutrophication on the morphological traits of plants (number of branches and leaves, height and height/branches). In linear mixed models, TN and TP were set as fixed factors and time as random factors; and the same model was also used to explore the effects of TN and TP on phytoplankton (Chl

a). Then, two-factor repeated measures ANOVA and general linear model were used to explore how plant density and fertilization affected TN, TP, Chl a and morphological traits. Similarly, two-way repeated ANOVA and general linear models were used to explore how plant density and fertilization affected plant-plant interactions (LRR and $NInt_A$). Finally, with $NInt_A$ as a fixed factor and time as random factors, a linear mixed model was constructed to explore the relationships between $NInt_A$ and LRR to test whether positive interactions contributed to changes in TN, TP and Chl a in water. Significant factors from the two-way repeated measures ANOVA were further investigated using Tukey HSD tests using the 'emmeans' package. The linear mixed models were built by the 'lmer' function in 'lme4' package, and its significance (p -value) and R^2 (R_M^2 and R_C^2) were calculated using the 'lmerTest' and 'MuMIn' packages, respectively. All statistical analyses were performed in R 4.3.0 (R Core Development Team, 2023).

3 | RESULTS

3.1 | Effects of neighbour density and nutrients on TN, TP, Chl a and morphological traits of macrophytes

The nutrient \times neighbour-density treatments significantly affected nutrient and Chl a concentrations and morphological traits of plants (Tables S1–S3). Fertilization resulted in an explosive growth of phytoplankton (Figure S1), especially in tanks without plant neighbours (mean Chl a concentration = $135 \pm 11 \mu\text{g L}^{-1}$ in second week; mean Chl a concentration = $80 \pm 4 \mu\text{g L}^{-1}$ in fourth week), significantly impeding the growth of macrophytes (Figures S2 and S3). At eutrophic and mesotrophic levels, Chl a increased significantly with TN and TP concentrations, but this did not occur under oligotrophic conditions (Figure S1). When comparing the control group ($n=0$) in different nutrient levels, that the number of branches, plant height and number of leaves were significantly lower in eutrophic conditions than in oligotrophic conditions (Table S4 and Figure S2). In eutrophic conditions, the number of branches, height and number of leaves decreased with increasing TN and TP concentrations (Figure S3, $p < 0.05$). In mesotrophic conditions, the number of branches and leaves and height decreased with increasing TN concentrations (Figure S3a,c,e; $R_M^2 = 0.21$, $p = 0.012$; $R_M^2 = 0.16$, $p = 0.022$; $R_M^2 = 0.16$, $p = 0.013$). Number of branches decreased significantly with increasing TP concentrations (Figure S3b; $R_M^2 = 0.13$, $p = 0.032$), while other traits had no significant relationship with nutrients ($p > 0.05$). In oligotrophic conditions, no traits had significant relationship with TN and TP ($p > 0.05$). In addition, in eutrophic and mesotrophic conditions, the ratio of height to number of branches increased significantly with increasing TN and TP concentrations (Figure S4, $p < 0.05$). However, the ratio of plant height to branch number was unrelated to TN and TP concentrations under oligotrophic conditions (Figure S4, $p > 0.05$).

Fertilization and neighbour density significantly affected TN, TP and Chl a concentrations. First-week fertilization significantly affected Chl a concentration; yet neighbour density had little influence on TN and TP across nearly all nutrient levels. However, neighbour density significantly reduced Chl a in the water during this period (Figure S5c, first week). Fertilization significantly affected Chl a in the second week (Figure 3) but there was no distinction in Chl a concentration between the mesotrophic and oligotrophic groups (Figure 3c, second week). Notably, neighbour density significantly reduced TN, TP, and Chl a concentrations across all nutrient levels (Figure 3, second week). In the third week, fertilization exhibited substantial impacts on Chl a (Figure S5, third week), but concentrations did not differ between mesotrophic and oligotrophic groups (Figure S5c, third week). Within all nutrient levels, neighbour density significantly reduced TN, TP, and Chl a concentrations, except TP in the oligotrophic group (Figure S5, third week). Significant changes in Chl a concentrations occurred in the fourth week under nutrient manipulation (Figure 3, fourth week); however, mesotrophic and oligotrophic groups did not differ (Figure 3c, fourth week). Within all nutrient levels, neighbour density significantly reduced TN, TP, and Chl a concentrations, except TP and Chl a concentrations in the oligotrophic group (Figure 3, fourth week). Furthermore, TN, TP, and Chl a concentrations substantially

declined with elevated total dry weight in both mesotrophic and eutrophic conditions (Figure S6a–c, $p < 0.05$), while only TN diminished noticeably with increased total dry weight in oligotrophic conditions (Figure S6a; $R^2 = 0.48$, $p = 0.001$).

As for the effects of fertilization \times neighbour on morphological traits, fertilization significantly changed morphological traits, but eutrophic and mesotrophic conditions did not differ (Figure 4, second and fourth week). Within nutrient levels, neighbour density significantly altered the morphological traits in the second week, except for oligotrophic conditions (Figure 4, second week). In the fourth week, neighbour density significantly altered plant morphology except for the number of branches in oligotrophic conditions (Figure 4, fourth week). In addition, morphological traits increased with increasing dry weight in eutrophic conditions (Figure S6d–f, $p < 0.05$); however, the relationship between morphological traits and dry weight did not differ between mesotrophic and oligotrophic levels (Figure S6d–f, $p > 0.05$).

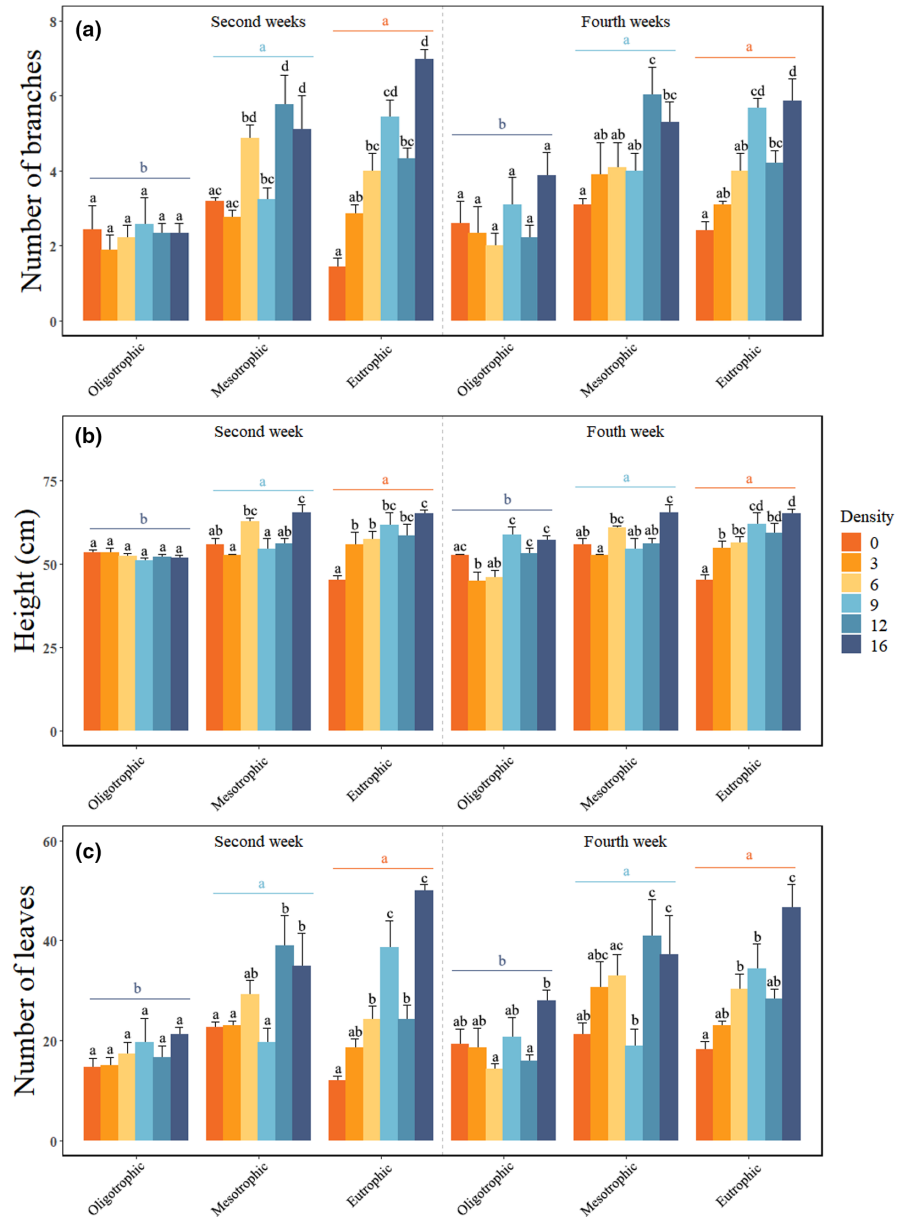
3.2 | Density-dependent SGH

Central species' dry weight was not correlated with neighbours in meso- and oligotrophic conditions (Figure S7a,b; $R^2 < 0.01$, $p = 0.806$; $R^2 = 0.10$, $p = 0.194$). However, the dry weight of the central species in the eutrophic conditions increased with the neighbour's dry weight (Figure S7c; $R^2 = 0.71$, $p < 0.001$).

Fertilization and neighbour density significantly affected plant-plant interactions (Table S5 and S6). Fertilization significantly altered LRR of TN, TP and Chl a in the second week (Figure 5, second week), yet no difference existed for LRR (Chl a) between mesotrophic and oligotrophic levels (Figure 5c, second week). Within nutrient levels, neighbour density significantly impacted LRR at the second week (Figure 5, second week), excluding LRR (TP) of mesotrophic level (Figure 5b, second week). For the results of the fourth week, fertilization significantly affected LRR of TN and TP, but had no significant effect on LRR of Chl a (Figure 5, fourth week). Within nutrient levels, neighbour density significantly modified LRR in the fourth week. Furthermore, LRR (TN), LRR (TP), and LRR (Chl a) significantly increased with elevated plant dry weight in eutrophic level (Figure S8a–c, $p < 0.05$), yet, no correlation was observed between morphological traits and dry weight in mesotrophic and oligotrophic levels (Figure S8a–c, $p > 0.05$).

Fertilization significantly altered the NInt_A of number of branches, height, and number of leaves in the second week (Figure 6, second week), yet, no distinction in NInt_A (number of leaves) existed between mesotrophic and oligotrophic levels (Figure 6c, second week). Within nutrient levels, neighbour density notably affected the NInt_A of morphological traits in eutrophic and mesotrophic levels in the second week, yet did not affect traits in oligotrophic conditions (Figure 6, second week). For the results of the fourth week, fertilization resulted in a notable variation in the NInt_A , specifically in the number of branches, height, and the number of leaves. However, there was no discernible difference in NInt_A between mesotrophic and oligotrophic levels during this period (Figure 6, fourth week). Furthermore, within nutrient levels, neighbour density significantly

FIGURE 4 Differences in morphological traits (mean \pm se) in neighbour density \times nutrient treatments in the second and fourth week of the experiment. Significant differences ($p < 0.05$) are indicated by different letters. Dark blue, sky blue and orange letters show the difference between oligotrophic, mesotrophic and eutrophic levels, respectively. Black letters indicate the difference caused by the neighbour density within the nutrient level.



altered the $NInt_A$ during the fourth week, excluding $NInt_A$ of height and the number of leaves (Figure 6b,c, fourth week). Additionally, in eutrophic conditions, the $NInt_A$ for the number of branches, height, and number of leaves was positively correlated with dry weight (Figure S8d-f; $p < 0.05$). However, morphological trait-dry weight correlations were non-significant at mesotrophic and oligotrophic levels (Figure S8d-f; $p > 0.05$). Moreover, our results revealed significant positive correlations between $NInt_A$ and LRR (Figure 7, $p < 0.05$).

4 | DISCUSSION

As per our hypothesis, our study showed that increasing eutrophication pressure negatively affects plant performance, which is shown by lower plant height and fewer branches and leaves at low plant density in eutrophic conditions. We found that $NInt_A$ of plant morphological traits increased from negative to positive with increasing

eutrophication, revealing that plant-plant interactions are inclined to shift from competition to facilitation with increasing environmental stress. In addition, increased neighbour density under eutrophic stress markedly increased branch count, leaf number; plant height and reduction rate of TN, TP and Chl a, suggesting that plant-plant facilitation is density-dependent. We also found that there are positive relationships between $NInt_A$ and LRR, indicating that plant-plant facilitation could buffer adverse effects caused by eutrophication, which may enhance the resilience of the macrophyte-dominated ecosystem and delay the collapse threshold of regime shift (Kéfi et al., 2016).

4.1 | Linking facilitation with ecological resilience to disturbance

Ecosystem resilience denotes the capacity of ecosystems to absorb disturbances and reconfigure under external stress, preserving their

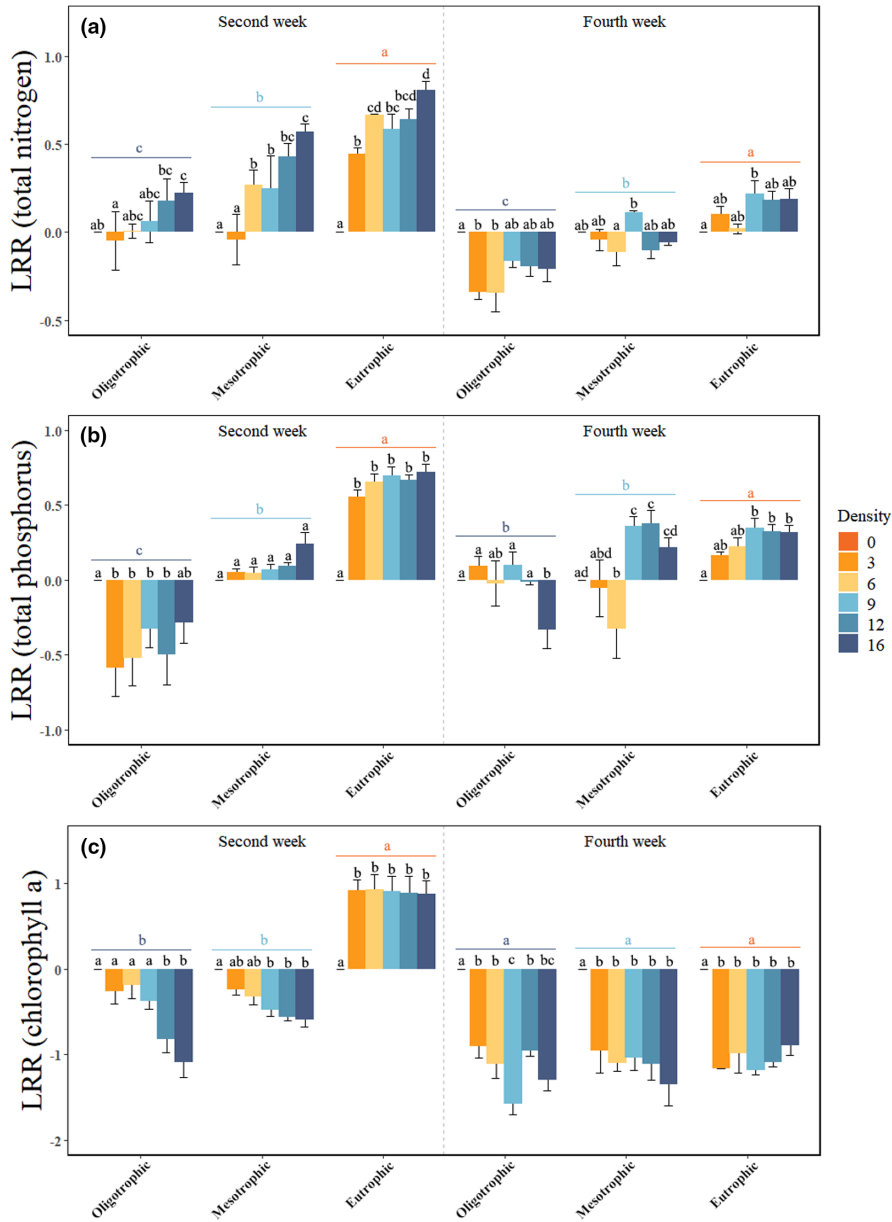


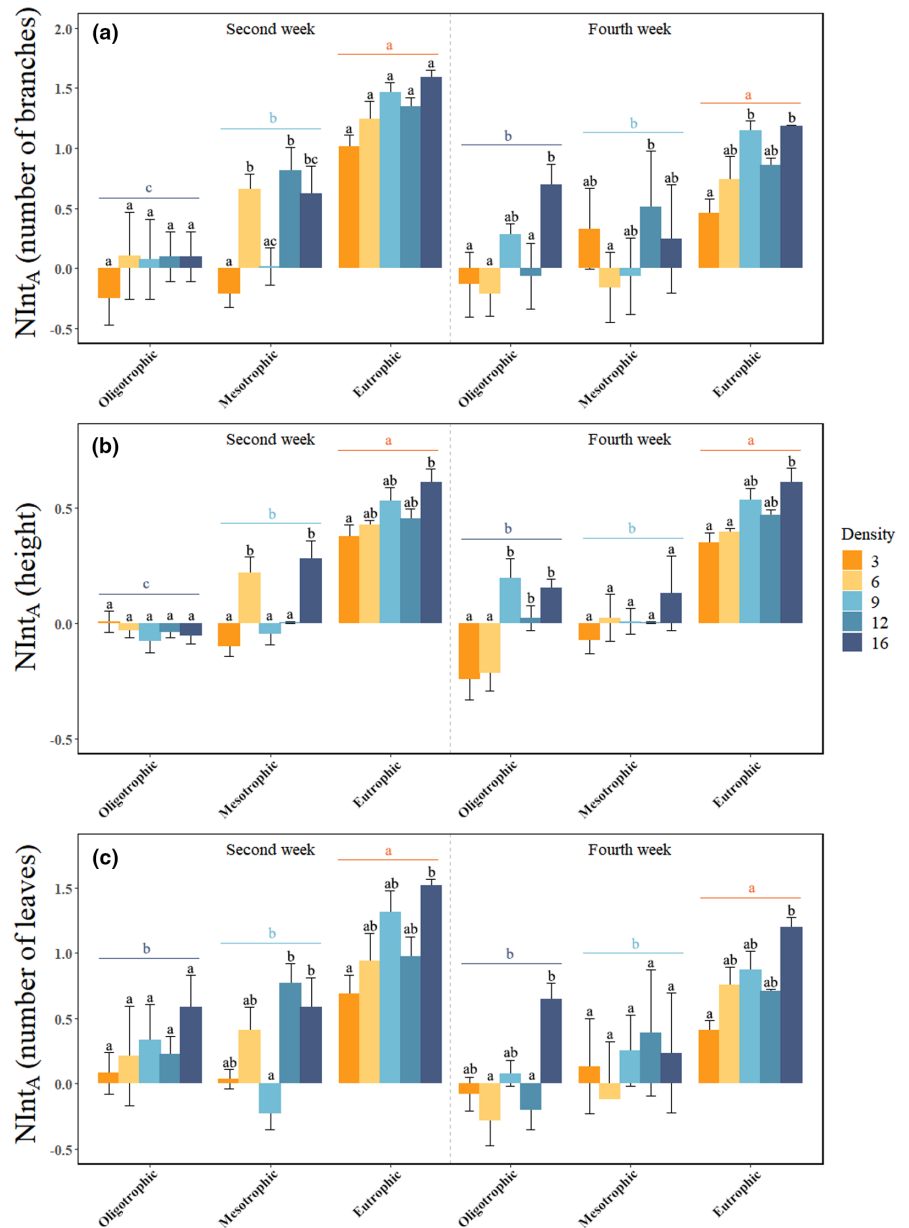
FIGURE 5 Differences in LRR (mean \pm se) in neighbour density \times nutrient treatments in the second and fourth week of the experiment. Significant differences ($p < 0.05$) are indicated by different letters. Dark blue, sky blue and orange letters show the difference between oligotrophic, mesotrophic and eutrophic levels, respectively. Black letters indicate the difference caused by the neighbour density within the nutrient level.

essential function and structure (Walker et al., 2004). Competition between submerged macrophytes and phytoplankton might catalyse certain species to gain advantage from the existence of neighbouring species by generating positive plant-environment feedbacks (Silveira & Thiébaud, 2020; Zheng et al., 2016). Strong positive feedback loops potentially lead to non-linear responses by lake ecosystems to external abiotic pressures, which substantially altered ecosystem functioning and services (Hilt et al., 2017; Scheffer & Carpenter, 2003). The ecological resilience of macrophyte-dominated states under eutrophic stress may be related to facilitation strength and multidimensional positive feedbacks (Kéfi et al., 2016), which are the result of species-species and species-environment interactions. Consequently, higher ecological resilience is probably related to high niche differentiation of submerged macrophyte communities (Weiher & Keddy, 1995). The multidimensional distribution in niche space enhanced resource use

and thereby increased ecosystem productivity (Mason et al., 2005). Thus, understanding the mechanisms by which density-dependent SGH stabilizes and disrupts ecosystems is critical for lake management. Inadequate macrophyte density would result in low ecological resilience in eutrophic conditions, increasing the risk for ecosystem collapse towards an algae-dominated turbid state (Bicudo et al., 2007). Conversely, escalating plant density may enhance positive interactions among plants, improving ecological resilience to fortify the system's resistance to disturbances. Therefore, high plant density is likely beneficial for the success of ecological restoration programs in eutrophic lakes.

Benefiting from plant-plant facilitation, submerged vegetation could still maintain high productivity during the early and even middle stages of eutrophication (Hillebrand et al., 2007), which may be attributed to the high species diversity, morphological complexity and regulation ability to maintain a constant element content in the

FIGURE 6 Differences in $NInt_A$ (mean \pm se) in neighbour density \times nutrient treatments in the second and fourth week of the experiment. Significant differences ($p < 0.05$) are indicated by different letters. Dark blue, sky blue and orange letters show the difference between oligotrophic, mesotrophic and eutrophic levels, respectively. Black letters indicate the difference caused by the neighbour density within the nutrient level.



macrophyte community (Cheng et al., 2023; Su, Chen, et al., 2019). Plant diversity effects on ecosystem functioning are one of the most classic topics in ecology and recent manipulative experiments often reported a positive effect of plant species diversity on biomass productivity (Liang et al., 2016; Zheng, Barry, et al., 2024). Interspecific facilitation is considered to be a key mechanism by which biodiversity affects ecosystem productivity (Cardinale et al., 2002; Danet et al., 2024). In addition, morphological complexity and stoichiometric homeostasis are positively correlated with macrophyte community biomass productivity, enhancing positive feedbacks to maintain a clear-water state (Cheng et al., 2023). Consequently, focusing on plant morphological traits in lake management could be instrumental in establishing 'underwater forests' with complex spatial structures, of immense importance in promoting the ecological resilience of clear-water states and curtailing the risk of regime shifts instigated by eutrophication.

4.2 | Density-dependent facilitation under eutrophication

Eutrophication represents a challenging condition for the proliferation of submerged macrophytes, and the global recession of submerged macrophytes from shallow lakes has been attributed to intensified eutrophication (Ansari et al., 2011; Zhang et al., 2017). Previous research has indicated that plants elongate their height to accommodate low-light conditions caused by eutrophication (Chen et al., 2016). However, some studies showed that deficiency in light availability suppresses nodes, branch quantity and plant height (Zhang et al., 2012). Our results have a similar result as eutrophication significantly reduced the number of branches, plant height and leaf number, but increased the ratio of plant height to branch number. This could be explained by the trade-off between plant survival and reproduction: plants may augment inter-node distance

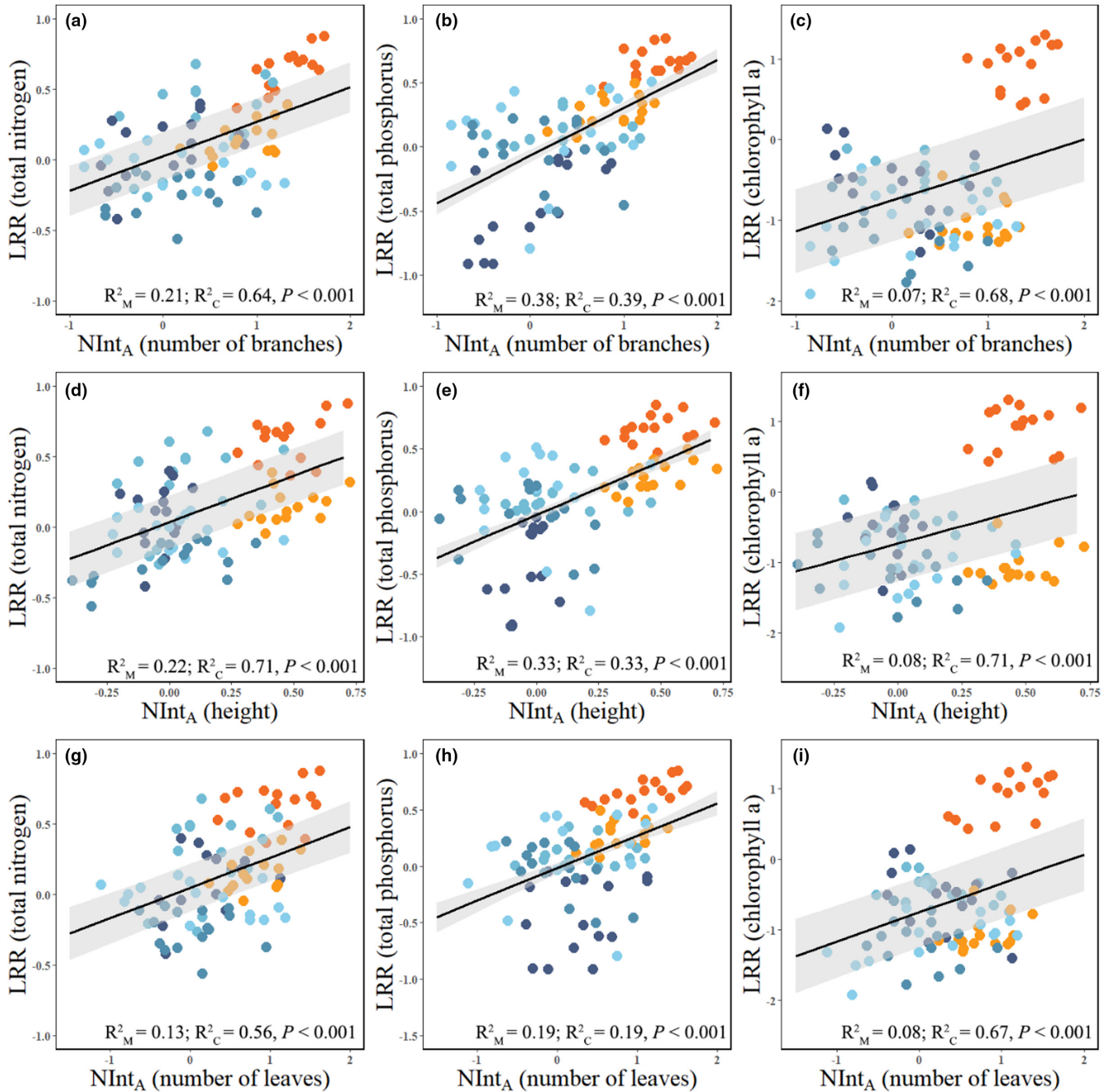


FIGURE 7 Relationships between log-response-ratio (LRR) and relative neighbour effect (Neighbour-effect intensity Index with Additive symmetry). Different colours represent different nutrient level and time. Each dot represents a tank. The R^2_M and R^2_C represent model variations explained by fixed effects and the combination of fixed and random effects, respectively.

to adapt to low-light availability at the expense of reducing the number of nodes and branches, thereby diminishing the plant's capacity to expand and colonize (Silveira & Thomaz, 2015). However, the appearance and increase of neighbour species enhanced the capacity for nutrient uptake and allelopathy of submerged macrophyte communities inhibited the growth of phytoplankton. Thus, the emergence and increase of neighbour species may lead to a cliff-like decline in phytoplankton. In oligotrophic conditions, light is no longer the limiting factor, leading to low reduction rate of Chl a concentration.

Competition and resource availability are vital determinants that sculpt plant community structure and species distribution (Grime, 1977; Zhang et al., 2015). The manifestation of density-dependent facilitation among plants in eutrophic conditions may stem from negative correlations between nutrients and light availability and 'competitive release' among submerged macrophytes—the transition from the primary contention among submerged macrophytes for nutrients to the rivalry between submerged macrophytes and phytoplankton for light (Levine et al., 2017). The emergence and augmentation of neighbouring species are likely to

suppress phytoplankton growth by decreasing nutrient availability, which results in a positive feedback loop of plant-water clarity (Su, Chen, et al., 2019) to promote the growth of morphological traits (height, number of branches and leaves) of submerged macrophytes and thus augment the macrophyte community's capacity for expansive colonization. Moreover, during the experiment, we found that at a higher neighbour density under eutrophic conditions, filamentous algae grew on the surface of the submerged macrophytes. Due to the higher specific surface area of filamentous algae (Mulbry & Wilkie, 2001; Xia et al., 2021), its ability to absorb nutrients is stronger, which may also be one of the reasons why the change rate of nutrients (LRR) in eutrophic level increased with density and was significantly higher than that in oligotrophic conditions. At present, there are also researchers trying to build a 'plant-filamentous algae' symbiotic system to deal with eutrophication (Xia et al., 2021). However, on the other hand, due to the weak allelopathic effect of submerged macrophytes on filamentous algae (Hilt & Gross, 2008), epiphytic filamentous algae may overproliferate, greatly reducing light availability for submerged macrophytes (Irfanullah & Moss, 2004; Tiling & Proffitt, 2017), and thus inhibiting their growth, or even lead to the death of plants. Therefore, in ecological restoration, it is essential to be aware of the overgrowth of filamentous algae to maintain a clean water state. In addition, submerged macrophytes can supply high-quality carbon resources (Gulati & Demott, 1997) to bacteria and flagellate organisms, which could provide polyunsaturated fatty acids (Tang et al., 2019) important for zooplankton growth (Tang et al., 2023) and thus promote energy flow in microbial food webs. Concurrently, plant-plant facilitation will also aid macrophytes to form more intricate spaces, potentially providing habitat for zooplankton and inhibiting sediment resuspension (Horppila & Nurminen, 2003; Jeppesen et al., 1998). Finally, facilitation arising from increasing neighbour density may also assist in mitigating mechanical damage to plants (Zhu et al., 2014, 2018) from the pressure of water level fluctuation and wind-driven waves (Madsen et al., 2001; Schoelynck et al., 2013).

5 | CONCLUSION

Our findings demonstrate that plant-plant facilitation under harsh conditions is density-dependent. Eutrophication significantly impedes plant growth, potentially hampering the reproduction and colonization of submerged macrophyte communities. Nevertheless, macrophyte species interactions tend to change from competition to facilitation with increasing pressure of eutrophication. Such facilitation is more prevalent with increasing plant density, which may mitigate negative impacts of eutrophication. That is, interactions among plants exhibited density-dependent facilitation under eutrophic conditions but not in mesotrophic or oligotrophic conditions. We suggest that the transition from macrophyte to algae-dominated states in shallow lakes may originate from the diminishment of positive interactions between plants under eutrophic stress. Thus, we

propose that future research should focus more on plant-plant interactions, particularly density-dependent facilitation under severe conditions, which contributes to the comprehension of regime shifts and offers a novel perspective for lake management.

AUTHOR CONTRIBUTIONS

Conceptualization, data interpretation: C.C., H.S., Y.L., S.X., Z.H., J.C., P.X. Developing methods, conducting the research: C.C., H.S., J.F.C., Q.R., Y.L., S.X., Z.H., N.X., Y.P., W.S. Data analysis, preparation of figures and tables: C.C., H.S., N.X., Y.P. Writing: C.C., H.S., W.S., Q.R., J.F.C., Y.P., N.X., Y.L., S.X., Z.H., J.C., P.X. All authors read and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest for this article.

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/9XfGuzZAVGXWNE6J2M5iMFs2Haz_BdBRqtQEgPZkiw, reference number: 10.5061/dryad.31zcrjwd.

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SUPPORTING INFORMATION

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

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