

Stoichiometric mechanisms of regime shifts in freshwater ecosystem

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ABSTRACT

Catastrophic regime shifts in shallow lakes are hard to predict due to a lack of clear understanding of the associate mechanisms. Theory of alternative stable states suggests that eutrophication has profound negative effects on the structure, function and stability of freshwater ecosystems. However, it is still unclear how eutrophication destabilizes ecosystems stoichiometrically before a tipping point is reached. The stoichiometric homeostasis (H), which links fine-scale process to broad-scale patterns, is a key parameter in ecological stoichiometry. Based on investigation of 97 shallow lakes on the Yangtze Plain, China, we measured nitrogen (N) and phosphorus (P) concentrations of the aboveground tissues of common submerged macrophyte species and their corresponding sediments. We found submerged macrophytes showed significant stoichiometric homeostasis for P (H_P) but not for N (H_N). Furthermore, H_P was positively correlated with dominance and stability at the species level, and community production and stability at the community level. Identifying where macrophyte community collapse is a fundamental way to quantify their resilience. Threshold detection showed that macrophyte community dominated by high- H_P species had a higher value of tipping point (0.08 vs. 0.06 mg P L⁻¹ in lake water), indicating their strong resilience to eutrophication. In addition, macrophytes with high H_P were predominant in relative oligotrophic sediments and have higher ability in stabilizing the water environment compared to those low- H_P ones. Our results suggested that ecosystem dominated by homeostatic macrophyte communities was more productive, stable and resilient to eutrophication. Eutrophication-induced stoichiometric imbalance may destabilize the ecosystem by altering the community structure from high-to low- H_P species. Efforts should be focused on maintaining and restoration of high homeostatic communities to make ecosystem more resilient, which can significantly improve our understanding of the critical transition mechanisms.

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1. Introduction

Perturbations from climate change and anthropogenic activities worldwide have extensively altered nitrogen (N) and phosphorus (P) cycling in various ways (Galloway et al., 2008; Marklein and Houlton, 2012; Liu et al., 2013; Penuelas et al., 2013). Since N and P are commonly limited elements of primary producers in natural

ecosystems (Elser et al., 2010; Harpole et al., 2011), eutrophication is predicted to considerably influence structures and functions of freshwater, marine and terrestrial ecosystems (Chapin et al., 1986; Sardans et al., 2012). In freshwaters, for instance, nutrient enrichment favors algae with high growth rates and frequently leads to shifts from a clear water state dominated by submerged macrophytes to a turbid water state dominated by phytoplankton, especially in shallow lakes (Scheffer et al., 2001; Beisner et al., 2003). Additionally, such shifts can cause degradation of ecological functions and services, with significant negative effects on human well-beings (Mäler, 2000; Hilt et al., 2017).

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Submerged vegetation is the main primary producers in shallow lakes and plays a fundamental role in stabilizing the freshwater ecosystems (Carpenter and Lodge, 1986; Jeppesen et al., 1998). Aquatic plants influence the hydrology and sediment dynamics through their direct effects on water flow and modify the environment to be more favorable via various positive interactions. For instance, dense macrophytes can provide structurally complex niches for large-size zooplankton and compete nutrients with algae (Jeppesen et al., 1998). Besides, it can reduce sediment resuspension and secrete allelopathic substances (Van Donk and van de Bund, 2002; Stansfield et al., 1997). However, eutrophication in recent decades has caused the disappearance of submerged macrophytes and switched to the turbid water state. Although these processes have been documented in several cases (Bayley et al., 2007; Ibelings et al., 2007; Tátrai et al., 2009) and examined using model simulations (Carpenter, 2005; Genkai-Kato and Carpenter, 2005), it still remains unclear how eutrophication destabilizes ecosystems stoichiometrically.

Stoichiometric homeostasis is the regulation ability of an organism to maintain a constant element content and ratios regardless of changes in nutrient availability (Sternner and Elser, 2002; Yu et al., 2010; Leal et al., 2017). Plants can buffer the external nutrient supply mismatch by multiple physiological mechanisms to maintain the stability of the body nutrient levels and the associated functioning, including excreting enzymes into the soil, nutrient resorption and biomass allocations within organisms (Killingbeck, 1996; Peng et al., 2016; Lambers et al., 2015). The stoichiometric homeostasis (regulation ability) depends on the resource limitation, physiological constraints and growth rate potential (Sistla et al., 2015). It is expected that high- H species have high competitiveness in poor nutrients while low- H species have high growth rate and can take advantage of nutrients when they are abundant (Frost et al., 2005). On a larger scale, stoichiometric homeostasis has been proved to be correlated with ecosystem stability, dominance and production (Yu et al. 2010, 2015). However, to our knowledge, there has been no report attempting to unravel the mechanisms of alternative stable states from a stoichiometric perspective. Furthermore, we note that both stoichiometric homeostasis (H) and ecological resilience represent the ability to maintain its original state at organism and ecosystem levels, respectively. Both concepts reflect variations in biological functions and hence can be used as indicators of organism/ecosystem response to environmental fluctuations (Elmqvist et al., 2003; Scheffer et al., 2015; Yu et al., 2015). However, it is still unknown whether stoichiometric homeostasis linking fine-scale process would be correlated with ecological resilience in broad-scale patterns in terms of regime shifts. Thus, it is important to clarify the links between macrophytes' ability of regulating stoichiometry and the structure, stability and resilience of lake ecosystems in response to eutrophication.

It is vital for management and conservation to understand the mechanisms of keeping a resilient clear water state (Elmqvist et al., 2003; Suding et al., 2004). Resilience here is the ability of an ecosystem to maintain key functions and processes encountering external perturbations (Holling, 1973). Phenomenally, the transition of predominant primary producers to phytoplankton is generally associated with collapse in both abundance and coverage of macrophyte community (Scheffer et al., 1993). Thresholds for the collapse represent a boundary parameter of the regime shifts, and a higher threshold implicates a more flexible ecological space and a larger domain of attraction (Scheffer et al., 2001; Andersen et al., 2009). Thus, it should be an effective way of quantifying ecosystem resilience to predict where a critical collapse threshold is reached (Andersen et al., 2009; Boada et al., 2017). Succession of macrophyte communities is a long-term process, which can serve as a clue to examine the slow responses of ecosystem state (Hughes et al., 2013). As stoichiometric homeostasis is tightly correlated

with species' production and stability (Yu et al. 2010, 2011), it is likely that eutrophication may erode resilience of the ecosystem by depressing high homeostatic macrophyte communities with high ecosystem production and stability.

Here, based on an investigation of 97 shallow lakes on the Yangtze Plain (Fig. 1), we first examined the strength of the stoichiometric homeostasis of submerged macrophytes by measuring N and P concentrations of their aboveground tissues. Then, we determined if stoichiometric homeostasis was correlated with species dominance and stability at the species level, as well as with production and stability at the community level. We hypothesized that there was a strong linkage of stoichiometric homeostasis in submerged macrophytes with regime shifts of a shallow lake ecosystem from clear to turbid states in the face of eutrophication.

2. Materials and methods

2.1. Study sites and field sampling

The Yangtze Plain, one of the three largest plains in China, contains numerous shallow lakes with different nutrient levels. In the present study, 97 lakes in the middle and lower reaches of the Yangtze River were surveyed in the growing season during 2013–2014 (Fig. 1). As the lakes suffered from severe degeneration, submerged macrophytes were absent from 51 lakes. In the 46 macrophytic lakes, we sampled in macrophytic region using the modified belt transect method (Vondracek et al., 2014), with 418 sampling sites in total. The number of sampling sites in each macrophytic lake were determined based on the area of macrophyte distribution. In order to establish stoichiometric relationships between submerged plants and its surrounding resources, 13 macrophytic lakes with more abundant coverage and species richness were investigated in detail in 2014. The lake area and mean water depth ranged from 16.9 to 2537.2 km² and 1.4 to 4.1 m, respectively (Table S1 for details).

In this study, we targeted on six common submerged macrophytes widely distributed in the Yangtze lakes: *Potamogeton maackianus*, *Potamogeton malaianus*, *Myriophyllum spicatum*, *Ceratophyllum demersum*, *Hydrilla verticillata* and *Vallisneria spiralis*, as their biomass comprised 98.2% of total submerged macrophytes in the study area. Submerged macrophytes were sampled using a rotatable reaping hook covering 0.2 m², with 3 times at each sampling site. The plants were washed, sorted by species and then weighed to determine the fresh weight. The aboveground parts of the six species were collected and placed in cloth bags with waterproof labels. Corresponding water samples were taken from 0.5 m below the surface, placed in a cooler and taken back to the laboratory for further analysis. In order to probe the stoichiometric homeostasis coefficients of submerged macrophytes, the upper 0–10 cm of sediments were collected in 2014, with 181 sediment samples in total. The sediment samples were collected using a columnar sampling instrument (acrylic glass tube, 5 cm inner diameter).

2.2. Laboratory analysis

The samples of macrophytes and sediments were oven dried at 80 °C for 48 h to constant weights and then ground into fine powder before elemental analyses. For total C and N concentration, both plant and sediment samples were measured using element analyzer (Flash EA 1112 series, CE Instruments, Italy). For total P concentration, plant and sediment samples were firstly digested using sulfuric acid/hydrogen peroxide and acid/perchloric, respectively. Then, the total P concentrations were determined using the ammonium molybdate ascorbic acid method for both plant and

sediment samples (Sparks et al., 1996). Total N and total P in the water column were analyzed according to standard methods (Huang et al., 1999). Specifically, total N and total P (mg L^{-1}) were measured as nitrate and ortho-phosphate after digestion with $\text{K}_2\text{S}_2\text{O}_8$ (at 120°C for 30 min). The concentration of orthophosphate in the digested samples was determined colorimetrically using molybdenum blue method.

2.3. Data analysis

Stoichiometric homeostasis coefficient (H) can be diagnosed by plotting the logarithms according to the following equation (Sternier and Elser, 2002): $\log(y) = \log(c) + (1/H)\log(x)$, where y is the P (or N) content of plants, x is the P (or N) content of the resources and c is a constant. As submerged plants absorb nutrients mainly from sediment via roots rather than water column via leaves (Best and Mantai, 1978; Carignan and Kalff, 1980; Smith and Adams, 1986), sediment total nutrient contents (N and P) were used as the resource to explore the stoichiometric homeostasis.

Species dominance was expressed by the biomass of this species as a proportion of the total biomass in a quadrat. Species stability was calculated as the ratio of average species biomass to the associated standard deviation. Community H was calculated by the weighted mean of species H across all submerged species in one quadrat according to the following equation (Yu et al., 2010):

$$\text{Community } (H) = \sum_{i=1}^n \text{relative_biomass}_i \times H_i$$

where n is the species number in a quadrat and i takes the value from 1 to n . Community production was the total biomass of all living submerged species within a quadrat (averaged by each lake),

and community stability was calculated as the ratio of the mean biomass to the associated standard deviation for the 13 lakes investigated in 2014. Then, linear regression was used to examine the relationships between the regulation ability and species dominance and stability, as well as the relationships between community H and community production and stability. All data sets analyzed above were obtained in 2014.

To explore whether stoichiometric homeostasis is associated with ecological resilience, thresholds determined under different stoichiometric community structures (high- H species vs. low- H species) were used to assess resilience, stability and the risk of an upcoming transition (Boada et al., 2017). Specifically, we examined whether community structures influence where the thresholds occur in response to total P in the water column. We combined the data sets of 2013 and 2014 with a total number of 418 quadrats to make the result more robust. We performed this analysis of change point detection using the package “strchange” in R 3.4.2 (R Core Team, 2017) for each community structure. The method detects structural change in linear regression models, using a moving window (minimal segment size setting, $h = 0.15$) along the nutrient gradients to generate a sequential F -test. A function named “breakpoints” was used to determine the locations of the changes based on residual sum of squares and Bayesian information criterion (BIC). Because change point detection requires discrete biomass data, we used the mean values of macrophyte biomass in every $0.01 \text{ (mg L}^{-1}\text{)}$ portion of water total P.

3. Results

3.1. N and P homeostasis coefficient (H) of submerged macrophytes

Stoichiometric homeostasis coefficients represents the ability of an organism to maintain relatively stable internal concentrations of

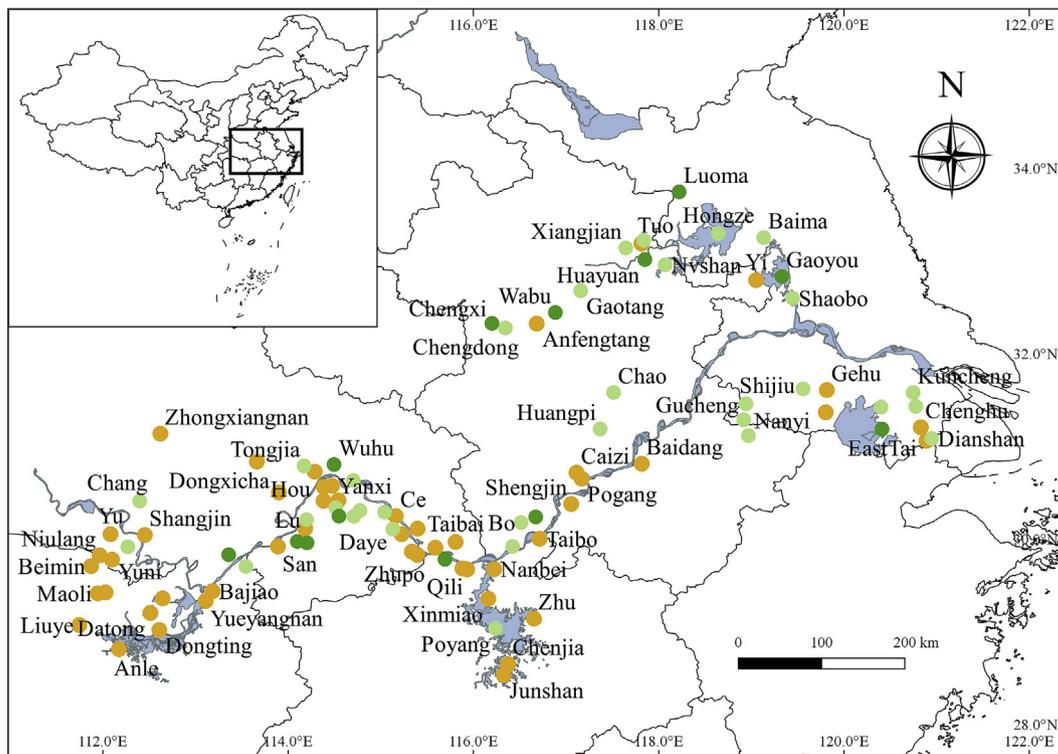


Fig. 1. Locations of 97 sampled lakes in the Yangtze floodplain. Symbols of yellow circles represent macrophyte-absent lakes; green circles represent macrophyte-present lakes. Specially, a detailed investigation of 13 macrophytic lakes (represented by the dark green circles) was conducted in 2014 to evaluate strength of stoichiometric homeostasis in six common macrophyte species. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

elements. We obtained it by plotting the logarithm of plant N and P contents with sediment nutrient contents, respectively. In this study, the stoichiometric homeostasis coefficients of P (H_P) for the six plant species (*P. maackianus*, *P. malaianus*, *V. natans*, *M. spicatum*, *C. demersum* and *H. verticillata*) ranged from 1.29 to 3.73 (Fig. 2), with an average of 2.40. However, no significant homeostasis coefficients of N (H_N) were detected, with the exception of significant H_N (i.e., 6.82) for *H. verticillata* (Table S2).

At the species level, the H_P of submerged macrophytes exhibited significant positive relationships with species dominance ($R^2 = 0.94$, $P = 0.0015$) and stability ($R^2 = 0.72$, $P = 0.0324$; Fig. 3 a, b). At the community level, community H_P of submerged macrophytes also exhibited significant positive relationships with community production ($R^2 = 0.36$, $P = 0.0305$) and stability ($R^2 = 0.54$, $P = 0.0045$; Fig. 3 c, d).

3.2. Linking the P regulation ability with community succession and ecological resilience

As the H_P values of *P. maackianus*, *P. malaianus* and *V. natans* were higher than those of *M. spicatum*, *C. demersum* and *H. verticillata*, we classified the former group as “high- H_P species” and the latter as “low- H_P species”. Threshold analyses showed that submerged vegetation biomass in the shallow Yangtze lakes exhibited two dramatic different states both in high- and low- H_P communities (Fig. 4). Results showed collapse of macrophyte community biomass was occurred when the water column total P crossed a tipping point (threshold). The mean biomass of low H_P community collapsed when water column total P crossed 0.06 mg L^{-1} . The biomass sharply decreased from $1149.85 \pm 271.87 \text{ g m}^{-2}$ to $192.45 \pm 119.27 \text{ g m}^{-2}$. By contrast, the

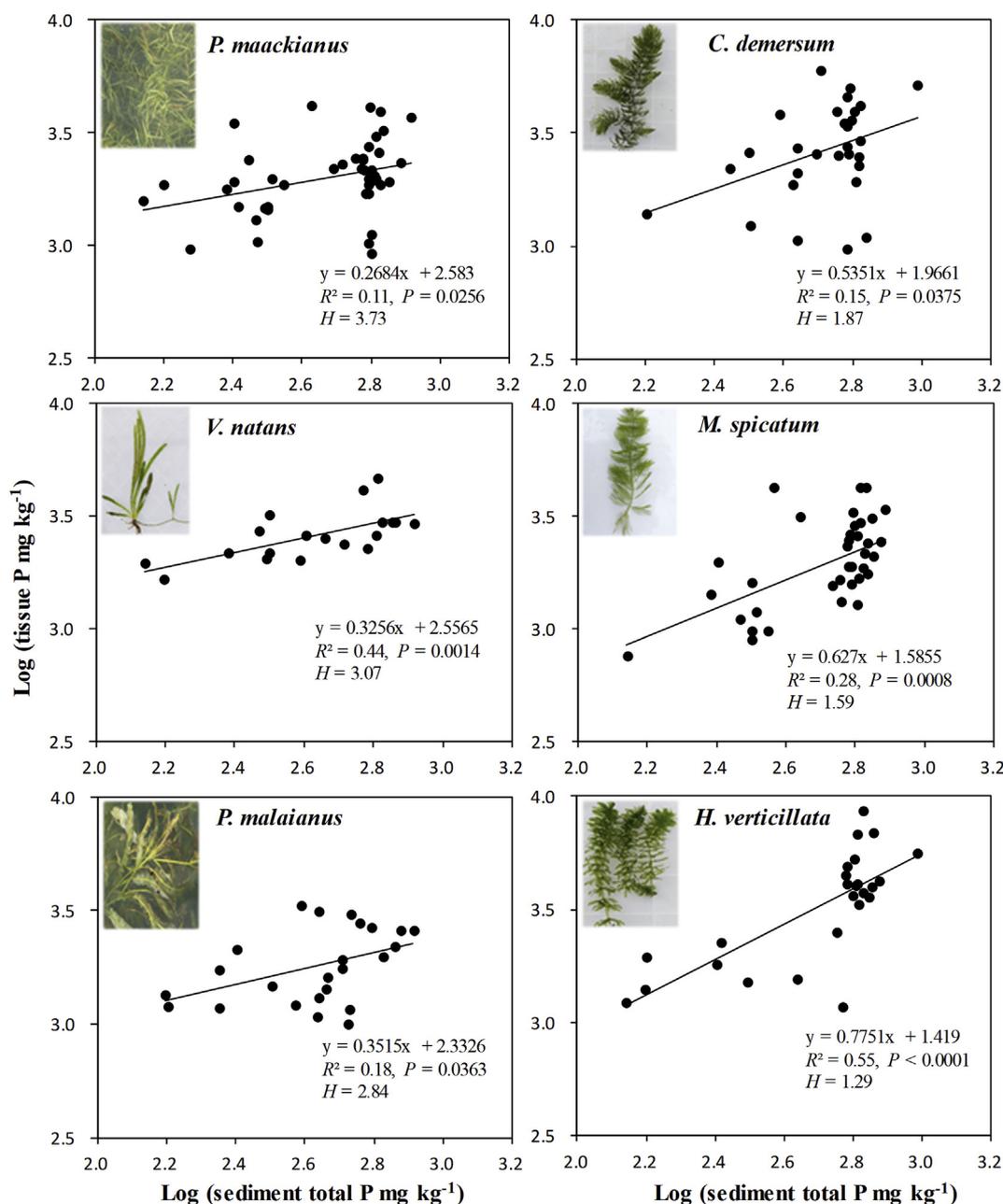


Fig. 2. The relationship between sediment total P and aboveground tissue P of submerged macrophytes. Stoichiometric homeostasis coefficient (H) were obtained according to the following equation: $\log(y) = \log(c) + (1/H)\log(x)$, where y is the P content of plants, x is the P content of the sediment and c is a constant.

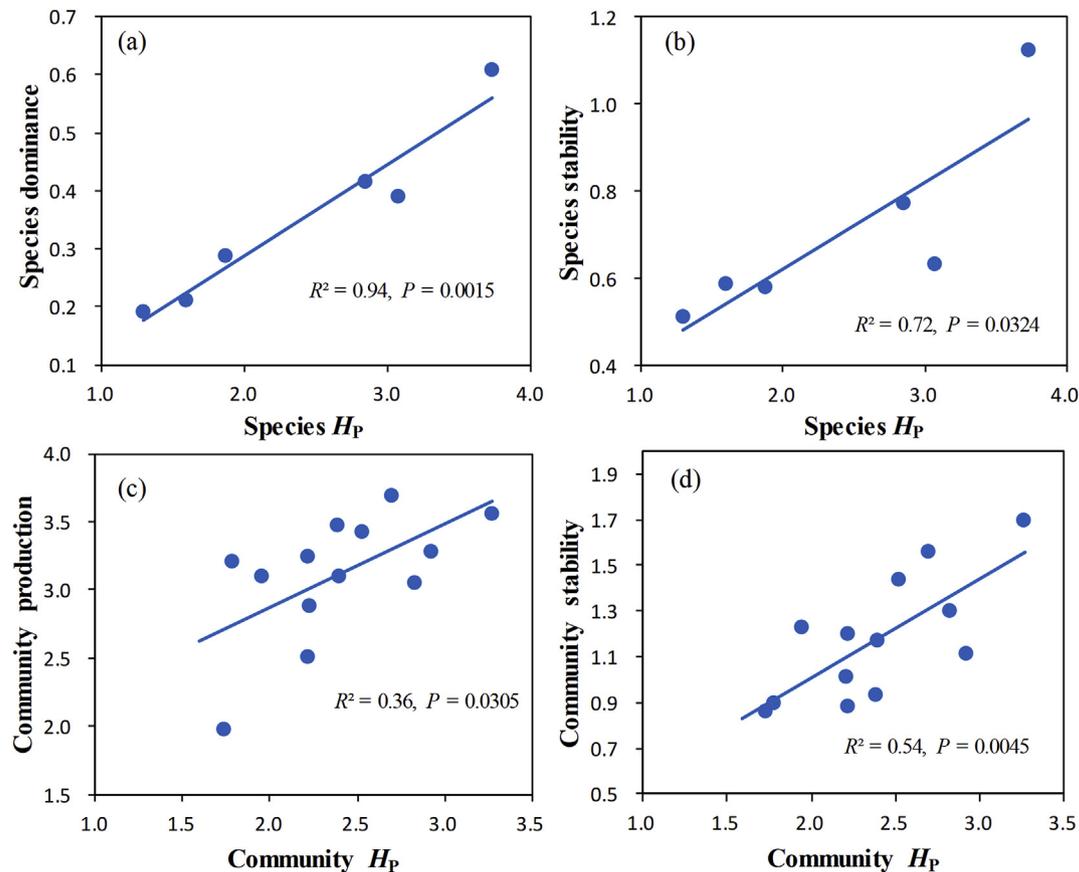


Fig. 3. Relationships between species H_p (stoichiometric homeostasis coefficient of P) and (a) species dominance and (b) stability at the species level and relationships between community H_p and (c) community production and (d) stability at the community level. Species dominance was expressed by the relative biomass in a quadrat in the field. Species stability and community stability were calculated by the ratio of the mean to its associated standard deviation, respectively. Community production was the total biomass of all living submerged species within a quadrat and was log10 transformed before linear regression analysis.

high H_p community was still present when water total P crossed 0.06 mg L^{-1} , with biomass around 1006.86 g m^{-2} . When water nutrient level beyond 0.08 mg L^{-1} , high H_p community also dropped from $1208.32 \pm 175.64 \text{ g m}^{-2}$ to $142.95 \pm 154.61 \text{ g m}^{-2}$. Our results confirmed the existence of regime shifts in both communities. Thresholds were found at higher levels of the stressor (water total P content) for the high- H_p community. The results were consistent and robust even when the intervals of water total P were changed to 0.02 mg L^{-1} (Fig. S1).

There were no significant differences of water total N and P between high- and low- H_p species dominated communities, while significant differences of sediment total N and P, secchi depth and chl a were observed between the two communities (Fig. 5). Furthermore, sediment total P was negatively correlated ($R^2 = 0.80, P = 0.0002$) with the dominance of high- H_p species, while it was positively correlated ($R^2 = 0.70, P = 0.0013$) with that of low- H_p species (Fig. S2).

4. Discussion

4.1. P vs. N availability in shaping stoichiometric homeostasis

The stoichiometric homeostasis coefficient (H) has been designed to reflect the ability of stoichiometric regulation in varying nutrient environments (Sterner and Elser, 2002). Many studies have shown that H is a powerful indicator for this in diverse organisms, including microbes, fungi, plants, and animals (Persson et al., 2010; Golz et al., 2015; Rodríguez et al., 2016; Li et al.,

2018). Individual stoichiometric traits are also linked to ecosystem production and stability (Yu et al., 2010). Previous studies have implied that aquatic vascular plants had a strong ability of stoichiometric regulation (Demars and Edwards, 2007; Li et al., 2013; Su et al., 2016). However, stoichiometric homeostasis is often species and element specific, and plant nutrients also respond to external environmental fluctuations to varying degrees. In our study, significant positive relationships were observed between plant tissue P and sediment total P concentrations (Fig. 2), whereas plants N, except for *H. verticillata*, showed no significant relationship with sediment N (Table S2). These results indicated that growth of macrophyte might be more closely correlated with P than N in freshwater ecosystem processes. For *H. verticillata*, P homeostasis (1.29) was much lower than N homeostasis (6.82), which was consistent with previous studies of terrestrial plants (Yu et al. 2010, 2011). This suggests that the structural elements with high concentrations are generally stable and not sensitive to environmental changes (Han et al., 2011).

In the present study, only homeostatic coefficient of P (H_p) of submerged macrophytes was significantly correlated with ecosystem production and stability (Fig. 3). This was inconsistent with those previous studies in terrestrial environments (Yu et al. 2011, 2015). Such a difference in the ability of stoichiometric regulation (N vs. P) between aquatic and terrestrial ecosystems may arise from different rates of nutrient accumulation. Terrestrial ecosystems are frequently influenced by atmospheric N deposition, while global freshwater ecosystems have accumulated more P than N from increased anthropogenic P inputs in

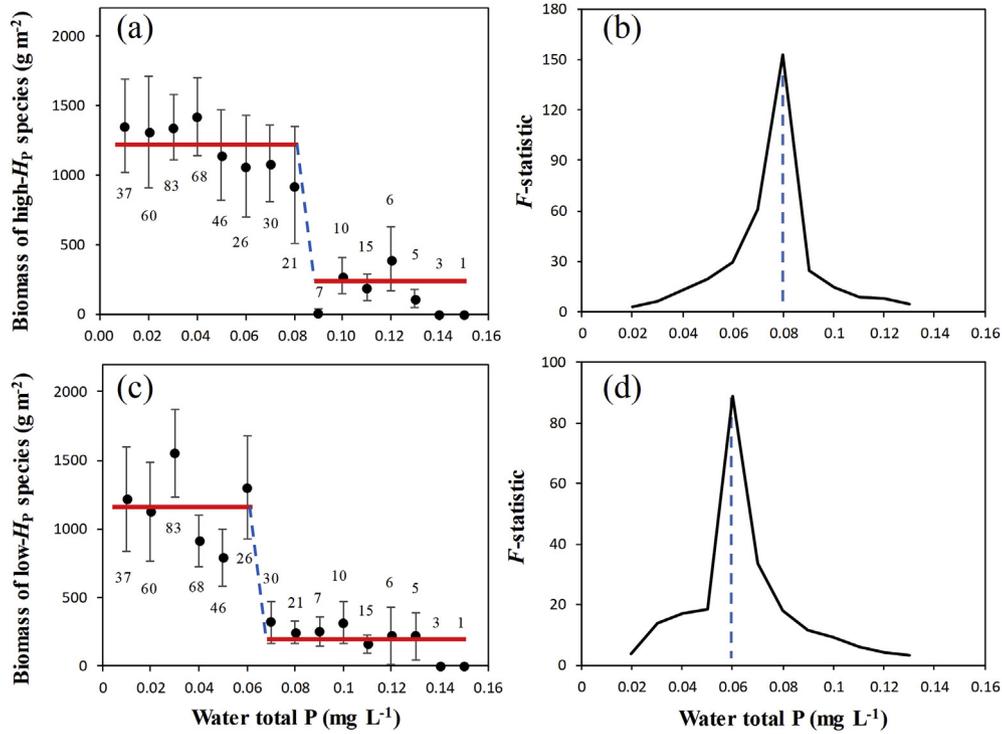


Fig. 4. Plots of macrophyte biomass and water total phosphorus for two different community structures: (a) high- H_p species and (c) low- H_p species. Change point analysis results for (b) high- and (d) low- H_p species. Black dots with standard error bars show the mean macrophyte biomass (mean \pm se) in every 0.01 mg L⁻¹ portion of total phosphorus. The red horizontal lines represent the mean macrophyte biomass before and after the threshold. The sequential F -statistic (minimal segment size setting, $h = 0.15$) was performed to test for a change in the mean and the peak F value indicated a regime shift. Dashed lines indicate the locations of thresholds. Number around the error bar was the sample number in each interval. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

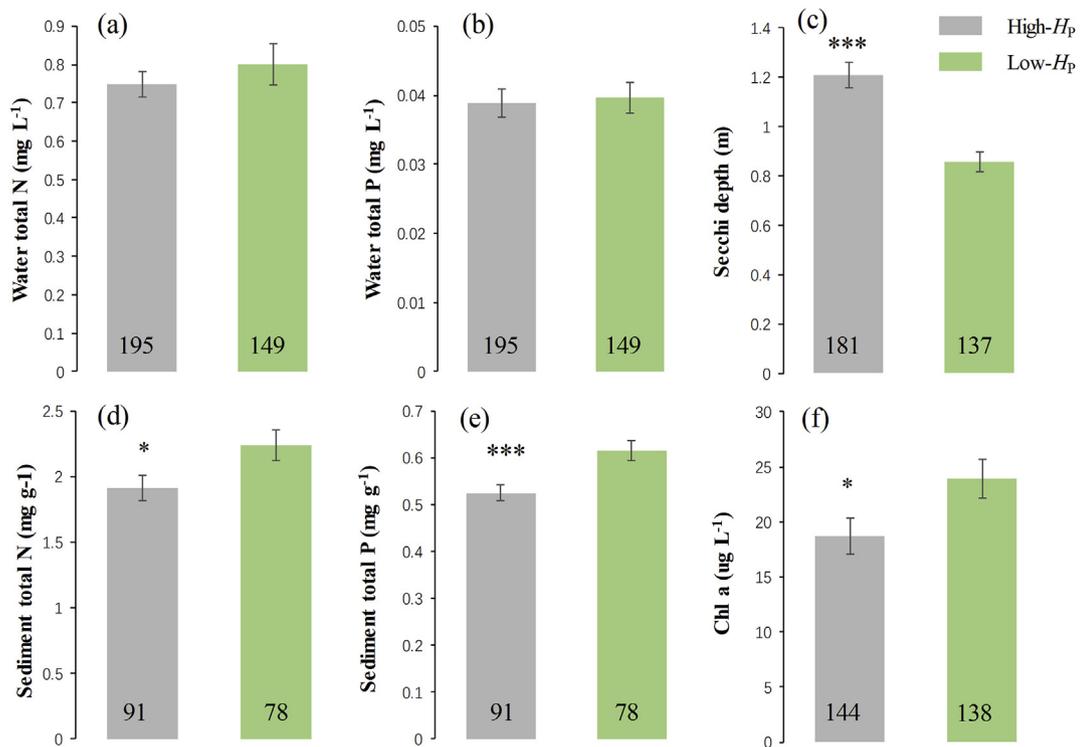


Fig. 5. Difference of (a) water total N, (b) water total P, (c) secchi depth, (d) sediment total N, (e) sediment total P, (f) chl a in high- and low- H_p species dominated communities. Number in the histogram was the sample number and error bar indicates standard error (mean \pm se). * indicates $P < 0.05$, *** indicates $P < 0.001$.

recent decades (Yan et al., 2016). Moreover, as freshwater ecosystems in pre-industrial times were considered to be P limited (Schindler, 1977; Sterner, 2008; Elser et al., 2007), the long-term selective pressure might have led to the presence of macrophytes with high capacities of acquiring and sequestering P over N, and thus leading to a high adaptability to P-limited environments (Güsewell and Koerselman, 2002).

4.2. Community structure changes with the progress of eutrophication

Because the ability to cope with elemental imbalance is species specific, phosphorus enrichment (eutrophication) should favor the growth of species with low P stoichiometric regulation ability in freshwater ecosystems. Our results showed that species with high- H_P were predominant when the sediment nutrients were low, while species with low- H_P were predominant when the sediment nutrients were high (Fig. 5d and e). The species with high- H_P values were suppressed by increased sediment P availability, ultimately dominated by low- H_P species during the process of eutrophication (Fig. S2). Plants with flexible stoichiometric properties can accumulate and store elements in excess of their immediate needs (Garbey et al., 2004; Demars and Edwards, 2007). This “luxury” uptake might be an ecological adaptive strategy that benefits the plant later when the elements are no longer available. However, species with homeostatic stoichiometry are often predominant in relative oligotrophic and stable environments because of their lower growth rates and the higher energetic costs of maintaining a stable stoichiometry in highly variable environments (Yu et al., 2011; Li et al., 2018). It is suggested that H_P can serve as an important stoichiometric indicator for predicting succession of macrophyte communities in the face of global change and anthropogenic activities.

4.3. A schematic model underlying regime shifts

Water total P was generally regarded as the driving factor for regime shifts from clear to turbid water in shallow lakes (Scheffer and Carpenter, 2003; Wang et al., 2014). Excessive phosphorus in water column is directly related to many unpleasant phenomena, e.g., increased biomass of phytoplankton, dominance of bloom-forming algal species, changes in macrophyte species composition, oxygen depletion and decrease in water transparency (Smith and Schindler, 2009). In the present study, we documented a shift from clear to turbid states in both high- and low- H macrophyte communities. However, the thresholds of water total P concentrations were substantially higher (0.08 vs. 0.06 mg L⁻¹) in high-homeostasis systems (Fig. 4). Our results indicated that stoichiometric homeostasis could strongly determine the buffer capacity of macrophyte communities. Results from species level stability, community level stability and threshold detection, all converged to give us a clear understanding of how stoichiometric homeostasis mediated the resilience to eutrophication. Specifically, macrophyte communities with strong stoichiometric homeostasis are more resilient to eutrophication than low homeostatic communities.

Submerged aquatic macrophytes can markedly improve local ecological environment through various positive interactions, which in turn benefit themselves. These interactions form a positive feedback loop: more vegetation results in higher water clarity, which is a necessary condition for catastrophic regime shifts (Scheffer et al., 2001; Kéfi et al., 2016). We found there are no differences of water total N and P between high- and low- H_P species dominated communities. However, communities dominated by high- H_P species tend to have lower chl a and higher water clarity,

indicating their higher capacity of stabilizing the local environment. In relative oligotrophic conditions where high- H_P species dominate, the positive feedback loops keep the system far away from the tipping point. However, in eutrophic conditions, the high- H_P species are replaced by low- H_P ones, which is accompanied by environmental degradation, decreases in community production and stability.

Based on our results, we presented a schematic model to explain the mechanisms and processes of regime shifts in the Yangtze floodplain shallow lakes (Fig. 6). In initial relative oligotrophic conditions, the ecosystem was dominated by high- H_P species with higher production and stability. With the progress of eutrophication, the high- H_P species were gradually replaced by the low- H_P ones. Homeostatic macrophytes tend to have relative lower growth rate and conservative usage strategy of nutrients (Yu et al., 2011; Li et al., 2018). In addition, restoration of homeostatic macrophytes can be prevented by the enhanced turbidity, grazing by herbivorous fish, water level fluctuations and lack of seeds or propagules in the sediment (O'Donnell et al., 2015; Hilt et al., 2008; Van Donk and Otte, 1996; Geest et al., 2005). It is expected that macrophytes with high- H_P values show lower threshold of nutrient level and higher equilibrium biomass in the backward recovery trajectory. On the other hand, the width of bistable regions indicates the strength of ecological resilience (Dakos et al., 2015; Muthukrishnan et al., 2016). Ecosystem dominated by high- H_P species has a higher nutrient threshold and thus a wider bistable region (F2-F2') than those dominated by low- H_P species (F1-F1'). Changes in macrophyte communities suggested that the flexible portion of the ecosystem domain decreased when affected by a disturbance. Thus, eutrophication-induced stoichiometric imbalances destabilized the ecosystems by changing the community structure from high- to low- H_P species, causing more easily transition of a system to an alternative turbid state. Although physiological mechanisms underlying these changes is still open for further study, our study provides a new perspective in analyzing the relationships between nutrient stoichiometry and ecosystem functions.

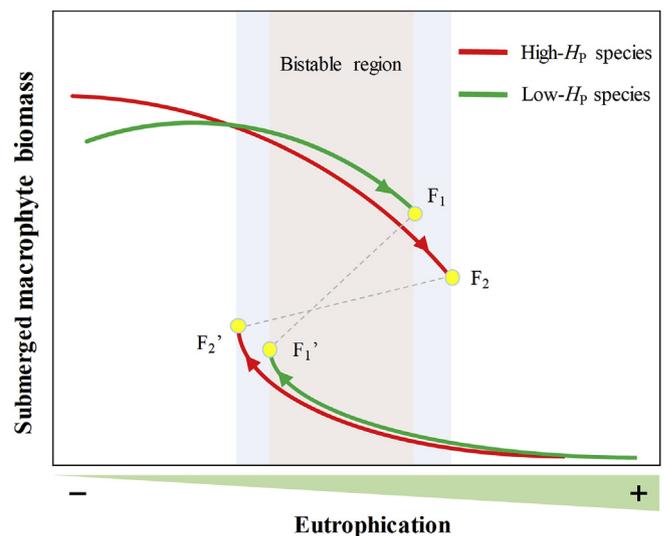


Fig. 6. A schematic model to explain the mechanisms and processes of regime shifts in shallow lakes. Ecosystem dominated by high- H_P species has high production, stability and resilience (indicated by the high threshold value of nutrients) than system dominated by low- H_P ones. The ecosystem dominated by high- H_P species owned a larger bistable region, with a lower abundance at the end of forward crash trajectory but higher equilibrium abundance along backward recovery trajectory due to its conservative nutrient use strategy and lower growth rate.

5. Conclusion

In the present study, we put forward, from the perspective of stoichiometry, a novel mechanism to elucidate the dynamics of structure, stability and resilience of lake ecosystems with eutrophication. Our results showed that regulation ability of P stoichiometry in submerged macrophytes was not only a powerful indicator to predict the structure and stability of the ecosystem, but also linked to species succession and ecosystem resilience in the face of external perturbations. Ecosystems dominated by high- H_P species tend to have a more stable regime, while those dominated by low- H_P species are more opportunistic and vulnerable to external perturbations. That is, eutrophication destabilizes freshwater ecosystems by inhibiting homeostatic macrophyte communities. Collapse of low- H_P species can be served as an early-warning signal for the regime shifts from clear to turbid state. Also, it is expected that low- H_P species can recover more quickly and thus can be used as pioneer species in restoration ecology. Our findings contribute to understanding the role of stoichiometric homeostasis in determining ecosystem structure, stability and resilience of macrophyte-dominated freshwater lakes. The present results are practically important for lake management and restoration in the increasingly eutrophic world.

Declaration of interest

The authors declare that there are no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.watres.2018.11.024>.

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