Ecological Processes

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The effects of biodiversity gradient on plant mass and metabolism of individual submerged macrophytes

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Abstract

Background: The effects of biodiversity on community function and services are frequently studied in the history of ecology, while the response of individual species to biodiversity remains great elusive. In this study, we determined the biodiversity effects on community productivity as well as species level plant mass and carbon (C) and nitrogen (N) metabolism of eight submerged plants. These macrophytes in Lake Erhai were selected and planted in a water depth of one meter along a diversity gradient of 1, 2, 4 or 8 species. Then, the community productivity or species level plant mass, soluble protein, free amino acid and soluble carbohydrate were correlated to species richness to determine the biodiversity effects on community and single species.

Results: The results showed that the community level biomass was positively correlated to plant species richness although the species level plant mass of individual species responded differently to the overall plant species richness. Namely, only one plant mass positively correlated to species richness and the others decreased or showed no significant correlation with the increase of species richness. The soluble proteins of most macrophytes were positively correlated to species richness; however, both the free amino acid and soluble carbohydrate of the plants were negatively or not significantly correlated to species richness.

Conclusions: These results indicated that the selection effects might dominate in our aquatic communities and the negative impacts of biodiversity on C and N metabolism of the macrophytes increased with the increase of species richness, which might result from the strong competition among the studied species. The biodiversity effects on the plant mass, and C and N metabolism of individual submerged species were first reported in this study, while more such field and control experiments deserve further research.

Keywords: Species richness, Productivity, Competition, Submerged macrophyte, Metabolism, Biodiversity

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Introduction

The growth and reproduction of submerged macrophytes are determined by many biotic and abiotic factors (Bornette and Puijalon 2011; Geist 2011; O'Hare et al. 2018), and there is a wealth of research on this topic. For example, abiotic factors as light, temperature, nutrient, sediment, CO_2 availability, water current, water level fluctuation, global change and biotic factors as interaction between plants, invasive species, herbivores, anthropogenic disturbance, biodiversity are always involved in these research programmes (Bornette and Puijalon 2011; Bakker et al. 2016; Hussner et al. 2017; Hilt et al. 2018; Sagerman et al. 2020). The ecosystem function and services affected by biodiversity are frequently assayed (Jiang et al. 2008; Emmerson et al. 2001; Giller et al. 2004; Hassler et al. 2014; Duffy et al. 2017; Ampoorter et al. 2020). For example, a positive diversity-productivity relationship is predominant in large scale studies or meta-analyses (Liang et al. 2016; Duffy et al. 2017; Ampoorter et al. 2020), which is usually explained by complementarity or sampling effects (Loreau and Hector 2001; Lefcheck et al. 2015). However, the pattern of species level plant mass over a species richness gradient remains largely unknown, although the average species level plant mass of individual plants in different species richness was measured in some previous studies (Hector et al. 2002; Hille Ris Lamber et al. 2004; Roscher et al. 2007; Marquard et al. 2009). In this type of experiments, the whole communities consist of the single plant species, which is indeed in the species pool. In addition, each species may respond differently to species richness because of the great differences among species (Firn et al. 2007; Jacob et al. 2010; Roscher et al. 2013). For this reason, some species may benefit from the increase of biodiversity to promote their plant mass, some species may suffer from the increase of biodiversity to reduce their plant mass, and some species may keep their plant mass stable with the increase of biodiversity (Wu et al. 2018). Accordingly, the responses of species level plant mass of individual plants to different species richness deserve further attention (Marquard et al. 2009; Wu et al. 2018).

For plant species, their growth is affected and reflected by their carbon (C) and nitrogen (N) metabolism (Cao et al. 2009; Yuan et al. 2016; Yu et al. 2017). Therefore, the growth conditions of plants can be indicated by their C and N metabolism. However, the effects of biodiversity on plant C and N metabolism are not well documented to our best knowledge, although other factors affecting plant C and N metabolism are frequently reported, such as NH_4^+ stress and low light availability (Cao et al. 2009), water depth (Yuan et al. 2016), high nitrogen loading (Yu et al. 2017), etc. To address this knowledge gap, it is necessary to determine the effects of biodiversity on plant C and N metabolism. Furthermore, whether C or N metabolism of the individual plant species responds differently to species richness, as species level plant mass of individual plants does because species are species-specific (Firn et al. 2007; Jacob et al. 2010; Wu et al. 2018, 2020). Moreover, whether the patterns of biodiversity effects on C or N metabolism of the individual plant species are in accordance with those of their species level plant mass.

We determined the C and N metabolism of the studied submerged macophytes through measuring the contents of the soluble protein, free amino acid and soluble carbohydrate of these plants as former researchers (Cao et al. 2009; Yuan et al. 2016; Yu et al. 2017). In this study, we hypothesize that (1) species level plant mass of individual species increases with overall species richness as community biomass due to complementarity effects (Loreau and Hector 2001; Lefcheck et al. 2015); and (2) all of the soluble protein, free amino acid and soluble carbohydrate of the submerged plants increase with overall species richness because of complementarity effects (Loreau and Hector 2001; Lefcheck et al. 2015). To test these hypotheses, we conducted a field pot experiment in 2018 to study the effects of biodiversity on species level plant mass as well as C and N metabolism of submerged plants in a biodiversity experiment in Lake Erhai. Furthermore, we discussed the feasibility of explaining the relationship between diversity and productivity (hereafter DPR) through the change of species level plant mass responding to species richness.

Materials and Methods

DPR experiment

The field experiment was conducted from August to October in 2018 (16 weeks), at Hongshan Bay (25°86′N, 100°14′E) in Lake Erhai, Dali City, Yunnan Province, China. This bay is characterized by light winds and waves. The study area is located in a warm plateau climate with an average annual temperature of 15.7 °C, a maximum temperature of 34 °C and a minimum temperature of –2.3 °C. The annual precipitation, sunshine duration and frost free period are 1024 mm, 2345 hours and 228 days, respectively. Eight common native submerged species in Lake Erhai were selected in this experiment (Ye et al. 2018). They are *Ceratophyllum demersum*, *Myriophyllum spicatum*, *Potamogeton maackianus*, *Stuckenia pectinata*, *Hydrilla verticillata*, *Vallisneria natans*, *Potamogeton nodosus* and *Potamogeton lucens*. All collected submerged macrophytes were washed and brushed softly with enough tap water and then the apical unbranched shoots (15 cm in length and similar in morphology) (clonal ramet with three leaves for *V. natans*) were then cut for planting. The number of plant species was controlled in every pot with a

circular area of 706.5 cm^2 (soil surface), 25 cm depth and pre-weighed 8 kg of sediment in the west littoral zone of Lake Erhai (Organic matter: 15.3–19.4 g kg^{-1}; total nitrogen: 1.52–1.78 g kg^{-1}, total phosphorus: 0.16–0.23 g kg^{-1} and pH: 6.12–6.93, about 15 cm thick soil layer). Each plant was planted in 5 cm depth. Plants were randomly cultivated with 1, 2, 4 or 8 selected species in communities (pots). Each diversity level was replicated eight times. In this experiment, we used four levels of diversity (1, 2, 4 and 8 species) and eight replicates, resulting in a total of 32 pots. Every pot was received 12 g plant cuttings, where the plant biomass was equally divided for each kind of species. All pots were suspended at one meter water level using a vinyl coated chain. The depth was measured from the top of the pot to the water surface. The pots were protected from fishes and other big aquatic animals by nets. Moreover, other appropriate care was carried out to minimize any disturbance. For example, other weeds (all plants not planted initially) were carefully removed from the pots when they were still small enough. For each pot, plants (roots and shoots) were harvested sixteen weeks later when roots were separated from soil by soaking the pot in water for 40 minutes and gently washing the soil away. Individual plant in each pot was dried at 70 °C for 72 h and measured as its species level plant mass. The total weight of all species level plant mass in each pot was considered its community level biomass. During experiment phase, the water level fluctuated between −10 cm and +20 cm.

Physiological analysis

For the single plant in every pot, the dry plant was ground into powder with a pestle and mortar. About 30 mg of the powder was extracted with 10 ml 80% ethanol at 80 °C. After centrifugation, the supernatant was used for free amino acid (FAA) and soluble carbohydrate (SC) determination. The FAA was determined by ninhydrin colorimetry method using alanine as a stand (Yemm and Willis 1954). The SC was determined by phenol method using glucose as a standard (Yemm and Cocking 1955). The soluble protein (SP) was determined using Coomassie brilliant blue G-250 (Bradford 1976) with bovine serum albumin as a stand.

Data analysis

Statistical analyses were conducted using the software package R 3.5.2 (R Core Team 2018). Although linear fitting is often used to indicate the relationship between biodiversity and productivity for most of DPR experiments, we used best fit curve to describe their correlation as some non-linear relationships were observed in some previous research (Waide et al. 1999; Duffy et al. 2017; Ampoorter et al. 2020; Wu et al. 2021). The best model was selected by using the Akaike's information criterion (AIC) procedure through comparing the AIC values of the six common models (Linear, Quadratic, Exponential growth, Power, Rational and Logarithm). Accordingly, Spearman's Rank Correlation Coefficient was used to analyze the relationships between community biomass or plant species level mass and plant species richness. Relationships between SP, FAA and SC of the individual plant species and the species richness in the experiment were also analyzed by Spearman's Rank Correlation Coefficient.

Results

Responses of Community productivity and species level plant mass

Our results showed that the species richness was significantly positively correlated to community biomass (productivity) (Fig. 1; $R^2 = 0.57$, $p < 0.0001$). With regard to the species level plant mass, only plant mass of *C. demersum* was positively correlated with the species richness (Fig. 2A). However, plant masses of *P. maackianus* and *P. lucens* were not significantly correlated to the species richness (Fig. 2C, H, $R^2 = 0.01$, $p = 0.51$ and $R^2 = 0.01$, $p = 0.64$, respectively) and plant masses of the other five macrophytes were negatively correlated with the species richness (Fig. 2B, D–G, $p < 0.05$).

C and N metabolism

The SP contents of most submersed plants, especially of *S. pectinata*, were markedly positively correlated to species richness (Fig. 3B–G, $p < 0.05$) except those of *C. demersum* and *P. maackianus*, which demonstrated no significant correlation with the species richness (Fig. 3A, 3C, $R^2 = 0.14$, $p = 0.37$ and $R^2 = 0.13$, $p = 0.17$, respectively). However, the FAA contents of most submersed macrophytes, especially of *S. pectinata*, were prominently negatively correlated to the species richness (Fig. 4, $p < 0.05$) except that of *P. maackianus*, which exhibited no significant correlation with the species richness (Fig. 4C, $R^2 = 0.19$, $p = 0.26$), and that of *P. nodosus*, which increased firstly and then dropped with the species richness (Fig. 4G, $R^2 = 0.51$, $p = 0.01$). Similarly, the SC contents were distinctly negatively correlated to the species richness for *M. spicatum* and *P. nodosus* (Fig. 5B, 5G, $p < 0.05$) or displayed no significant correlation with the species richness for *C. demersum*, *P. maackianus* and *H. verticillata* (Fig. 5A, 5C, 5E, $p > 0.05$), while the SC contents of *V. natans* increased firstly and then dropped with the species richness (Fig. 5F, $R^2 = 0.65$, $p = 0.01$).
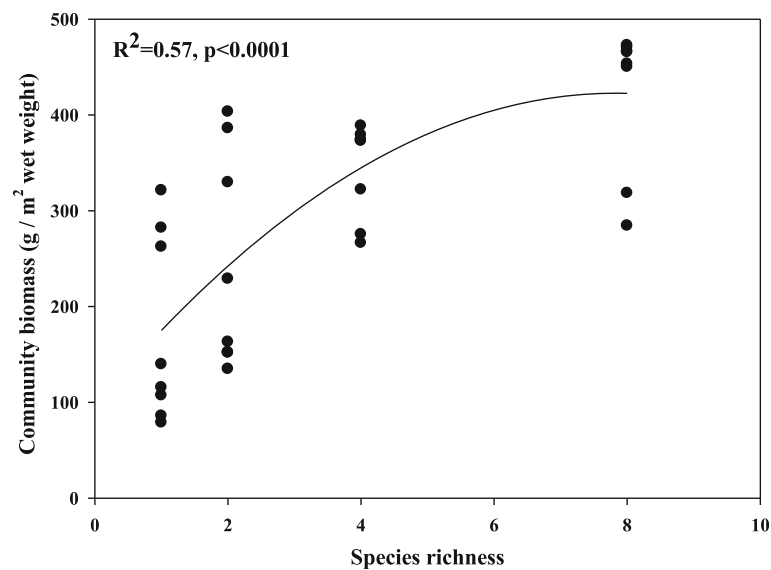
Fig. 1 The relationship between community productivity and plant biodiversity in an aquatic macrophytes experiment, which was conducted from August to October 2018 at Hongshan Bay in Lake Erhai, Dali City, Yunnan Province, China

Discussion

Positive linear pattern of DPR

In this experiment, the results imply that community level biomass is significantly positively correlated with the species richness in the aquatic environment. These positive relationships are in accordance with most of the results of previous studies and recent meta-analyses (Tilman et al. 1996; Loreau and Hector 2001; Adler et al. 2011; Lefcheck et al. 2015; Grace et al. 2016; Mandal et al. 2018; Luo et al. 2019; Rita and Borghetti 2019). The positive linear pattern of DPR results from the over-yielding usually caused by complementarity effects or selection effects in high biodiversity communities (Loreau and Hector 2001). However, contrary to Wu et al. (2018), our results clearly suggest that the selection effect is dominated in this aquatic experiment as the plant mass of only one species increased with plant biodiversity, while those of other species decreased or kept static with plant biodiversity (Fig. 2). The results obviously indicate that strong competition increases among the studied species with species richness. But we do not know when complementarity effects or selection effects occur. So, which factor(s) determine either the complementarity effects or the selection effects, which play an important role in the over-yielding in DRP experiments, might be an ecological hotspot in the near future.

Competition among species

As stated above, only plant mass of *C. demersum* increased with plant biodiversity, while those of other species decreased or kept static with plant biodiversity (Fig. 2). In this sense, plant mass of individual species may

benefit from or suffer from or keep relative stable with the increase of biodiversity. We can speculate that the over-yielding in high biodiversity is the trade-off of all species. This result agrees well with the obversations of Ye et al. (2018) in Lake Erhai, where they suggested that the dominant species at the depth of one meter in the west littoral zone of Lake Erhai was *C. demersum*, which has the most competitive ability and can outperform other submerged species. Therefore, we can speculate that only the biomass of *C. demersum* increased with species richness and those of the other species declined with plant biodiversity is due to either the strong competition stress of *C. demersum* or the strong competition stress among the study species. Generally, plants firstly develop physiological adaptations responding to adverse environments (Hessini et al. 2009; Yuan et al. 2016; Sasidharan et al. 2018), such as the changes of many kinds of antioxidant enzymes, SC and FAA. Under stress conditions, the defense systems of plants can be overwhelmed and many types of antioxidant enzymes are induced to remove reactive oxygen species in plant cells (Alscher et al. 2002; Wu et al. 2009). Accordingly, the contents of SP in plant species increase with the increase of stress because all antioxidant enzymes are SPs. The SP contents of our study species were positively correlated with species richness (Fig. 3), which indicates that both the competition stress (suffered by these submerged macrophytes) and antioxidant enzymes (produced by these submerged macrophytes) increase with plant biodiversity. On the contrary, the FAA and (or) SC concentrations of the study species declined with the species richness (Figs. 4 and 5). This suggests that the
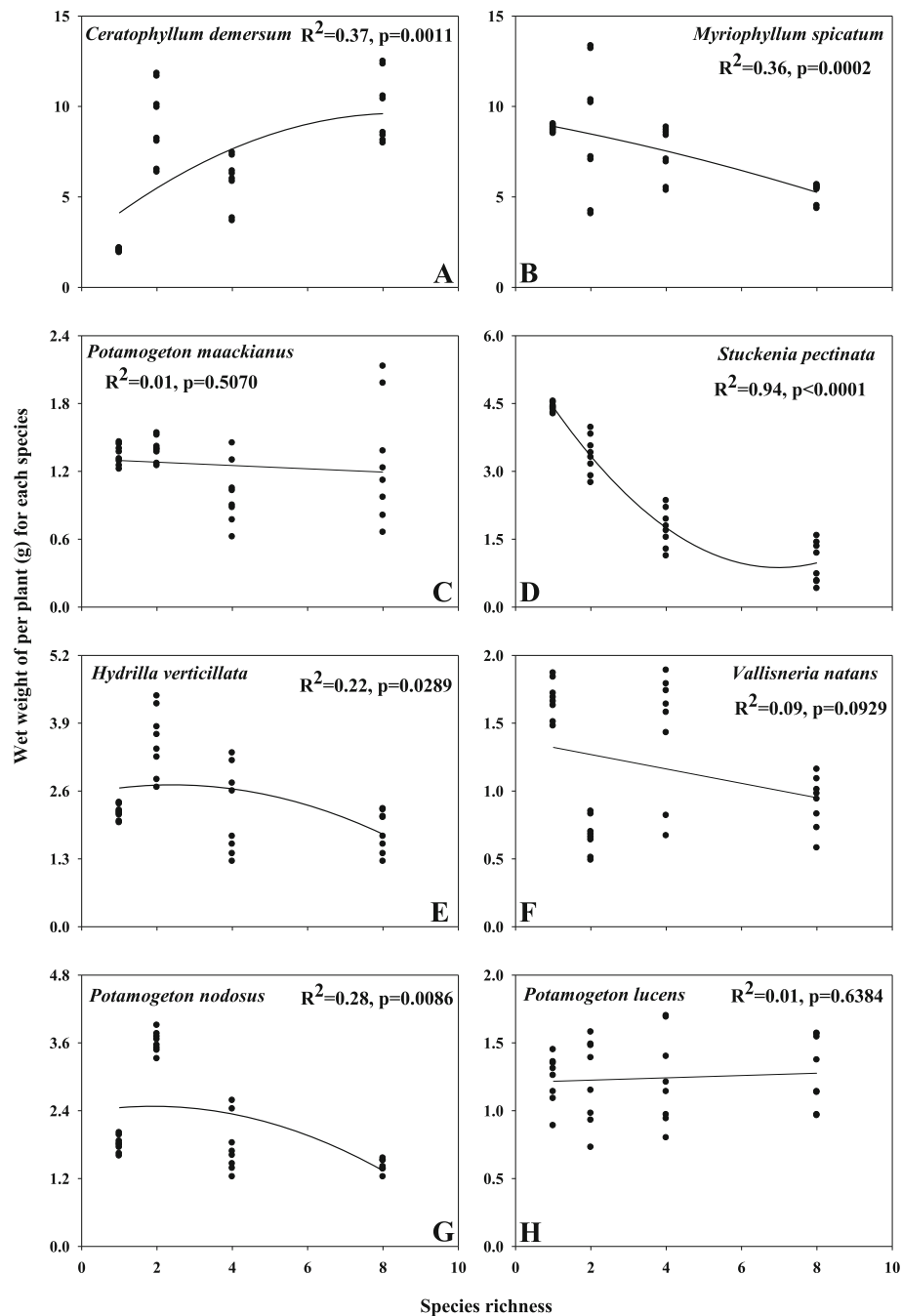
Fig. 2 The species level plant masses of individual species along an aquatic plant biodiversity gradient in Lake Erhai. Eight common native submerged species were selected in this experiment, see Materials and Methods

production of FAA and (or) SC is inhibited in the study macrophytes when the competition stress, resulting from high plant biodiversity, is strong (Cao et al. 2009; Yuan et al. 2016; Yu et al. 2017). Thus, the biomass production and growth of the plants can be greatly affected, as observed in our study, because FAA and SC are important intermediates and buffering pool of C and N

metabolism (Myers and Kitajima 2007; Yuan et al. 2016). These results are partially opposite to our two hypotheses, indicating most studied macrophytes suffered from the increase of biodiversity in our experiment. This might because that the light competition among these submerged species in this mesotrophic lake (Geist 2011; Ji et al. 2017; Ye et al. 2018) increased with biodiversity
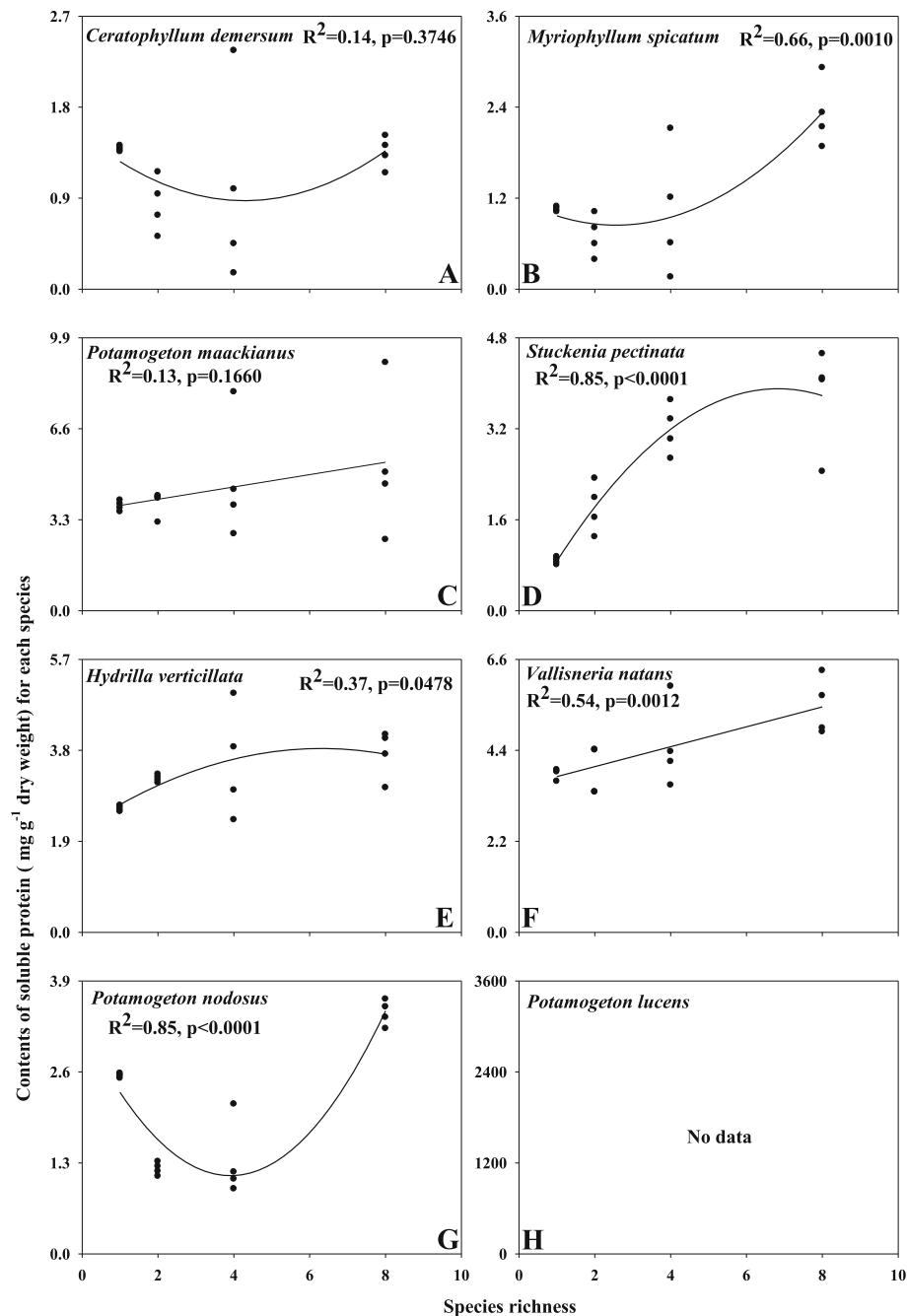
Fig. 3 The plant soluble protein of individual species along an aquatic plant biodiversity gradient in Lake Erhai. Note: No data means that the sample is too small to be measured and the follows are the same

due to over-yielding (Clark and Tilman 2008; Borer et al. 2014; Cerabolini et al. 2016), as observed in our study.

Different responses of individual species

Our results showed that different species responded differently to species richness and even the different measured parameters of the same species responded

diversely to the species richness in our aquatic communities, which agrees well with much previous research (Hector et al. 2002; Hille Ris Lamber et al. 2004; Roscher et al. 2007; Marquard et al. 2009; Wu et al. 2018, 2020). This result therefore implies that both plant species and plant variables cannot equally benefit from high plant species richness because of the great differences among species and the index-specificity within a species (Firn
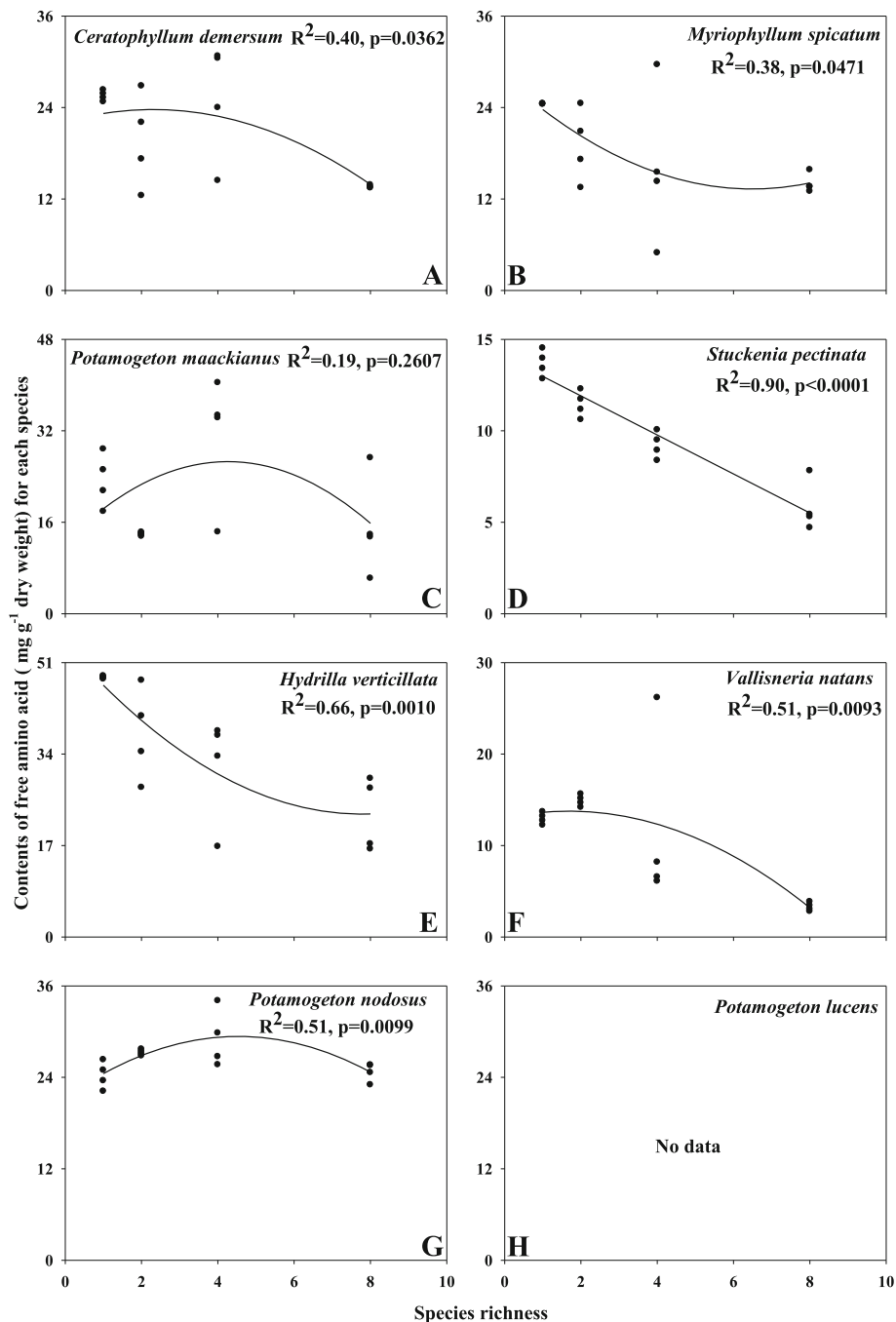
Fig. 4 The plant free amino acid of individual species along an aquatic plant biodiversity gradient in Lake Erhai

et al. 2007; Jacob et al. 2010; Roscher et al. 2013; Wu et al. 2018, 2020). This might be a good explanation of the formation of distinct function species (Whittaker 1965; Odum 1983), such as dominant, sub-dominant, companion, keystone, rare and redundant species, within a community in real nature because of their different benefits from biodiversity. However, this phenomenon cannot be observed within such a short experimental

period and more extensive and intensive studies are needed to prove this. Accordingly, the four DRP patterns are very reasonably and frequently observed because the pattern is determined by tradeoffs between the plant masses of all species, which are actual species in the species pool consisting of the whole communities (Wu et al. 2018). Furthermore, the interplay of multiple particular abiotic and biotic experimental conditions makes the
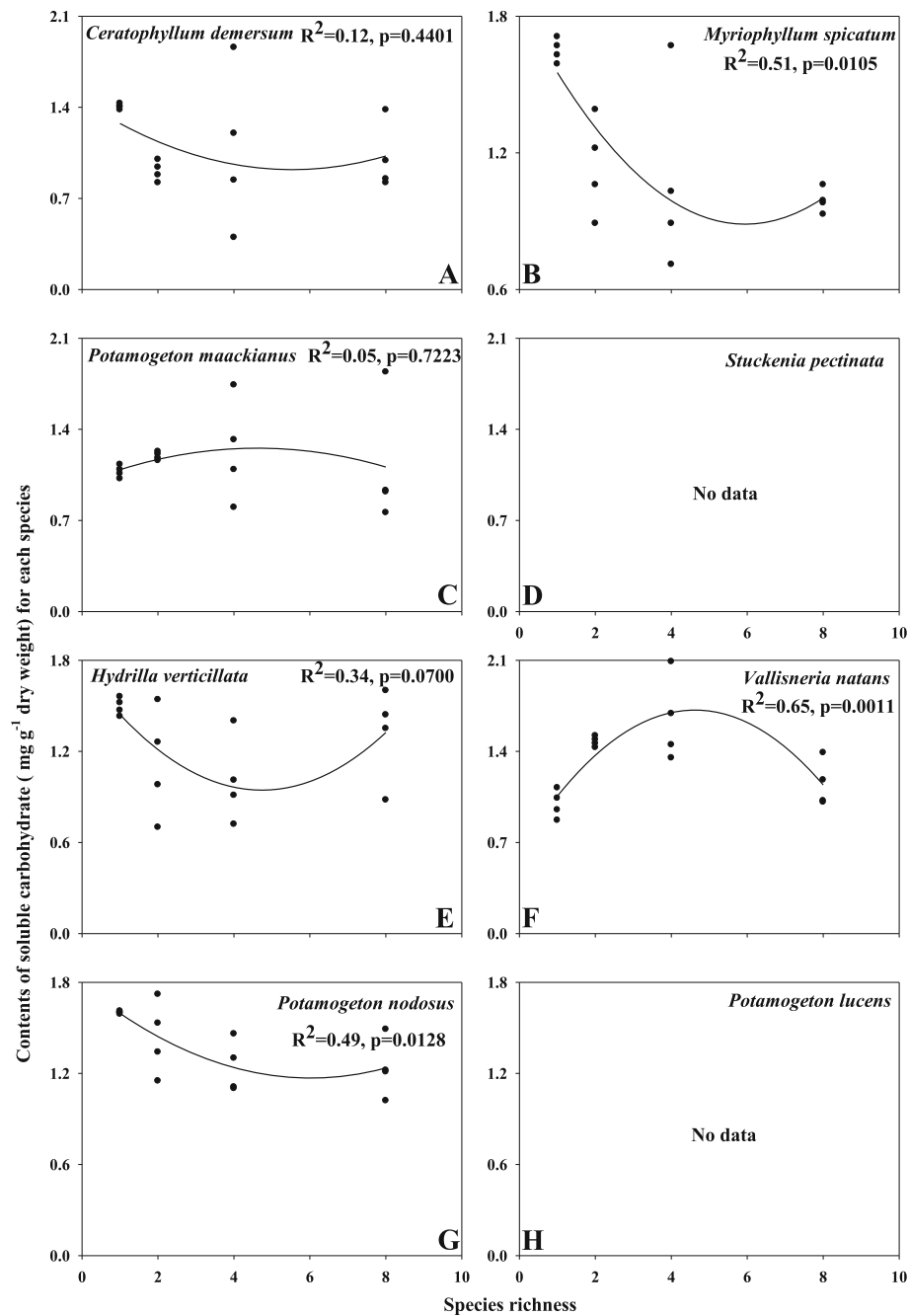
Fig. 5 The plant soluble carbohydrate of individual species along an aquatic plant biodiversity gradient in Lake Erhai

pattern of the DPR more complicated (Byrnes et al. 2014; Lefcheck et al. 2015). This might be the reason that there are no explicit explanations of the other three DPR patterns except the positive linear DPR pattern. However, the pattern of species level plant mass over the biodiversity gradients can be readily obtained whatever the abiotic or biotic factors change. This might make species level plant mass a great advantage over others in terms of

mechanic explanations of DPR patterns though there are some little design flaws (e.g. less species) in our experiment. Therefore, we argue that a type of DPR pattern could be interpreted by analyzing the trends of species level plant mass over the biodiversity gradient. This might be a good alternative mechanism explaining the complicated DPR patterns and more extensive experiments are needed to further prove our hypothesis.

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Conclusion

Community productivity was significantly positively correlated with plant biodiversity due to the selection effect. However, the relationships between species level plant mass, plant SP, FAA and SC and species richness are more complicated. The negative effects of biodiversity on the most of the studied species are attributed to the strong competition, especially light competition, among these submerged macrophytes. The analyses of the plant species level response to species richness might be a good alternative mechanism explaining the complicated DPR patterns, which are affected by many intricate factors.

Abbreviations

C: Carbon; N: Nitrogen; DPR: The relationship between diversity and productivity; FAA: Free amino acid; SC: Soluble carbohydrate; SP: Soluble protein

Authors' contributions

QLY and WAP initiated the study and wrote the main manuscript; QLY, ZHY, ZW, LL, YSY and LF were responsible for the field experiment and laboratory analysis; WYH and HF for data analysis; WYH and SCL for literature research; BZX for manuscript revision; and all authors contributed to discussion on the field survey and final version of the draft. The authors read and approved the final manuscript.

Availability of data and materials

Please contact the author for data requests, and the data will be available online upon your request

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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