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Original Articles

Eutrophication promoted the change of macrophyte community from R strategy to C strategy in Lake Taihu

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ABSTRACT

Functional traits effectively reflect plants' ecological strategies in response to environmental changes. This study investigated how lake eutrophication influences macrophyte communities ecological strategies by analyzing leaf functional traits along the eastern littoral zone of Lake Taihu. Using Grime's CSR framework (C: competitive; S: stress-tolerant; R: ruderal), we compared strategies among different macrophyte life forms (submerged, floating-leaved, and emergent) across a eutrophicaiton gradient. The study sites exhibited varying degrees of eutrophication (from mesotrophication to heavy eutrophication), with significant differences in nutrient contents and light availability. The macrophyte community was predominantly characterized by C and R strategies, with dominance shifting from R to C as eutrophication increased. Different life forms showed distinct responses: Submerged macrophyte transitioned from R to C strategies, floating-leaved macrophytes decreased C strategies proportion with increased S strategies while emergent macrophytes remained stable. Environmental factorss influenced community strategies indirectly through macrophyte traits, with C and S strategies negatively correlation with underwater light availability but positively with nutrient levels. while R strategy showed opposite correlations.This study revealed that reduced underwater light availability, rather than increased nutrient levels, was the primary driver of changes in macrophyte ecological strategies under eutrophication.

1. Introduction

Plants adapte to their environments by changing their functional traits, which reflect the characteristics and functions of ecosystems (Diaz et al., 2016, Wright et al., 2004). The environmental filtering theory (Keddy, 2009) suggested that only species from the regional species pool that met specific selection criteria could enter and establish successfully within local communities. The traits allowing plants to endure environmental changes plays a crucial role in facilitating this filtering process (Diaz et al., 2004). The values of functional traits of different plants determined which ecological strategies to adopt. For example, a larger leaf area allows for greater light capture, increasing photosynthetic capacity, while the presence of thorns reduces herbivory. Therefore, analyzing functional traits helped us understand the ecological strategies that plants used to adapt to their surroundings (Cross et al., 2015, Rosado and de Mattos, 2017).

Ecological strategy is a collection of plant functional traits. Grime proposed three main ecological strategies for plants adaptation, such as competitive (C, palnts grow rapidly and larger to acquire more resources), stress-tolerant (S, plants survive under harsh conditions), and ruderal (R, plants focuse on regeneration and reproduction) strategies, collectively known as CSR strategies. These strategies represents fundamental trade-offs between competition, resorces stress and disturbation. Pierce et al. (2017) developed a strategy calculation tool called StrateFy, which evaluated changes in CSR strategies based on a global assessment of three common leaf traits, such as leaf fresh weight, leaf dry weight and leaf area. This method relied on easily measurable plant traits and effectively explained various ecological strategies and

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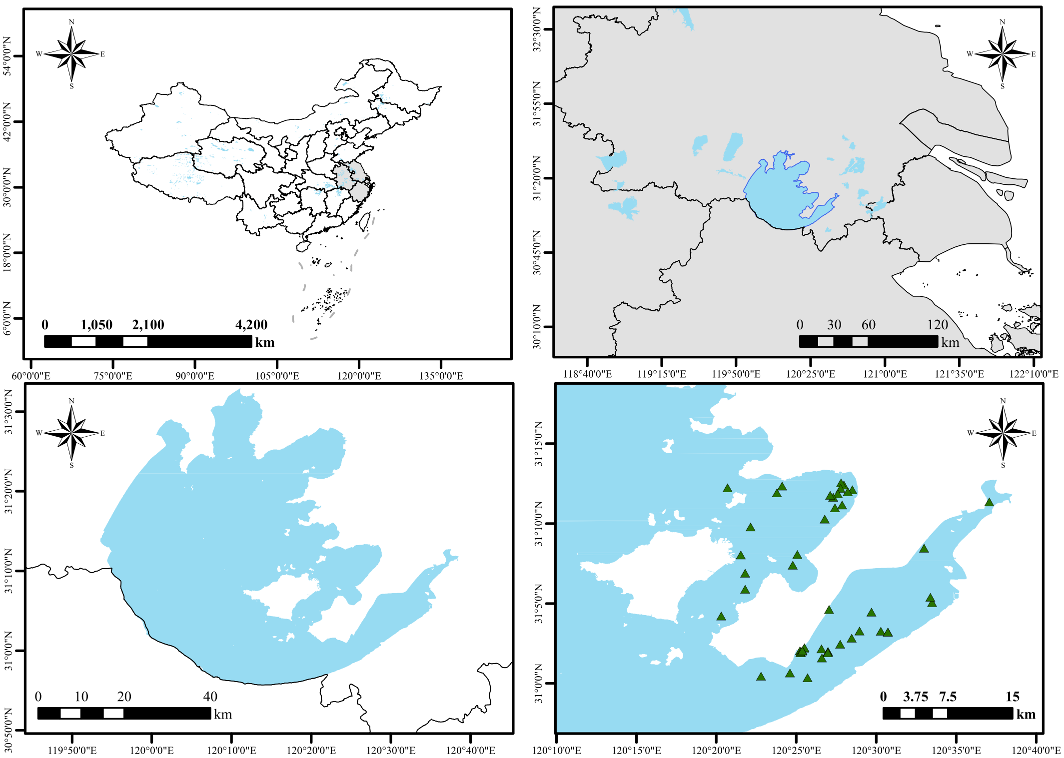

Fig. 1. Location of Lake Taihu and distribution of sampling sites.

functional trade-offs. Currently, this approach for determining CSR strategies based on leaf size and economic traits was widely accepted, superseding other plant functional traits in various contexts, such as species invasion, succession gradients and climatic regions (Barba-Escoto et al., 2019, Han et al., 2023). The effects of nutrient and light variations on plant traits and CSR strategies had been extensively studied. For instance, higher nitrogen levels reduced nutrient stress, increasing the proportion of C strategies in temperate grassland plants (Li et al., 2024). In contrast, shading can promoted R strategies among drought-resistant shrubs (Escobedo et al., 2021). However, most researches had focused on terrestrial plants, with limited studies on aquatic macrophytes.

Eutrophication is one of the most important and persistent water quality problems in freshwater ecosystems (Ansari et al., 2011, Le Moal et al., 2019). deterioration in water quality associated with nutrient enrichment brings serious ecological and socioeconomic problems, severe impacts on aquatic organisms, which poses a significant environmental challenge for lakes (Qin et al., 2013, Zou et al., 2020). Eutrophication poses a significant environmental challenge for lakes. As lakes become more eutrophic, nutrient concentrations in the water rise, reducing nutrient stress for aquatic macrophytes (Guan et al., 2010). However, eutrophication can also led to excessive phytoplankton growth, which decreases light availability underwater (Gao et al., 2020). As a result, aquatic macrophytes in these lakes would encounter a paradox of reduced nutrient stress alongside increased light stress. Macrophytes could be divided into various life forms, each with a unique relationship to the water column, such as emergent macrophytes extended above the water surface, floating-leaved macrophytes spread their leaves on the water, and submerged macrophytes live entirely underwater. That meant the effects of eutrophication would differ among these groups. We hypothesized that different levels of eutrophication may drive changes in the development of ecological strategies and in a shallow lake, with variations in strategies differing among life forms (Zhao et al., 2022). The primary objectives of this study were: (1) to identify patterns of CSR strategy changes in communities and among various life forms across different eutrophication gradients, and (2) to determine the key factors influencing the CSR strategies of aquatic macrophytes in Taihu Lake.

To test this hypothesis, we chose Lake Taihu, located in the middle and lower reaches of the Yangtze River in Eastern Plains ecoregion of China, to survey macrophytes fuctional traits and their ecological strategies. Lake Taihu is a large, shallow lake with varying nutrient statuses across different regions (Qin, 2002), of which that would provide an ideal platform to investigate the mechanisms driving changes in macrophyte ecological strategies (Qin et al., 2013). We measured key functional traits of various species and life forms under different nutrient conditions and calculated their CSR strategies

2. Materials and methods

2.1. Study area

Our research was conducted at Lake Taihu (31°30′N, 120°18′E) in the lower Yangtze River region of China. Lake Taihu is the third-largest freshwater lake in China, covering an area of 2338 km^2. It is characterized by a subtropical monsoon climate, with average annual temperatures ranging from 15 to 17 °C and average annual precipitation between 1010 and 1400 mm. As a typical shallow lake, it has an average depth of 1.89 m and a maximum depth of 2.6 m. Nutrient levels vary significantly across different regions of the lake (Qin et al., 2006). Lake Taihu once supported over 30 species of notable macrophytes (Duan et al., 2009, Luo et al., 2016, Zhao et al., 2022), According to the literature, typical aquatic macrophytes are as follows (Li et al., 2014, Qin et al., 2007). The submerged macrophytes include species such as *Zannichellia palustris, Myriophyllum spicatum, Potamogeton crispus, Vallisneria spiralis, Najas marina, Elodea canadensis, Cabomba caroliniana, Hydrilla verticillata, Potamogeton maackianus, Ruppia maritima,* and *Spirodelas polyrhiza.* The floating-leaved macrophytes include *Nymphaea tetragona, Nuphar pumila,* and *Trapa bicornis.* The emergent macrophytes mainly consist of *Phragmites australis, Sórghum halepense*, and *Nelumbo nucifera*. Submerged macrophytes are more sensitive to habitat availability, resulting in a greater diversity of species (Zhou et al., 2023).

Table 1
The standard of grading and classification.

Trophic level	Evaluation criteria	Qualitative evaluation
Oligotrophication	$\mathrm{TLI}\ (\sum) < 30$	Great
Mesotrophication	$30 \leq \mathrm{TLI}\ (\sum) \leq 50$	Good
Light eutrophication	$50 \leq \mathrm{TLI}\ (\sum) \leq 60$	Lightly polluted
Moderate eutrophication	$60 < \mathrm{TLI}\ (\sum) \leq 70$	Moderately polluted
Heavy eutrophication	$\mathrm{TLI}\ (\sum) > 70$	Heavily polluted

These macrophytes were primarily found in the northern and eastern bays of the lake (Li et al., 2014, Qin et al., 2007).The Lake Taihu basin was one of the most densely populated and economically developed regions in China. It supported 4.8 % of the national population and contributed 11.6 % of the gross domestic product (GDP), even though it occupied only 0.38 % of the country's total land area. The rapid economic growth and population increase had led to eutrophication of Taihu Lake, resulting in a significant decline in both the number and distribution of aquatic macrophyte species (Zhao et al., 2017). The remaining aquatic macrophytes were concentrated in the eastern parts of Xukou Bay and East Taihu Bay.

2.2. Sample collection and analysis

This survey was conducted from August to October 2023 and from

Table 2
Water environment parameters across different eutrophication levels in Lake Taihu.

Trophic level	WD (m)	SD (m)	SD/ WD	pH	TSS (mg/l)	Chl *a* (ug/l)	COD (mg/l)	NO_x^--N (mg/l)	NO_2^--N (mg/l)	NH_4^+-N (mg/l)	PO_4^{3-}-P (mg/l)	TN (mg/L)	TP (mg/L)	K	TLI
MT	1.46 ± 0.39^{a}	1.26 ± 0.36^{a}	0.75 ± 0.06^{a}	8.97 ± 0.61^{a}	4.22 ± 2.69^{a}	3.77 ± 6.81^{a}	1.51 ± 0.87^{a}	0.06 ± 0.14^{a}	0.003 ± 0.007^{a}	0.08 ± 0.06^{a}	0.007 ± 0.009^{a}	0.43 ± 0.23^{a}	0.03 ± 0.02^{a}	5.86 ± 1.12^{a}	40.24 ± 6.26^{a}
LE	1.55 ± 0.45^{a}	1.02 ± 0.28^{b}	0.69 ± 0.05^{ab}	8.28 ± 0.807^{b}	16.83 ± 43.96^{a}	17.37 ± 13.87^{b}	2.84 ± 0.77^{ab}	0.06 ± 0.033^{a}	0.002 ± 0.002^{a}	0.06 ± 0.07^{a}	0.006 ± 0.004^{a}	0.62 ± 0.27^{ab}	0.06 ± 0.08^{a}	11.27 ± 0.89^{b}	54.87 ± 2.86^{b}
ME	1.53 ± 0.44^{a}	0.61 ± 0.23^{c}	0.50 ± 0.05^{b}	7.79 ± 0.46^{b}	12.72 ± 11.52^{a}	9.91 ± 7.40^{ab}	3.82 ± 0.91^{b}	0.06 ± 0.02^{a}	0.003 ± 0.003^{a}	0.09 ± 0.07^{a}	0.004 ± 0.003^{a}	0.59 ± 0.14^{ab}	0.03 ± 0.01^{a}	11.77 ± 1.02^{b}	65.14 ± 2.80^{c}
HE	0.92 ± 0.71^{b}	0.32 ± 0.12^{d}	0.48 ± 0.07^{b}	7.64 ± 1.03^{b}	21.10 ± 25.36^{a}	6.22 ± 9.70^{b}	5.33 ± 2.45^{c}	0.06 ± 0.04^{a}	0.004 ± 0.003^{a}	0.14 ± 0.13^{a}	0.008 ± 0.007^{a}	0.88 ± 0.48^{b}	0.05 ± 0.03^{a}	13.94 ± 0.57^{b}	75.72 ± 5.42^{d}

Note: The following abbreviations are used for environmental parameters related to different levels of eutrophication: Mesotrophication (MT), Light eutrophication (LE), Moderate eutrophication (ME), and Heavy eutrophication (HE). Other terms include water depth (WD), transparency (SD), the ratio of secchi depth to water depth (SD/WD), total suspended solids (TSS), chlorophyll *a* (Chl*a*), chemical oxygen demand (COD), nitrate nitrogen (NO_x^--N), nitrite nitrogen (NO_2^--N), ammonia nitrogen (NH_4^+-N), orthophosphate (PO_4^{3+}-P), total nitrogen (TN), total phosphorus (TP), and the Trophic Level Index (TLI). Different letters (a, b, c, d) indicate significant differences as determined by the Tukey test ($p < 0.05$).

Table 3
Changes in traits and strategies of different life forms of macrophytes along the eutrophication gradient.

Life-form	TLI	LA(cm^2)	LFW (g)	LDW (g)	LDMC (g/g)	SLA (mm^2/mg)	Height (m)	Weight (g)	SSD (cm^3/g)	SDMC (g/g)	C(%)	S(%)	R(%)	Strategy
Submerged	**MT**	9.70 ± 17.30	0.22 ± 0.39	0.01 ± 0.02^{a}	0.1 ± 0.060^{a}	126.24 ± 91.86^{a}	0.73 ± 0.55^{a}	5.96 ± 5.99^{a}	15.21 ± 10.76^{ab}	0.11 ± 0.06	14.06 ± 15.44^{a}	4.31 ± 13.75^{a}	81.63 ± 19.53a	**R**
	LE	3.85 ± 5.22	0.09 ± 0.13	0.01 ± 0.01^{ab}	0.13 ± 0.05^{ab}	85.38 ± 40.20^{ab}	0.91 ± 0.54^{a}	5.35 ± 4.97^{a}	29.41 ± 51.55^{b}	0.12 ± 0.07	12.44 ± 12.71^{a}	10.46 ± 21.60^{ab}	77.1 ± 22.41^{a}	**R/CR**
	ME	7.64 ± 7.10	0.16 ± 0.15	0.03 ± 0.03^{bc}	0.16 ± 0.04^{b}	65.90 ± 25.59^{b}	1.58 ± 0.71^{b}	12.10 ± 11.91^{b}	11.38 ± 7.39^{a}	0.51 ± 2.18	22.83 ± 15.88^{b}	6.39 ± 9.78^{ab}	70.78 ± 20.79^{ab}	**R/CR**
	HE	6.97 ± 5.53	0.22 ± 0.20	0.03 ± 0.03^{c}	0.13 ± 0.06^{ab}	87.97 ± 71.42^{ab}	1.25 ± 0.89^{b}	15.11 ± 12.02^{b}	20.96 ± 15.89^{ab}	0.10 ± 0.06	25.36 ± 21.90^{b}	15.49 ± 22.60^{b}	59.15 ± 29.09^{b}	**R/CSR**
floating-leaved	**LE**	76.9 ± 99.56^{a}	4.55 ± 6.39^{a}	0.54 ± 0.79	0.17 ± 0.07	31.25 ± 8.30^{ab}	2.33 ± 1.65	56.55 ± 63.37	12.18 ± 5.11	0.11 ± 0.05	51.76 ± 17.64^{a}	22.12 ± 22.73^{a}	26.12 ± 13.30	**C/CSR**
	ME	29.11 ± 41.67^{b}	1.25 ± 2.32^{b}	0.18 ± 0.3	0.18 ± 0.05	38.10 ± 18.04^{a}	2.19 ± 1.66	49.65 ± 37.79	10.09 ± 3.55	0.15 ± 0.15	40.26 ± 16.17^{b}	25.73 ± 22.64^{ab}	34.01 ± 18.40	**CSR**
	HE	13.61 ± 11.78^{b}	1.37 ± 1.98^{b}	0.23 ± 0.31	0.2 ± 0.05	25.72 ± 13.94^{b}	1.37 ± 0.54	26.28 ± 12.75	12.62 ± 3.22	0.09 ± 0.02	26.14 ± 11.15^{b}	44.29 ± 36.77^{b}	29.57 ± 33.28	**S/CSR**
Emergent	**LE**	110.35 ± 21.56	2.55 ± 1.21	0.82 ± 0.24	0.32 ± 0.04	26.92 ± 4.51	1.94 ± 0.87	20.08 ± 48.47	4.53 ± 1.51	0.14 ± 0.07	56.87 ± 23.13	21.99 ± 4.55	24.51 ± 11.94	**C/CSR**
	ME	694.33 ± 779.04	22.34 ± 25.45	3.58 ± 3.85	0.17 ± 0.03	39.24 ± 9.63	1.4 ± 1.09	51.01 ± 53.44	13.78 ± 1.66	0.14 ± 0.05	58.79 ± 32.06	18.87 ± 13.14	33.91 ± 33.39	**C/CSR**
	HE	202.91 ± 627.31	8.85 ± 28.08	1.57 ± 4.21	0.26 ± 0.11	40.7 ± 19.28	1.29 ± 0.73	84.77 ± 146.46	12.36 ± 10.08	0.17 ± 0.08	45.22 ± 21.54	31.29 ± 20.75	23.49 ± 18.54	**C/CSR**

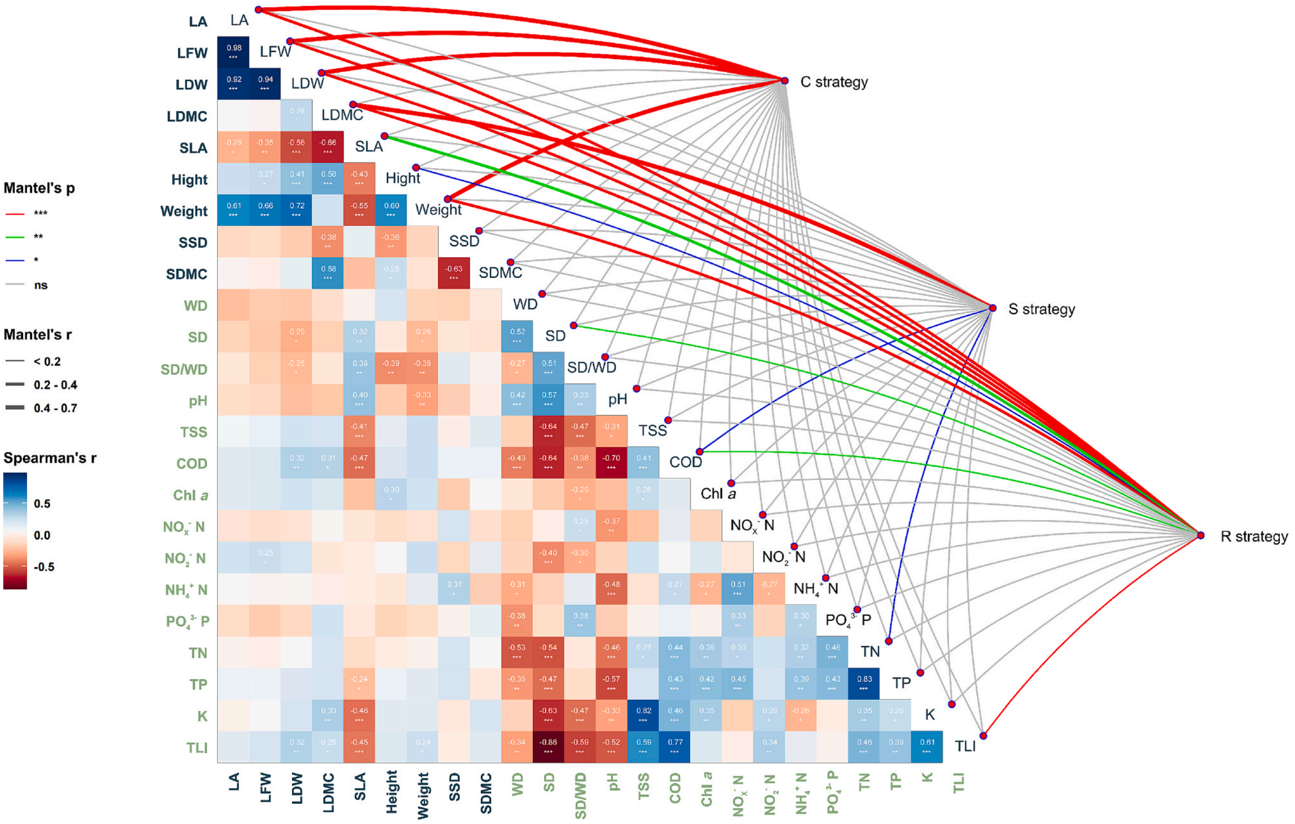

Fig. 2. Relationships among community strategies, functional traits, and environmental changes.The lower left section of the figure features a color gradient that represents the Spearman correlation coefficients between community trait indices and environmental factors. In the axes, black indicates community traits, while green represents environmental factors. Asterisks (*) denote the significance levels between factors ($p < 0.05$, $p < 0.01$, $p < 0.0001$), with correlation coefficients (r^2) displayed numerically within the rectangles. On the right side, the Mantel test results illustrate the relationships among community strategies, environmental factors, and functional traits. The thickness of the lines indicates the strength of the correlation (R^2): red signifies extremely significant correlations ($p < 0.001$), blue indicates highly significant correlations ($p < 0.01$), green denotes significant correlations ($p < 0.05$), and gray represents non-significant correlations ($p > 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

April to August 2024 in areas with dense populations of aquatic macrophytes in East Taihu Bay and Xukou Bay(Fig. 1). Sampling sites were chosen along a transect extending from the shoreline to the edge of the macrophyte distribution zone, with each site spaced more than 50 m apart. At each location, water samples were collected using a water sampler and transported back to the lab for chemical analysis. To obtain comprehensive samples of both submerged and floating-leaved macrophytes, a Petersen grab sampler (0.5 m × 0.38 cm, area = 0.19 m^2) was utilized. For emergent macrophytes, a sampling area was defined with a quadrat (0.5 m × 0.5 m, area = 0.25 m^2) and complete above-ground and below-ground specimens were collected using a spade. All samples were taken back to the laboratory within 24 h for measurement. To reduce disturbance to the water body during sampling, water depth (WD) was measured using a Speedtech SM-5 portable depth sounder and Secchi depth (SD) with a Secchi disk. Additionally, a calibrated multi-parameter water quality analyzer (YSI ProQuatro, HACH, USA) was used to measure pH on-site. Light intensity at the water surface and at a depth of 20 cm was recorded using an underwater quantum scalar photometer (Apogee MQ510, Logan, UT, USA). The water's light attenuation coefficient (K, m^{-1}) was then calculated using the following formula:

$$K = \frac{\ln I_0 - \ln I_z}{Z}$$

In this context, Z represents the water depth (20 cm for this study), while I_0 and I_z refer to the light intensity at the water surface and at a depth of 20 cm below the surface, respectively.

The collected plants were thoroughly rinsed with tap water and sorted by species. Use the Flora Reipulicae Popularis Science and Wikipedia to identify aquatic macrophyte species (IB-CAS 2019). Using a precision balance with an accuracy of 0.01 g, we weighed the total biomass of each species within the sampling area to calculate both species-specific biomass density and community biomass density (total fresh weight/sampling area). Five complete individuals from each species were selected and laid out on a table for measurement. The height of each individual was measured with a ruler, and their fresh weight was recorded on the balance. All leaves were removed and weighed to determine the total leaf fresh weight (LFW). The leaves were then spread flat, and photographs were taken with an Epson scanner (Epson Scan2, Epson, JPN) to allow for leaf area calculation using ImageJ software (National Institutes of Health, USA). The fresh weight of the stem (SFW) was also recorded, and stem volume (V) was measured through water displacement (Li et al., 2019). Next, leaf and stem samples from each plant were placed in an oven and dried at 55 °C until they reached a constant weight. We then measured the dry weights of the leaves (LDW) and stems (SDW). From these measurements, we calculated several metrics: leaf dry matter content (LDMC = LDW/LFW), specific leaf area (SLA = LA/LDW), stem density (SSD = SDW/V), and stem dry matter content (SDMC = SDW/SFW).

Immediately after sampling, water samples were taken to the laboratory for chemical analysis. The following indicators were measured using standard methods (Association 1926): total suspended solids (TSS), chlorophyll *a* from phytoplankton (Chl*a*), ammonium nitrogen (NH_4^+-N), nitrate nitrogen (NO_X^--N), nitrite nitrogen (NO_2^--N), chemical oxygen demand (COD), total nitrogen (TN), and total phosphorus (TP). TP was determined through colorimetric analysis after converting the samples to orthophosphate using $K_2S_2O_8$ and NaOH. TN and TP were

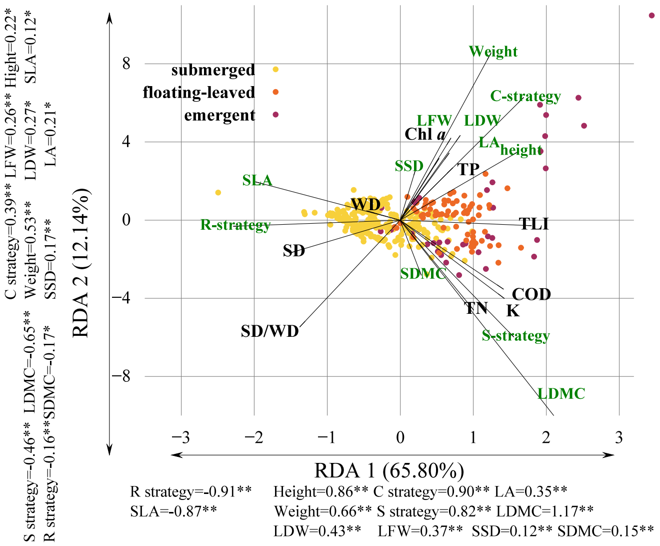

Fig. 3. Redundancy analysis (RDA) of individual traits and strategies of macrophytes along environmental changes. In the figure, abbreviations adhere to previously established definitions in the literature. Points represent the life form types of sampling sites, while black text indicates the scores for each environmental factor, and green text represents the scores for community traits and strategies. The correlation coefficients of each factor with the RDA axes, along with their significance, are illustrated in the figure, with positive and negative correlations denoted by +/- . Significance levels are marked with asterisks: * indicates $p < 0.05$ and ** indicates $p < 0.01$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

digested simultaneously. After digestion, TN was measured as nitrate, with absorbance readings taken at 220 nm.Water samples were filtered using Whatman GF/C glass fiber filters (pore size 0.45 μm), and ammonium nitrogen (NH_4^+-N) was analyzed using the Nessler method. For NO_X^--N analysis, the filtered water was treated with H_3O_3S and HCl, and absorbance was measured at both 220 nm and 275 nm. Nitrite nitrogen ((NO_2^--N) was measured by adding $C_6H_5(NH_2)SO_3H$, CH_3COONa, HCl, and $C_{10}H_9NH_2$ to the filtered water, with absorbance measured at 520 nm. The chemical oxygen demand (COD) was assessed using titration.

To calculate total suspended solids (TSS), the GF/C filter was first weighed (W_1) after incineration in a muffle furnace at 550 °C for 2 h. The volume of filtered water (V_1) was then dried in an oven at 110 °C for 24 h until a constant weight (W_2) was achieved. TSS was calculated using the following formula: $(TSS)=(W_2-W_1)/V_1$.

2.3. *Eutrophication level assessment of lakes*

This study used the Trophic Level Index (TLI) to evaluate the eutrophication levels in different regions of Lake Taihu. The TLI was proposed by the China Environmental Monitoring Station in 2001 (Wang et al., 2002) and has since been widely applied in assessing lake eutrophication across China (Wang et al., 2019).

$$TLI(\sum) = \sum_{j=1}^{m} w_j$$

In this formula, $TLI(\sum)$ represents the overall trophic state index, W_j denotes the weight of the trophic state index for the j-th parameter, and TLI (j) indicates the trophic state index for that specific parameter.

Using Chl*a* as the baseline parameter, the normalized weight of the j-th parameter can be calculated with the following formula:

$$W_j = r_{ij}^2 / \sum_{j=1}^{m} r_{ij}^2$$

In the equation, r_{ij} represents the correlation coefficient between the j-th parameter and the baseline parameter Chl*a* while m denotes the number of evaluation parameters.

The calculation formula for the trophic state index of each project is as follows (Table 1):

$TLI(Chla) = 10(2.5 + 1.086\ln Chla);TLI(TP) = 10(9.436 + 1.624\ln TP)$.

$TLI(TN) = 10(5.453 + 1.694\ln TN)$; $TLI(SD) = 10(5.118 – 1.94\ln SD)$.

$TLI(COD) = 10(0.109 + 2.661\ln COD)$.

2.4. *Data calculation*

Community traits were evaluated using the community-weighted mean (CWM) trait value. CWM was calculated based on the average trait values of species within a sample and the biomass of each species. The formula for CWM is as follows:

$$CWM = \sum_{i=1}^{S} Pi \times Ti$$

where T_i represents the trait value of the i-th species among the S species in the community, and P_i was the relative biomass of the i-th species (the proportion of the species' biomass to the total biomass in the sample). This means that the CWM calculation incorporates both the individual trait values and their contributions based on biomass, thus providing a weighted assessment of the community's traits.

The CSR strategy was calculated using the "StrateFy" software by entering three leaf traits: Leaf Area (LA), Leaf Dry Matter Content (LDMC), and Specific Leaf Area (SLA). This process assessed the ecological strategies for various species and life forms of macrophytes, as described by Pierce et al. (2017).

Additionally, the community strategy was determined using the community-weighted mean (CWM) approach. This method combined species-specific trait values with their relative biomasses to provide a comprehensive evaluation of the community's ecological strategies. The reliability and effectiveness of the "StrateFy" software had been well-supported by experiments conducted around the world (Dayrell et al., 2018, Li and Shipley 2017, Wang et al., 2018).

2.5. *Data analysis*

All species were categorized into three life forms: emergent macrophytes, floating-leaved macrophytes, and submerged macrophytes. Data were analyzed using one-way analysis of variance (ANOVA) with SPSS 19.0 (SPSS Inc., Chicago, IL, USA). Tukey's test was performed for multiple comparisons ($p < 0.05$) to evaluate the significance of differences between the groups. The relationship between CSR strategies and explanatory factors, including environmental variables and plant traits, was assessed using the Spearman test and the Mantel test from the vegan R package. Redundancy analysis (RDA) was conducted with CANOCO5 to examine the relationships among plant traits, CSR strategies, and environmental factors, excluding environmental parameters that contributed insignificantly to the total variation ($p > 0.05$) and had a variance inflation factor (VIF) greater than 10. The proportion of each strategy calculated by "StrateFy" was arranged in the ternary chart, and Origin2024 (Origin Lab Corporation, Northampton, MA, USA) was used to draw the box chart and ternary chart under different eutrophication degrees. Additionally, we carried out an enhanced regression tree analysis using the "gbm" package in R to determine the relative importance of leaf traits in the dynamic changes of C/S/R values (Cheong et al., 2014). This ecological modeling technique generates multivariate regression trees through machine learning, allowing us to quantify each factor's contribution to the response variable (Cheong et al., 2014, Zhou et al., 2021). Variance partitioning analysis was performed using the "vegan" package in R to assess the contributions of light and nutrient variations to plant strategies (Yu et al., 2022). The selected plant traits in the models were primarily based on their relative importance and results from the redundancy analysis. To clarify the

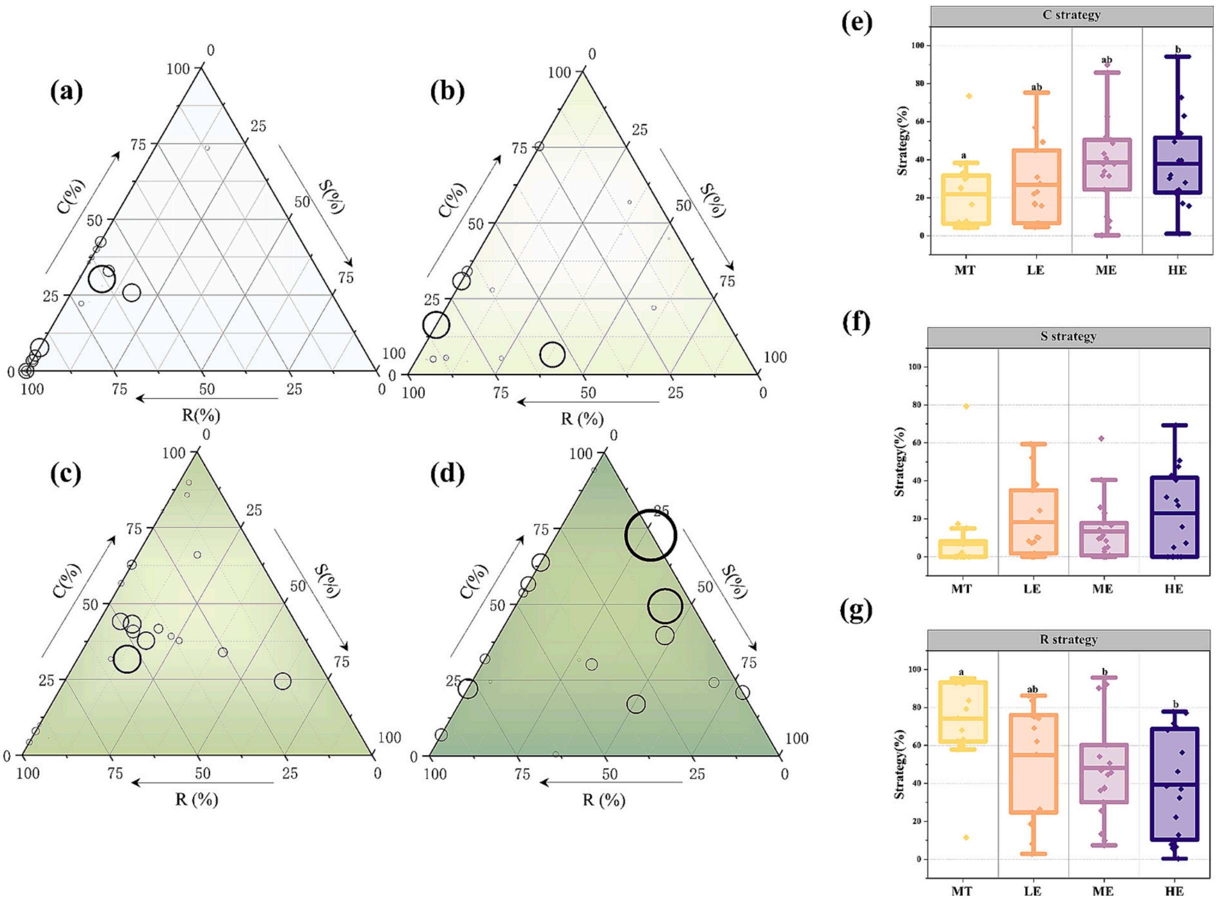

Fig. 4. Changes in macrophyte community strategies at different eutrophication levels. The light blue color represents the mesotrophication (MT) state (a), the light green represents the light eutrophication (LE) state (b), the green corresponds to the moderate eutrophication (ME) state (c), and the dark green indicates the heavy eutrophication (HE) state (d). The size of the circles reflects the biomass of the community. The three graphs on the right illustrate the proportional changes of the C strategy (e), S strategy (f), and R strategy (g) in macrophyte communities across varying levels of eutrophication. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

complex pathways of influence, we employed Partial Least Squares Structural Equation Modeling (PLS-SEM) to estimate the causal network among latent variables (Fan et al., 2016, Xie et al., 2024). PLS-SEM calculations were performed using SmartPLS 4 (SmartPLS GmbH, Germany). This study emphasizes the factors affecting plant strategies and their interactions, highlighting the driving forces behind variations in these strategies. PLS-SEM relaxes the assumption of multivariate normality during parameter estimation, making it particularly suitable for exploratory research with small sample sizes and effective in assessing interactions among variables. All visualizations were created using Origin 2024 (Origin Lab Corporation, Northampton, MA, USA).

3. Results and analysis

3.1. Variation of environmental parameters under different levels of eutrophication

The eutrophication status along the Taihu Lake macrophyte beds could be classified into four levels: Mesotrophication (MT), Light eutrophication (LE), Moderate eutrophication (ME), and Heavy eutrophication (HE) (Table 2). Specifically, values for transparency, pH, and the depth/transparency ratio all showed significantly decrease with increasing eutrophication levels ($p < 0.05$). In contrast, variables such as The water's light attenuation coefficient (K), chemical oxygen demand (COD), and total nitrogen (TN) significantly increase with higher eutrophication levels ($p < 0.05$). However, changes in NO_X^-N, NO_2^--N, NH_4^+-N and PO_4^{3-}-P were not significant ($p > 0.05$).

3.2. Differences in individual traits and strategies among various life forms of macrophytes

Submerged macrophytes could be found across all four levels of nutrient level; however, floating-leaved and emergent macrophytes were not present in the mesotrophication (MT) condition. As eutrophication intensifies, the leaf dry weight (LDW), height, and weight of submerged macrophytes increased significantly. The specific leaf area (SLA) and stem density (SSD) initially declined before increasing, reaching its lowest point during moderate eutrophication (ME) ($p < 0.05$). Additionally, the C strategy and S strategy of submerged macrophytes increased significantly, while the R strategy showed a decrease significantly ($p < 0.05$).

In floating-leaved macrophytes, both leaf area (LA) and leaf fresh weight (LFW) significantly declined with increasing eutrophication level. The C strategy also decreased significantly ($p < 0.05$), while the S strategies increased significantly. R strategies remained relatively unchanged. Emergent macrophytes showed no significant modifications in functional traits or ecological strategies across the different levels of eutrophication (Table 3).

3.3. Relationship between macrophyte community traits and strategies and their environment

For each community, the weighted average of all species' traits and ecological strategies was calculated to serve as indicators of functional traits and ecological strategies. The Spearman method was employed to

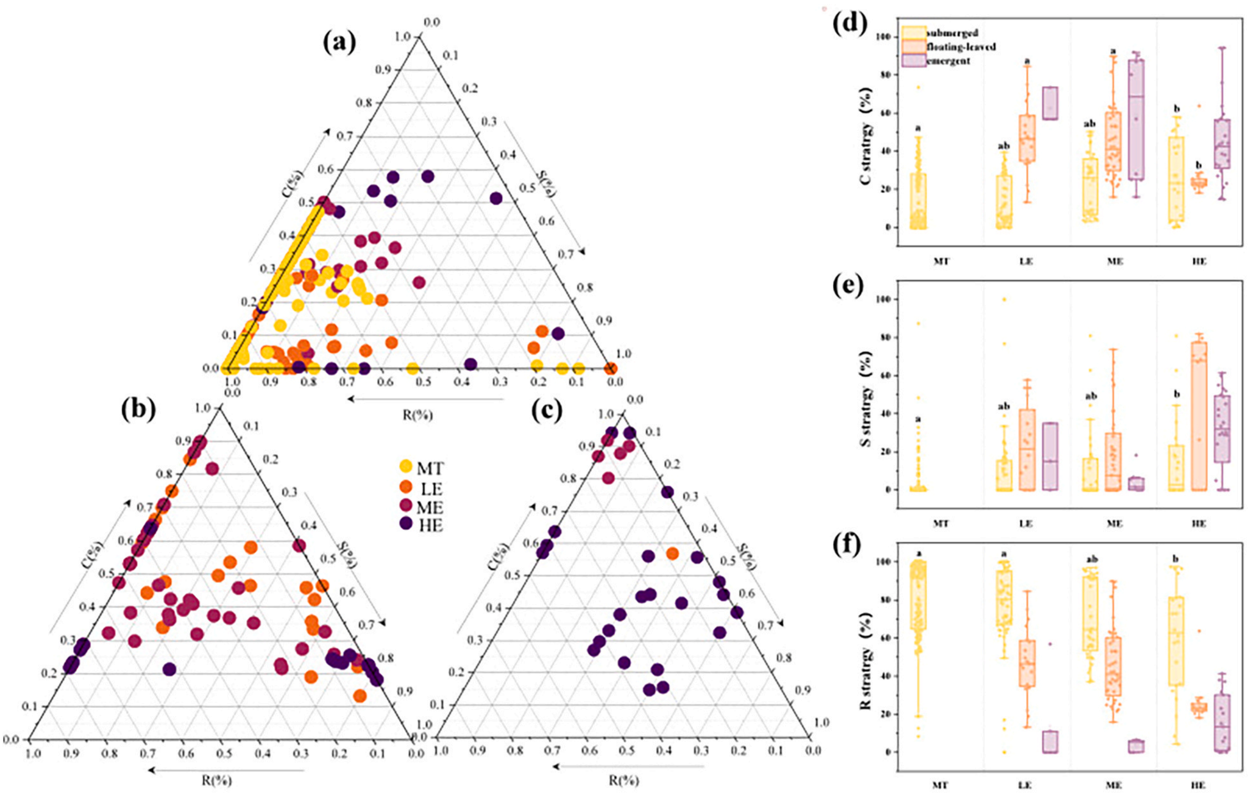

Fig. 5. Strategy distribution of aquatic macrophytes by life form at varying eutrophication levels. The three graphs on the left show the strategy distribution of submerged macrophytes (a), floating-leaved macrophytes (b), and emergent macrophytes (c) across different levels of eutrophication. Yellow indicates the mesotrophication (MT), orange represents the light eutrophication (LE), purple signifies the moderate eutrophication (HE), and blue-purple denotes the heavy eutrophication (HE).The three graphs on the right illustrate the changes in the C strategy (d), S strategy (e), and R strategy (f) for each type of aquatic macrophyte at varying eutrophication levels. Yellow corresponds to submerged macrophytes, orange is for floating-leaved macrophytes, and purple refers to emergent macrophytes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

examine the correlation between these traits and the environment, while the Mantel test revealed relationships between different ecological strategies and functional traits as well as variations in environmental conditions (Fig. 2). At the community level, the C strategy was significantly influenced by leaf traits (LA, LFW and LDW) and biomass ($p < 0.05$). The S strategy was significantly affected by the leaf trait named leaf dry matter content (LDMC) and nutrients (COD and TN) ($p < 0.05$). Meanwhile, the R strategy showed significant relationships with multiple leaf traits (LA, LFW, LDW, LDMC, SLA, height, and weight), as well as environmental factors such as light (SD) and nutrients (COD and TLI) ($p < 0.05$).

3.4. Changes in individual traits and strategies of macrophytes in response to environmental variation

A redundancy analysis (RDA) was conducted to identify significant environmental variables influencing aquatic macrophyte community traits and strategies (Fig. 3). The results indicate that RDA1 explains 65.80 % of the total variance, while RDA2 accounts for 12.14 %, together explaining 77.94 % of the variance (Fig. 4).

The main environmental variables regulating macrophyte strategies and traits include TLI, SD/WD, TN and COD. RDA1 is negatively correlated with the R strategy ($r = -0.91$, $p < 0.01$) and positively correlated with the S strategy ($r = 0.82$, $p < 0.01$) and C strategy ($r = 0.90$, $p < 0.01$). Additionally, RDA2 shows a negative correlation with the S strategy ($r = -0.46$, $p < 0.01$) and R strategy ($r = -0.16$, $p < 0.01$), and positively with the C strategy($r = 0.39$, $p < 0.01$).

3.5. Changes in macrophyte community strategies with lake eutrophication

The distribution of community strategies in relation to increasing eutrophication levels was depicted using Grime's triangular diagram (Fig. 4). In the mesotrophication (MT) and light eutrophication (LE) communities, the R strategy predominates, with average strategy compositions of C:S:R = 18:7:78 (Fig. 4a) and C:S:R = 27:18:55 (Fig. 4b), respectively.

Although species in the moderately eutrophic community predominantly select the R strategy (C:S:R = 38:13:48) (Fig. 4c), there is a gradual shift in community strategy proportions from the R strategy toward the C strategy. When the lake reaches heavy eutrophication (Fig. 4d), the proportions of C and R strategies become almost equal (C:S:R = 37:22:39). Furthermore, as the degree of lake eutrophication increases, the range of changes in aquatic macrophyte community strategies also expands.

3.6. Changes in strategies of macrophytes by life form

The responses of different life forms of aquatic macrophyte communities to lake eutrophication levels showed distinct variations. Submerged macrophytes (Fig. 5a) exhibited a higher proportion of the R strategy in the mesotrophication (MT) (81.63 %) compared to the light eutrophication (LE) (71.1 %), reaching a minimum of 59.15 % in the Heavy eutrophication (HE) condition. As eutrophication increased, there was a significant ($p < 0.05$) shift towards the C strategy.

In contrast, floating-leaved macrophytes exhibited strategy changes that differed from those observed in submerged macrophytes (Fig. 5b). Specifically, The proportion of the C strategy decreased significantly (p

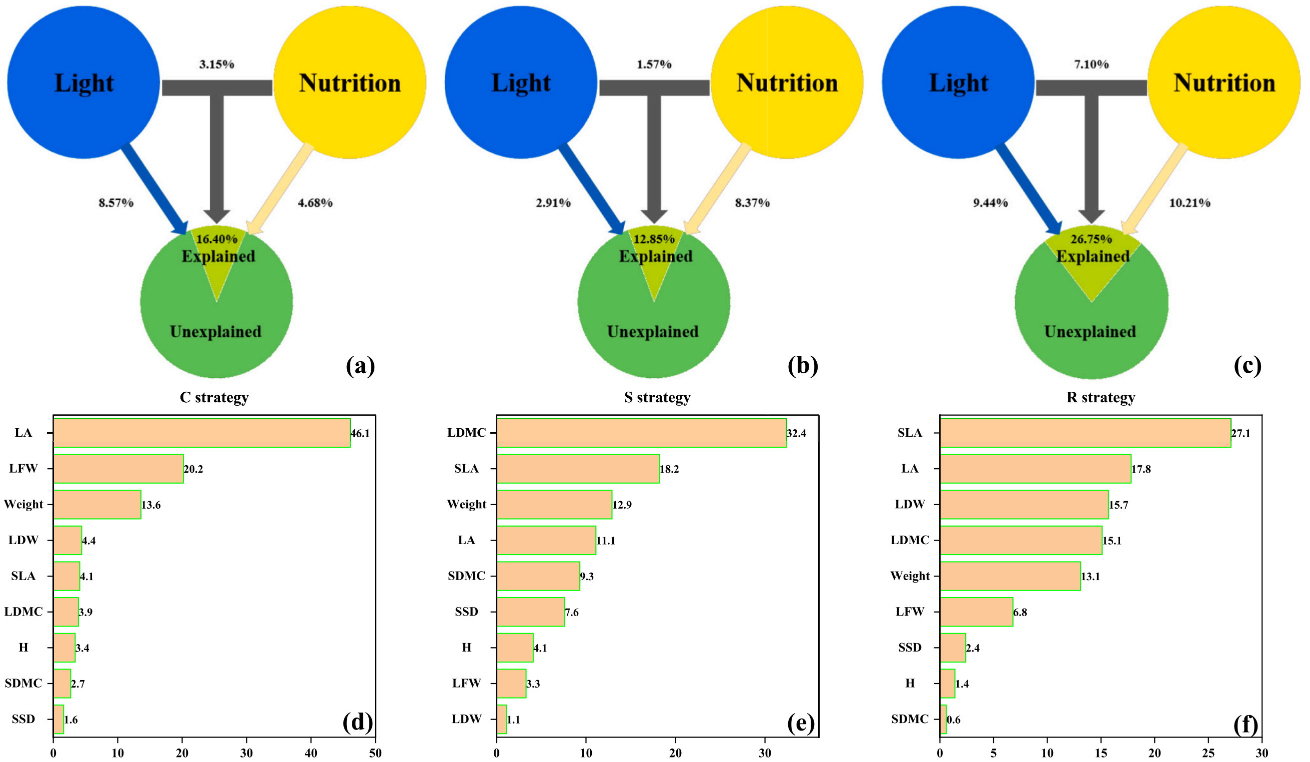

Fig. 6. Variance partitioning analysis demonstrated the percentage of variation in C, S, and R strategies that was explained by environmental factors and macrophyte community spatial structure (Fig. 6a, 6b, and 6c). In addition, enhanced regression tree analysis revealed the relative importance of macrophyte functional traits in explaining the variation in C, S, and R strategy scores (Fig. 6d, 6e, and 6f).

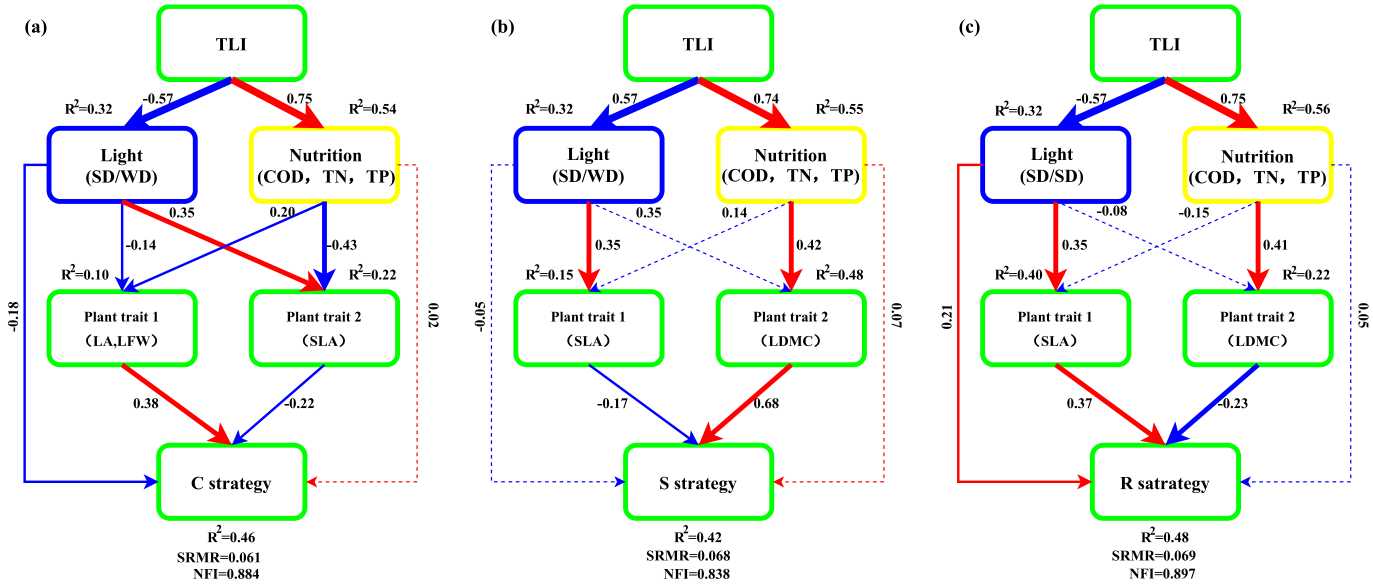

Fig. 7. Cascading relationships among C, S, and R Strategies with nutrient gradients, light and nutrient stress, and functional Traits. The partial least squares path model (PLS-PM) illustrated the primary pathways through which nutrient gradients, light and nutrient stress, and functional traits influenced macrophyte strategies. Environmental and trait selection was based on Mantel tests and Redundancy Analysis (RDA). Red arrows indicated positive causal relationships, while blue arrowed represent negative causal relationships; dashed lines indicated non-significant correlations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

< 0.05) with increasing eutrophication, while the S and R strategies remained stable, showing no significant changes ($p > 0.05$). For emergent macrophytes, no significant changes in any of the strategies were observed as eutrophication levels increased.

3.7. Factors influencing the distribution of CSR strategies in macrophyte communities

Variance partitioning analysis demonstrated that light and nutrient availability were the most significant factors influencing macrophyte

CSR strategies, collectively accounting for 16.4 %, 12.85 %, and 26.75 % of the variations in C, S, and R strategies, respectively (Fig. 6a, 6b, 6c). Enhanced regression tree analysis further revealed dynamic links between macrophyte functional traits and CSR strategy scores. Leaf area (LA), leaf fresh weight (LFW), leaf dry matter content (LDMC), and specific leaf area (SLA) as key traits driving variations in the C, S, and R strategies. Specifically, LA explained 46.1 % of the variation in the C strategy of macrophytes under different eutrophication levels (Fig. 6d). In contrast, LDMC accounted for 32.4 % of the variation in the S strategy (Fig. 6e), and SLA explained 27.1 % of the variation in the R strategy (Fig. 6f).

4. Discussion

Despite recent advancements in trait-based studies of macrophytes in shallow eutrophic lakes (Arthaud et al., 2012, Fu et al., 2014), understanding of ecological strategies among aquatic macrophytes remained incomplete. To address this gap, field sampling was conducted in Lake Taihu, which exhibits differences in trophic states, to investigate variations in ecological strategies among different life forms and species of macrophytes. Our findings indicated that increased levels of eutrophication led to a reduction in nutrient stress but an increase in light stress. Macrophytes at varying degrees of eutrophication displayed R/CR strategies, suggesting a shift in adaptive responses. Moreover, as eutrophication levels increased, a corresponding increase in the C strategy within macrophytes communities was observed. This study, grounded in CSR theory, provided valuable insights into the adaptive strategies and successional dynamics of aquatic macrophytes in shallow lake ecosystems undergoing eutrophication.

4.1. Strategy distribution across different eutrophication levels

4.1.1. Distribution of major strategies among aquatic macrophytes

We found that aquatic macrophyte species predominantly exhibit R/C strategies along the eutrophication gradient, which aligned with our hypothesis. Environmental filtering led to the convergence of leaf functional traits within communities and the differentiation of biological communities on a global scale (Bernard-Verdier et al., 2012, Ordoñez et al., 2009). Although the environmental conditions across the four studied eutrophication gradients differed, they still belonged to a unified biological community. The R strategy thrived under frequent disturbances by investing in opportunistic species that efficiently acquired resources and capitalize on reproductive opportunities. The complex and variable nutrient environment favors R strategies characterized by rapid growth and reproductive capacity (Albuquerque et al., 2020, Arthaud et al., 2012). Additionally, to better access nutrients in the water, macrophytes exhibited higher specific leaf area (SLA), which aligned with findings from leaf economic spectrum studies (Osnas et al., 2013, Wright et al., 2004). Furthermore, frequent disturbances from factors such as herbivory and water flow exacerbated the prevalence of R strategies, making them the dominant strategy in shallow eutrophic lakes (Albuquerque et al., 2020, Pierce et al., 2014).

4.1.2. Changes in macrophytes community strategies with increasing eutrophication

As eutrophication intensified, the ample availability of nutrients and competition for light prompted macrophytes to invest more in competitive strategies, resulting in a significant increase in C strategy scores (Li et al., 2024, Zheng et al., 2023). Importantly, shallow lake ecosystems may have lacked species classified as S-stress tolerators, which was markedly different from terrestrial plants. Numerous studies have shown that S strategies are typically associated with dry climates and resource-limited habitats, such as those found in China's plateau ecosystems (Zheng et al., 2023, Zhou et al., 2021). In contrast, the abundance of water resources in lake ecosystems likely accounted for this disparity (Volaire 2018).

4.2. Changes in macrophytes of different life forms along the eutrophication gradients

4.2.1. The increased degree of eutrophication brings about changes in both nutrient dimensions and light availability

Increasing eutrophication levels resulted in significant increases in nutrients such as TN and COD. Conversely, a marked decrease was observed in indicators of light availability, including SD, SD/WD, and K. These significant changes in nutrient and light availability caused by eutrophication lead to species turnover, resulting in shifts in community strategies (O'Hare et al., 2018, Stefanidis and Papastergiadou 2019). In our study, *Potamogeton malaianus* was the only submerged macrophyte species found across all four levels of eutrophication, with its C strategies showing significant changes as eutrophication increased, providing new insights for future research. Variations in functional traits among macrophyte life forms facilitated a flexible trade-off in CSR strategies to adapt to environmental changes. Specifically, as eutrophication intensified, submerged macrophytes gradually lose their dominance within the community, displaying a more competitive and stronger C strategy in heavy eutrophication (HE) conditions (Table 2). In contrast, emergent and floating-leaved macrophytes, due to their competitive advantages in nutrient-rich environments (higher height and LA, Table 2), became the dominant species (Stefanidis and Papastergiadou 2019).

4.2.2. The difference of strategies change among different life forms

However, the way strategies changed among different life forms varies. Submerged macrophytes were more sensitive and exhibited a stronger C strategy as eutrophication progressed (Table 2), while floating-leaved macrophytes showed a reduction in R strategy and an increase in S strategy (Table 2). This finding contrasted with our expectations. Previous studies indicated that anchored floating-leaved macrophytes, like *Trapa*, could respond to nutrient increases by reducing LA and increasing leaf number to enhance the leaf area of their blades, thereby improving total photosynthetic area (Li et al., 2009, Xie et al., et al., 2007). As LA was the most impactful trait affecting the C strategy, its reduction would have resulted in a significant decline in the C strategy (Fig. 6). Additionally, it is noteworthy that emergent macrophytes did not display differences in strategies along the eutrophication gradient. Eutrophication primarily impacts the functional traits and ecological strategies of aquatic macrophytes by reducing underwater light availability. Emergent macrophytes, predominantly distributed in shallow littoral zones, are susceptible to variations in subaquatic light conditions only during their spring emergence period. However, owing to lower spring temperatures that inhibit extensive algal proliferation, the reduction in underwater light penetration remains limited during this critical phenological phase. Following aerial emergence above the water surface, these macrophytes become liberated from light constraints. Notably, the elevated nutrient concentrations in both water column and sediments under eutrophic conditions cease to function as limiting factors, instead transforming into growth-promoting resources that positively stimulate the development of emergent vegetation. This adaptive advantage persists throughout their subsequent growth stages until seasonal senescence. These characteristics likely explain the observed lack of significant shifts in the ecological strategies of emergent macrophytes across varying eutrophication levels. The complex environment faced by aquatic ecosystems, such as herbivory, water flow disturbances, sediment composition and water deeps, also played a critical role in influencing emergent macrophyte classification (Ecke et al., 2016, Fares and Michelan 2024). This study was limited to the classification and analysis of Pierce's key leaf morphological traits (LA, LDMC, SLA), and did not effectively elucidate the trends in macrophyte chemical traits (such as starch, soluble sugars, cellulose, etc.). These knowledge gaps regarding chemical traits warrant further investigation in future research. Additionally, this study was limited to investigating water eutrophication as a variable, leaving other environmental factors underexplored. Future research should focus on more complex changes in aquatic environments to gain deeper insights.

4.3. Drivers of strategy change

4.3.1. Specific response path

The partial least squares path model (PLS-PM) revealed that light stress and nutrient stress collectively drove shifts in ecological strategies (Fig. 7), consistent with our hypothesis. Light had a significant direct impact on C and R strategies; increased light availability exerted negative and positive effects on the C and R strategies, respectively. Conversely, the direct influence of nutrients on CSR strategies was not significant. Changes in these two dimensions primarily affected macrophyte strategies indirectly by impacting key traits (Fig. 7), including an increase in leaf area (LA), indicating enhanced light resource acquisition by individual macrophytes. Trait analyses showed that as eutrophication intensified, communities responded to light stress through significant increases in LA and height. Meanwhile, specific leaf area (SLA) in the community decreased, as ample nutrient availability meant that SLA, a trait reflecting fast investment and high returns, is no longer the sole choice within the plant community (Reich and Cornelissen 2014, Silva et al., 2018). This aligns with other studies indicating that nutrient increases in high-altitude grasslands led to a shift towards increased C strategies (Li et al., 2024, Zheng et al., 2023). Eutrophication influenced macrophyte traits and CSR strategies by deducing light availability more than increasing nutrient level(Fig. 7).

4.4. Research contribution and deficiency

This study only encompassed mesotrophication to heavy eutrophication conditions, neglecting oligotrophication and hyper-eutrophication environments. Furthermore, adhering to Grime's framework, this study focused solely on resource stress (light and nutrients), while the influence of disturbance factors (e.g., grazing, hydrodynamic disturbance) remains under-explored. Further research is warranted, ideally employing mesocosm experiments to systematically investigate aquatic macrophytes CSR strategy shifts across both stress and disturbance gradients. Considering China's current lake management practices, the changes in aquatic macrophytes CSR strategies following the ten-year fishing ban in Lake Taihu, a scenario of reduced disturbance, also deserve further investigation. This study elucidated how macrophyte traits and ecological strategies responded to changes in light and nutrient levels under varying degrees of eutrophication. These findings not only enhanced our understanding of response mechanisms in lake ecosystems but also provide scientific foundations for lake management and conservation efforts. The research offers novel insights into aquatic vegetation restoration, supporting improved water remediation and lake management strategies. Future research should aim to validate these findings across broader environmental contexts and explore additional factors that may influence macrophyte ecological strategies.

5. Conclusion

For macrophyte communities, the increase in light stress and the alleviation of nutrient stress caused by rising levels of lake eutrophication significantly enhance the proportion of C strategies while weakening the proportion of R strategies.

Different life forms of macrophytes responded differently to changes in lake eutrophication levels. Submerged macrophytes were more sensitive, showing a significant reduction in R strategy and an increase in C strategy proportions as eutrophication intensifies. In contrast, floating-leaved macrophytes exhibited a smaller range of strategy changes, with a decrease in C strategy proportion and a significant increase in S strategy. Emergent macrophytes showed no significant difference.

The impacts of increased eutrophication levels indirectly influence community strategies by regulating functional traits. This affected overall community strategy shifting through changes in strategies of various life forms and the replacement of dominant species.

CRediT authorship contribution statement

Qiduo Yang: Writing – original draft, Visualization, Software, Methodology, Investigation, Data curation. **Yanhui Liu:** Writing – review & editing, Investigation, Data curation. **Hanhan Zhang:** Writing – review & editing, Investigation, Data curation. **Qingya Gong:** Writing – review & editing, Investigation, Data curation. **Ke Geng:** Investigation, Data curation. **Yaling Su:** Writing – review & editing, Methodology, Conceptualization. **Kuanyi Li:** Project administration, Methodology, Funding acquisition, Conceptualization. **Chunlei Yue:** Supervision, Resources, Methodology, Conceptualization. **Baohua Guan:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Data availability

The data that has been used is confidential.

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