



# The Biodiversity–Biomass Relationship of Aquatic Macrophytes Is Regulated by Water Depth: A Case Study of a Shallow Mesotrophic Lake in China

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The relationship between biodiversity and productivity (or biomass production) (BPR) has been a popular topic in macroecology and debated for decades. However, this relationship is poorly understood in macrophyte communities, and the mechanism of the BPR pattern of the aquatic macrophyte community is not clear. We investigated 78 aquatic macrophyte communities in a shallow mesotrophic freshwater lake in the middle and lower reaches of the Yangtze River in China. We analyzed the relationship between biodiversity (species richness, diversity, and evenness indices) and community biomass, and the effects of water environments and interspecific interactions on biodiversity–biomass patterns. Unimodal patterns between community biomass and diversity indices instead of evenness indices are shown, and these indicate the importance of both the number and abundance of species when studying biodiversity–biomass patterns under mesotrophic conditions. These patterns were moderated by species identity biologically and water depth environmentally. However, water depth determined the distribution and growth of species with different life-forms as well as species identities through environmental filtering. These results demonstrate that water depth regulates the biodiversity–biomass pattern of the aquatic macrophyte community as a result of its effect on species identity and species distribution. Our study may provide useful information for conservation and restoration of macrophyte vegetation in shallow lakes through matching water depth and species or life-form combinations properly to reach high ecosystem functions and services.

**Keywords:** biodiversity indices, biomass, water depth, macrophyte, freshwater ecosystem, life-form

## INTRODUCTION

The relationship between biodiversity and ecosystem function has been debated for decades in many ecosystems (Duffy et al., 2017). Productivity and biomass production are comprehensive reflections of the response of plants to the environment as a result of growth and reproduction and are often focused on as key features of ecosystem functions (Loreau et al., 2001;

Chisholm et al., 2013). The reported shapes of relationships between biodiversity and productivity (or biomass) (BPR pattern) vary greatly from positive or negative patterns in which biodiversity increases or decreases linearly with productivity (Wardle et al., 1997; Liang et al., 2016; Luo et al., 2019) to unimodal patterns in which biodiversity peaks at intermediate productivity (Dodson et al., 2000; Leduc et al., 2012; Craven et al., 2016), and in some cases, there is no correlation between them (Vila et al., 2003). A possible reason for this divergence is that data are often collected at different ecosystems (Bai et al., 2007; Hillebrand and Cardinale, 2010; Brun et al., 2019). Brun et al. (2019) demonstrate that biodiversity typically increases with productivity in forests although a unimodal pattern is shown in grasslands. However, those studies focus on terrestrial and marine ecosystems, such as phytoplankton and algae (Chen et al., 2019; De Raedt et al., 2019). Only a few studies investigate the BPR pattern of the macrophyte community. For example, Dodson et al. (2000) explore how macrophyte productivity influences macrophyte species richness by investigating several lakes in North America and find that the species richness presented a unimodal pattern on the productivity gradient. The pond study of Chase and Leibold (2002) also indicates that richness increases at low productivity but decreases at high productivity as a result of interspecific interaction and species identity. Recently, increasing studies prove that species identity (Roscher et al., 2007; Cui et al., 2019) and interaction (Michalet et al., 2006; Xiao et al., 2009) would be the underlying biological mechanisms that determine BPR patterns due to their great contribution to the community structure. It is demonstrated that interspecific interaction and species compositional difference have important effects on diversity patterns and productivity (Chase and Leibold, 2002; Chase and Ryberg, 2004). However, many studies confound the effects of species identity and interaction on the BPR pattern and treat them as a whole to explain the biological mechanism of the BPR pattern (Chase and Leibold, 2002; Chase and Ryberg, 2004). Previous BPR experiments used an analysis of variance method to separate the effects of species composition and diversity on the community structure. However, the method did not provide information on contributions of different species to the ecosystem structure. It is necessary to distinguish the effects of specific species identity and interspecific interaction on the BPR pattern for a better understanding of biological mechanisms of the BPR pattern. Therefore, we applied the diversity-interaction (DI) model proposed by Kirwan et al. (2009) to separate the contribution of different species and interspecific interactions to the community structure.

Furthermore, many abiotic factors, such as temperature, nutrition level, and water availability, affect the BPR pattern (Ma et al., 2010; Gravel et al., 2011). In terrestrial ecosystems, Palpurina et al. (2018) suggest that the type of nutrient limitation alters the BPR pattern in grasslands, and Garcia et al. (2018) find that changes in temperature influence the BPR pattern of microbial communities. In aquatic ecosystems, connectivity of the watershed and heterogeneity in the environmental factors are demonstrated to be prominent factors that affect the BPR pattern of the macrophyte community at a large scale (Chase and Leibold, 2002; Chase and Ryberg, 2004). However, the underlying abiotic

mechanism of the macrophyte BPR pattern on a local scale has not been explored yet. Although many environmental factors, such as light, temperature, nutrient content of water bodies, and substrate characteristics, affect the growth and distribution of aquatic vegetation (Barko and Smart, 1986; Jeppesen et al., 2000; Squires et al., 2002; Bornette and Puijalon, 2011), it is proved that water depth is the major factor influencing growth and community composition of macrophytes mainly due to the limitation of light availability in shallow lakes (Van Geest et al., 2003; Scheffer and van Nes, 2007; Dong et al., 2014; Fu et al., 2014). Spence (1967) and Hudon et al. (2000) find a distribution of species with different growth forms along the water depth gradient, which results in the zonation of the macrophyte community. To be specific, there is a sequence from emergent to floating-leaved and submerged vegetation with increasing water depth. Nevertheless, how environmental factors, especially water depth and its effect on macrophyte distribution, affect the BPR pattern of the macrophyte community is rarely studied.

In addition, most studies are based on species richness in the study of the BPR pattern (Whittaker, 1972). However, other biodiversity indices, such as diversity (e.g., Shannon–Wiener index and Simpson diversity) and evenness indices (e.g., Pielou evenness and Simpson evenness), are also important for the measurement of the BPR pattern. This is because these indices incorporate the proportional abundance of each species within the community (Lembrechts et al., 2018), which provides more adequate information on the contribution each species makes to the ecosystem function. Nonetheless, the ecological meanings these indices deliver are different. Species richness, the Shannon–Wiener index, and Shannon diversity are sensitive to the presence of rare categories in an ecological community (Bandeira et al., 2013; Maturo, 2018). Simpson diversity is primarily a measure of dominance concentration because it is a good indicator of the dominance of one or several species over other species (Whittaker, 1972). Evenness indices, the degree to which abundances are equitably divided among species, represents whether the abundance of a species in the community is regular. High evenness represents the uniform distribution of species in the community with similar abundance, and low evenness represents an uneven abundance of species in the community with the existence of dominant species (Schleuter et al., 2010). Chalcraft et al. (2008) demonstrate that different measures of biodiversity respond to productivity in different ways in grasslands. However, the aquatic ecosystem may perform dissimilar patterns from the terrestrial ecosystem due to the specific habitat (surrounded by a water column).

Aquatic macrophytes provide numerous ecological and economic services, such as offering a habitat and food to aquatic animals and birds, supplying raw materials for social production (Costanza et al., 1997; Jeppesen et al., 2012). Investigation of the BPR pattern of the aquatic macrophyte community is critical to understand the aquatic ecosystem function. Therefore, we conducted an investigation of Liangzi lake, which is located in the middle and lower reaches of the Yangtze River in China, suffers medium human disturbance, and conserves many rare and endangered species (Fang et al., 2006), to explore the biodiversity–biomass pattern of the

macrophyte community and its mechanisms under mesotrophic conditions. We hypothesized that (1) there are unimodal relationships between multiple measures of biodiversity and biomass; (2) both species identity and interspecific interaction shape the biodiversity–biomass pattern biomechanically; and (3) environmental factors, especially water depth, affects the community structure and biodiversity–biomass pattern.

## MATERIALS AND METHODS

### Study Area

The study was performed in Liangzi Lake (30°05′–30°18′N, 114°21′–114°39′E), Hubei Province, China (Figure 1). Liangzi Lake is the largest freshwater lake with the largest water storage capacity ( $14 \times 10^8$  tons) and water area (304.3 km<sup>2</sup>) in Hubei Province (Wang et al., 2019; Meng et al., 2020). It is under the mesotrophic level with average total nitrogen of 0.554 mg/L and average total phosphorus of 0.024 mg/L. Liangzi Lake features a subtropical monsoon climate with an annual average temperature of 17°C, an average annual precipitation of 1330 mm and a mean freezing period of 15 days. It is a typical macrophyte-dominated shallow lake (i.e., macrophyte is the main primary producer) in the middle reaches of the Yangtze River Basin with high macrophyte biodiversity, about 90 species during the last decade (Fang et al., 2006; Xie et al., 2015). The dominant submerged species are *Myriophyllum spicatum*, *Vallisneria natans*, *Ceratophyllum demersum*, *Potamogeton malaianus*, *Hydrilla verticillata*, etc., and there are many rare and endangered species in Liangzi Lake, such as *Ottelia alismoides* and *Ceratopteris thalictroides*. However, Liangzi Lake was seriously flooded in 2016 (Xu et al., 2018), which led to the degradation of submerged macrophytes in the central lake as well as being caused by flood in 2010 (Wang et al., 2019), only vegetation in the shore area has been restored after flood due to relative low water depth until 2018. Therefore, macrophytes were surveyed in the shore area of Liangzi Lake as shown in Figure 1.

### Plant Samples

From July 19 to August 7, 2018 (i.e., the growing season when macrophytes have maximal production), 78 aquatic macrophyte plots (1 m × 1 m) (Müllerová et al., 2020) were surveyed according to a typical sampling method on the shores of Liangzi Lake, where aquatic plants are widely distributed. To be specific, one or two plots were placed in small communities, and three to four plots were placed in communities with high species richness and complicated community structure. The species in each plot were recorded, and the coverage of each species was determined by visual estimation on a 22° scales (0.5, 1, 5, 10, 15, 20, . . . , 100%). Whole plants containing shoots and roots were collected and washed to remove sediment and surface residues. The plant samples were immediately brought to the National Field Station of Freshwater Ecosystem at Liangzi Lake (hereafter referred to as the Liangzi Lake National Station) for further measurement. The plant materials collected from each site were classified based

on species and life-form (i.e., submerged, floating-leaved, free-floating, and emergent plants) then oven-dried at 80°C for 72 h to obtain the biomass. Community biomass refers to the total biomass of all species in each plot in our study.

### Water Environment

First, water depth was measured in each plot. Then, incident photosynthetically available irradiance (400–700 nm) was measured three times at the air–water surface and different underwater depths using a fiber optic sensor (LI-250A, LI-COR, Inc.). Light attenuation for photosynthetically active radiation was valued as the light attenuation coefficient,  $K_d$  (m<sup>-1</sup>). Finally, physical and chemical parameters were measured at each site at 1 m underwater. Water temperature (T), dissolved oxygen (DO), conductivity (Cond), total dissolved solids (TDS), salinity (SAL) and pH of water samples were measured using a portable water quality monitor (PROPLUS, YSI, United States). Turbidity (Turb) and total suspended solids (SS) were measured using a turbidity meter (2100Q, HACH, United States) and a portable spectrophotometer (DR900, HACH, United States). Water samples were collected in 500-ml clean bottles, stored in a portable refrigerator and transported to Liangzi Lake National Station immediately for analyses of total nitrogen (TN) and total phosphorus (TP). TN and TP were analyzed in a flow injection analyzer (QC8500, LACHAT, United States).

### Biodiversity Indices

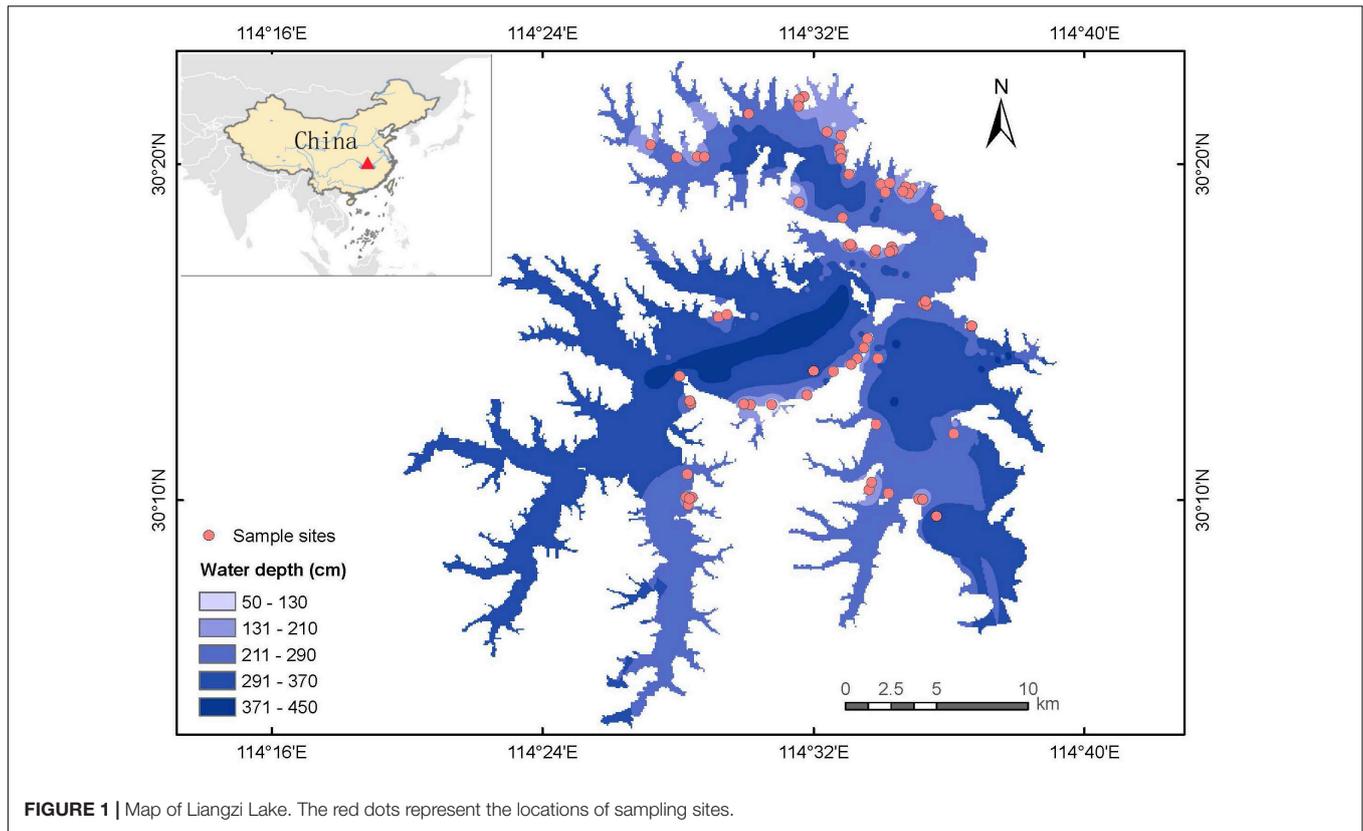
Seven biodiversity indices, including four diversity indices and three evenness indices, were computed as follows:

Richness	$R = S,$
Shannon–Wiener index	$SW = - \sum_{i=1}^S \left( \frac{C_i}{C} \ln \frac{C_i}{C} \right),$ (Shannon and Weaver, 1949)
Shannon diversity	$SD = e^{[- \sum_{i=1}^S \left( \frac{C_i}{C} \ln \frac{C_i}{C} \right)]},$ (Maturó, 2018)
Simpson diversity	$SiD = 1 - \sum_{i=1}^S \left( \frac{C_i}{C} \right)^2,$ (Simpson, 1949; Pielou, 1969)
Pielou evenness	$PE = \frac{- \sum_{i=1}^S \left( \frac{C_i}{C} \ln \frac{C_i}{C} \right)}{\ln S},$ (Pielou, 1969)
Shannon evenness	$SE = \frac{e^{[- \sum_{i=1}^S \left( \frac{C_i}{C} \ln \frac{C_i}{C} \right)]}}{S},$ (Sheldon, 1969)
Simpson evenness	$SiE = \frac{1 - \sum_{i=1}^S \left( \frac{C_i}{C} \right)^2}{S},$ (Morris et al., 2014)

where  $S$  is the species number of a plot,  $C_i$  is the coverage of species  $i$ , and  $C$  is the sum coverage of all species in a plot.

### DI Models

The DI model, improving diversity effects models proposed by Loreau and Hector (2001), separates the contribution of different species and interspecific interactions to ecosystem function (Kirwan et al., 2009). In our study, the DI model was employed to test how individual species and interaction between species pairs affect the biodiversity–biomass pattern by comparing hierarchical linear DI models (Kuebbing et al., 2015).



**FIGURE 1** | Map of Liangzi Lake. The red dots represent the locations of sampling sites.

The general formulation of the linear model is  $y = ID + DE + \epsilon$ , in which  $y$  is a community-level ecosystem function (here, biomass),  $ID$  is species identity effects, and  $DE$  is diversity effects. Four hierarchical linear DI models (Table 1) were used to test alternative hypotheses about the effect of species identities and interspecific interactions on the biomass in aquatic macrophyte communities (Kirwan et al., 2009; Kuebbing et al., 2015). By comparing the fit and analyzing the variance of these models, we can evaluate how species and interactions between pairwise species explain the BPR pattern (Kirwan et al., 2009).

The null model (M0) assumes that ecosystem function does not change with diversity but with a function of total abundance ( $M$ ) of the community. M1 adds an overall species identity term  $\beta_i P_i$ , a function of the production of each species in monoculture ( $\beta_i$ ) weighted by its proportion ( $P_i$ ) in the community on the basis of the null model. M1 tests the effects of each species individually on the biomass in the absence of species interactions ( $DE = 0$ ). M2 includes a pairwise interactions term  $\delta_{ij} P_i P_j$ , where  $\delta_{ij}$  is the strength of interspecific interaction between species  $i$  and  $j$ , and M2 turns to M3 when all pairwise species combinations have the same strengths of interspecific interaction ( $\delta_{AV}$ ). The above models constitute a hierarchy of complexity describing species identity and interaction effects. By comparing the fit of models in this hierarchy, we can test biological hypotheses about how species identity and interspecific interaction effects contribute to ecosystem function (Kirwan et al., 2009). The significant difference between M1 and M0 demonstrates that species differ in their individual monoculture performances, between M3 and

M1 demonstrates that there is a diversity effect on average, and between M3 and M2 demonstrates that separate pairwise interactions differ (Kirwan et al., 2009).

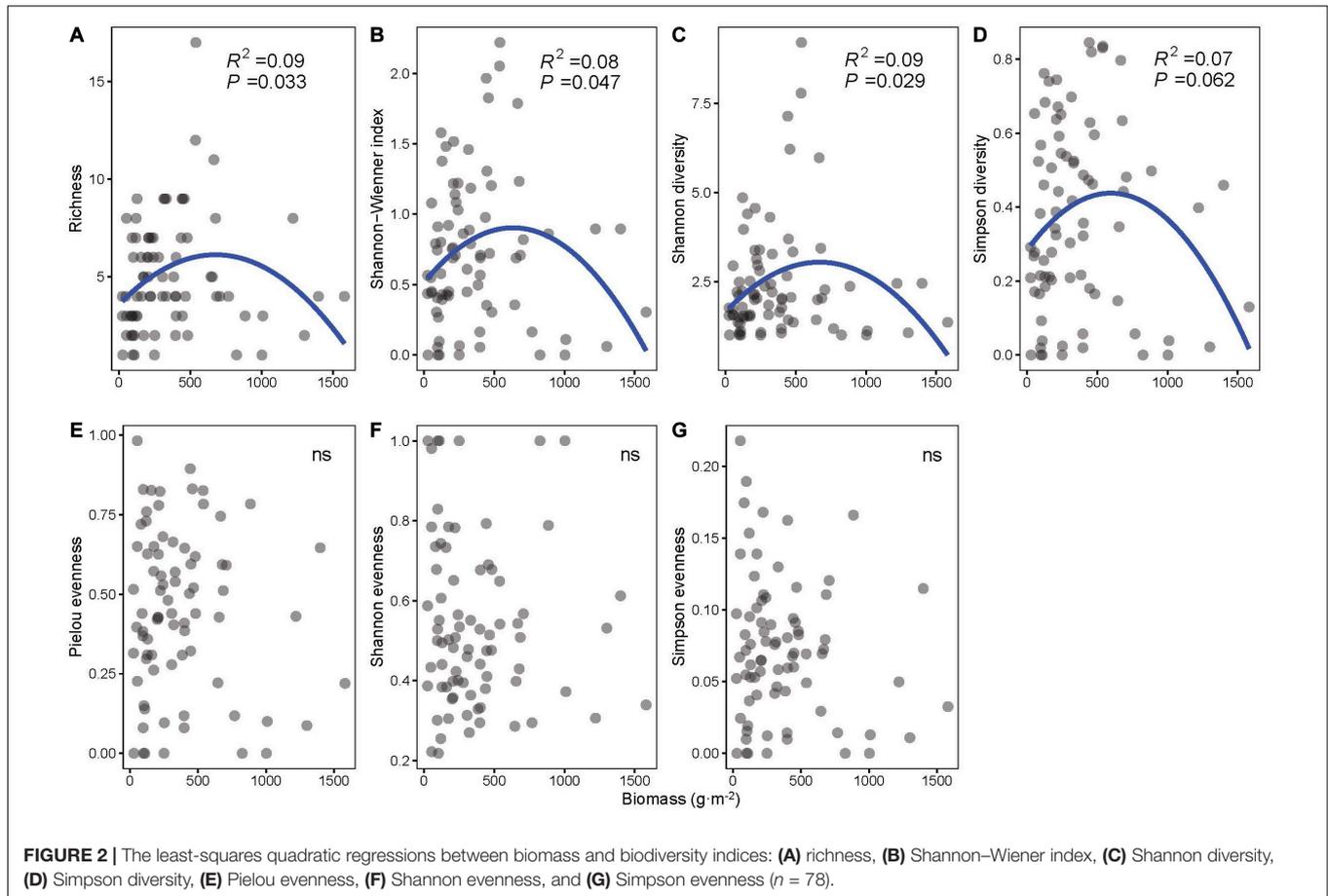
### Data Analyses

To examine the influence of the biomass of the macrophyte community on diversity indices (i.e., richness, Shannon–Wiener index, Shannon diversity, Simpson diversity, Pielou evenness,

**TABLE 1** | Hierarchical linear DI models.

Model	Formula
M0 Null model	$y = \alpha M + \epsilon$
M1 Species identity model	$y = \sum_{i=1}^S \beta_i P_i + \alpha M + \epsilon$
M2 Separate pairwise interactions	$y = \sum_{i=1}^S \beta_i P_i + \alpha M + \sum_{\substack{i,j=1 \\ i < j}}^S \delta_{ij} P_i P_j + \epsilon$
M3 Average interaction effect	$y = \sum_{i=1}^S \beta_i P_i + \alpha M + \delta_{AV} \sum_{\substack{i,j=1 \\ i < j}}^S P_i P_j + \epsilon$

*S* and *M* means species richness and total abundance of a community, respectively.  $P_i$  and  $P_j$  are the relative biomass of species  $i$  and  $j$ . The coefficient reflects the effect of total abundance on ecosystem function ( $y$ );  $\beta_i$  is the estimated performance of species  $i$  in monoculture;  $\delta_{ij}$  is the strength of interspecific interaction between species  $i$  and  $j$ ;  $\delta_{AV}$  is the average strength of interspecific interaction.



Shannon evenness, and Simpson evenness), we first fitted linear relationships using least-squares linear regressions in which the dependent variables are the biodiversity indices. We then performed least-squares quadratic regressions. We deem the relationship curvilinear if the quadratic term is significantly different from zero and the overall model is significant. We compared two statistical models to select the most appropriate fit to the data. The Akaike information criterion (AIC) was calculated to help select the best model for each of the biodiversity indices. The least-squares quadratic regressions were chosen finally due to the lower AIC value. DI models

**TABLE 2 |** Comparisons between hierarchical DI models testing biological hypotheses about the contribution of species identity and interspecific interactions to productivity.

Diversity–interaction hypothesis	Model comparison	$\Delta AIC$	$P$
Species differ in their individual monoculture performance	M1-M0	−67.24	<b>&lt;0.001</b>
There is a diversity effect on ecosystem functioning	M3-M1	−0.75	0.2157
Separate pairwise interactions differ	M3-M2	102.89	0.8654

*P* in bold indicates a significant difference between two models.

were fitted by ordinary multiple regression, and comparisons between hierarchical models were made using the differences in AIC (Connolly et al., 2013) with variance analysis testing its significance using the ANOVA function. Differences in communities with different dominant species in biomass and biodiversity were compared using one-way ANOVA by *post hoc* Bonferroni tests for multiple comparisons, respectively, with the R packages agricolae (Mendiburu, 2009).

Redundancy analysis (RDA) was used to rank the aquatic macrophytes of four life-forms and species on all environmental gradients by the R package vegan (Oksanen et al., 2007). Stepwise regression was performed to eliminate the collinearity of environmental factors and screen out the major factors that influence the BPR pattern. We used the natural log-response ratio,  $\ln(\text{biomass}/\text{biodiversity})$ , as the effect size metric for the relationship between biodiversity and biomass.

The least-squares linear regressions were performed to examine the effects of water depth on biomass (i.e., total biomass and the biomass of emergent, floating-leaved, and submerged plants) and diversity indices (i.e., richness, Shannon–Wiener index, Shannon diversity, Simpson diversity, Pielou evenness, Shannon evenness, and Simpson evenness) after comparison of models' AIC value with least-squares quadratic regressions. Notably, free-floating species were not included in this analysis due to their extremely low frequency (2 of 78 plots). The above

analyses were performed using R version 3.5.1 (R Development Core Team, 2011).

## RESULTS

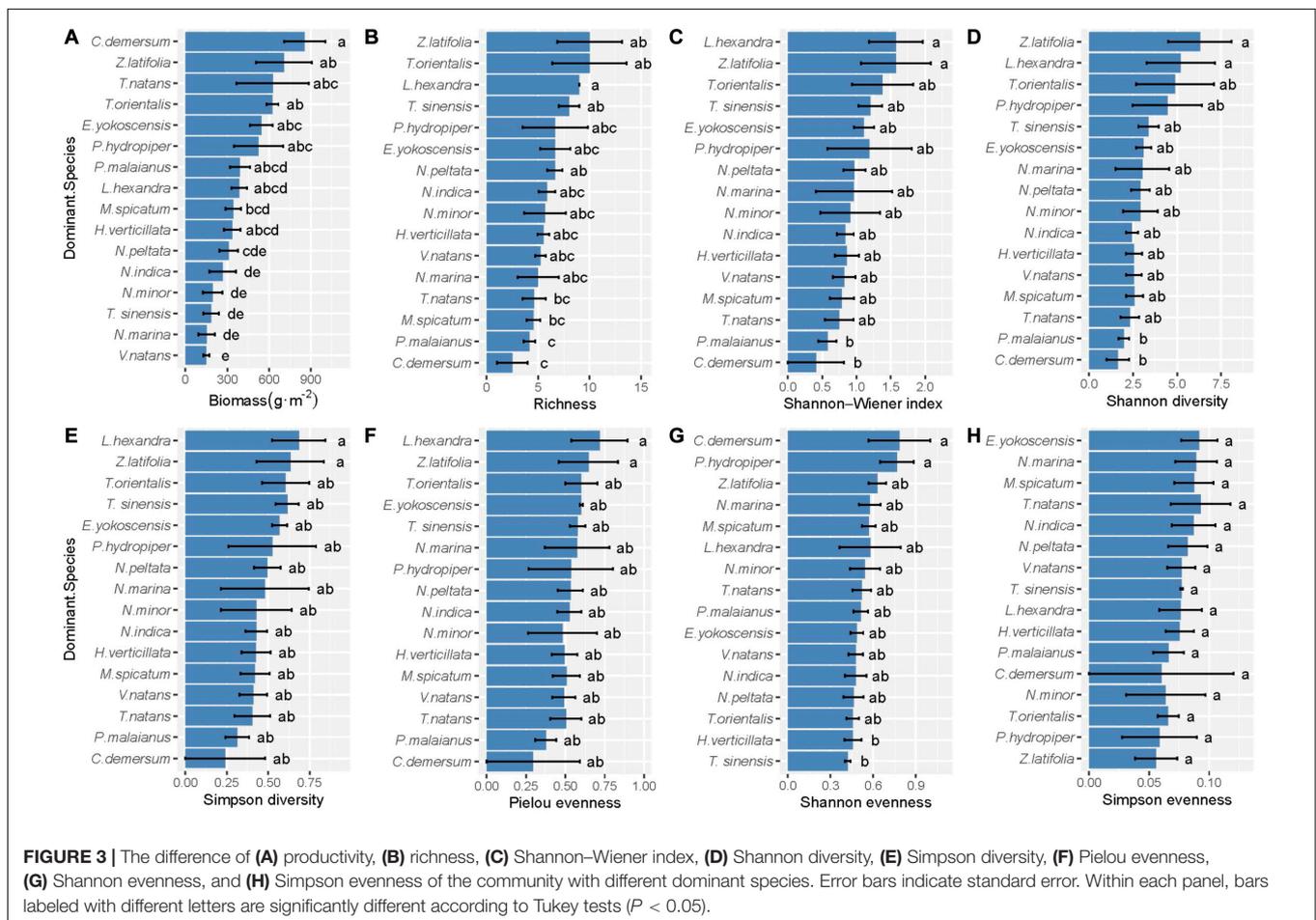
The present survey recorded 33 aquatic plant species, including 12 submerged species, seven floating-leaved species, two free-floating species, and 12 emergent species (Supplementary Table 1). The total biomass of all plots ranged from 48 to 1581 g m<sup>-2</sup>. The water depth was between 40 and 350 cm. The basic physical and chemical properties and nutritional conditions of the water body are given in Supplementary Table 2.

### The Biodiversity–Biomass Pattern and the Effect of Biological and Environmental Factors

Unimodal patterns were shown between community biomass and richness, the Shannon–Wiener index, Shannon diversity, and Simpson diversity ( $P < 0.1$  for all four indices, Figures 2A–D), and evenness indices (i.e., Pielou, Shannon, and Simpson evenness) had no significant relationship with biomass ( $P > 0.1$ , Figures 2E–G).

According to the comparison between hierarchical linear DI models, we found that species identity played an important role in the biodiversity–biomass pattern of the aquatic macrophyte community, which is proved by the significant difference between M1 and M0 (Table 2). However, we found no indication that pairwise interactions existed, on average or separately, by comparing M3 and M1, M3 and M2 (Table 2, full model results can be found in Supplementary Method). Moreover, the results of the one-way ANOVA show that the communities with different dominant species tended to have a disparate community structure (Figure 3). Emergent species-dominated communities had high diversity and biomass, and communities dominated by submerged species *C. demersum* had high biomass but low diversity (Figure 3).

Total nitrogen, water depth, and SS cumulatively accounted for 14.03 and 16.92% of the changes in coverage and biomass, respectively, of all macrophytes in the two axes of RDA (Supplementary Figure 1). TN positively affected the coverage ( $P < 0.001$ ) and biomass ( $P < 0.001$ ) of floating-leaved macrophytes but negatively influenced the coverage ( $P < 0.001$ ) and biomass ( $P < 0.001$ ) of submerged plants (Supplementary Figure 1). The biomass and coverage of emergent plants exhibited a negative relation with water depth ( $P < 0.001$ ) (Supplementary Figure 1). SS is positively correlated with



the growth of submerged plants ( $P < 0.001$ ) but negatively correlated with the growth of floating-leaved plants ( $P = 0.005$ ) (Supplementary Figure 1). After stepwise regression analysis, we found that water depth explained the most variation in many log-response ratio of biomass and diversity indices (i.e., richness, Shannon-Wiener index, Shannon diversity, Simpson diversity, and Pielou evenness,  $P < 0.05$ , Figures 4A–E) and significantly affected  $\ln$  (biomass/Simpson evenness) (Figure 4G). Water depth affected  $\ln$  (biomass/richness) most out of all biodiversity–biomass relationships (Figure 4).

## The Influence of Water Depth on Biomass and Biodiversity

The community biomass as well as the biomass of floating-leaved and submerged plants increased along the water depth gradient ( $P < 0.05$ , Figures 5A,C,D), and the biomass of emergent plants showed a decreasing trend with water depth ( $P = 0.097$ , Figure 5B). Meanwhile, water depth significantly

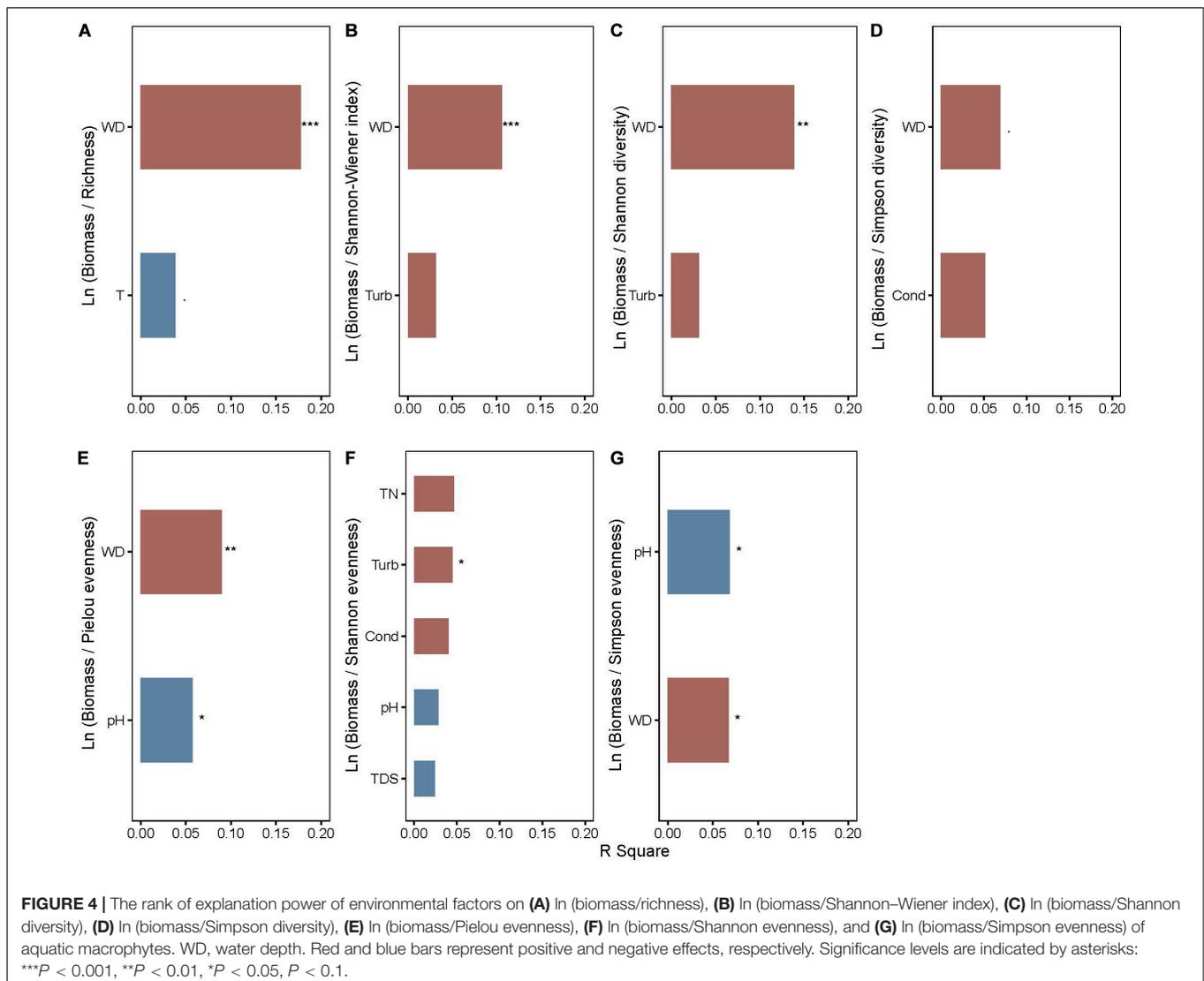
reduced most of diversity indices (i.e., richness, Shannon–Wiener index, Shannon diversity, Simpson diversity, and Pielou evenness;  $P < 0.05$ ) except two evenness indices (i.e., Shannon and Simpson evenness;  $P > 0.1$ ) (Figure 6).

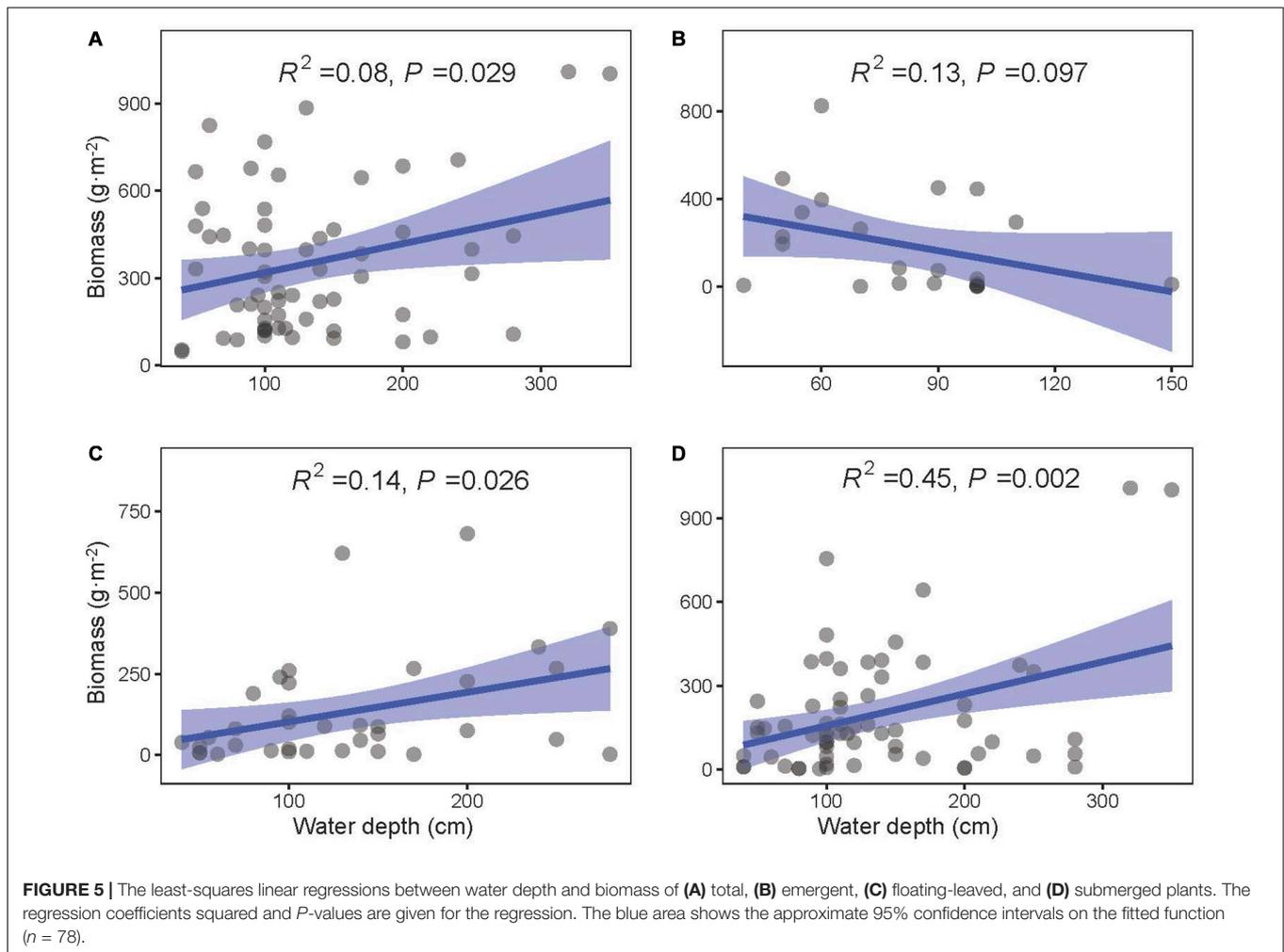
Overall, emergent plants distributed in shallow water (30–120 cm) and floating-leaved plants occupied a wider range of water depth (30–300 cm), and submerged plants distributed in all water depth (30–360 cm) (Figure 7A). The yields of emergent, floating-leaved, and submerged plants peaked at 30–60, 180–240, and 300–360 cm, respectively (Figure 7B).

## DISCUSSION

### The Biodiversity–Biomass Pattern and the Biotic and Abiotic Mechanisms

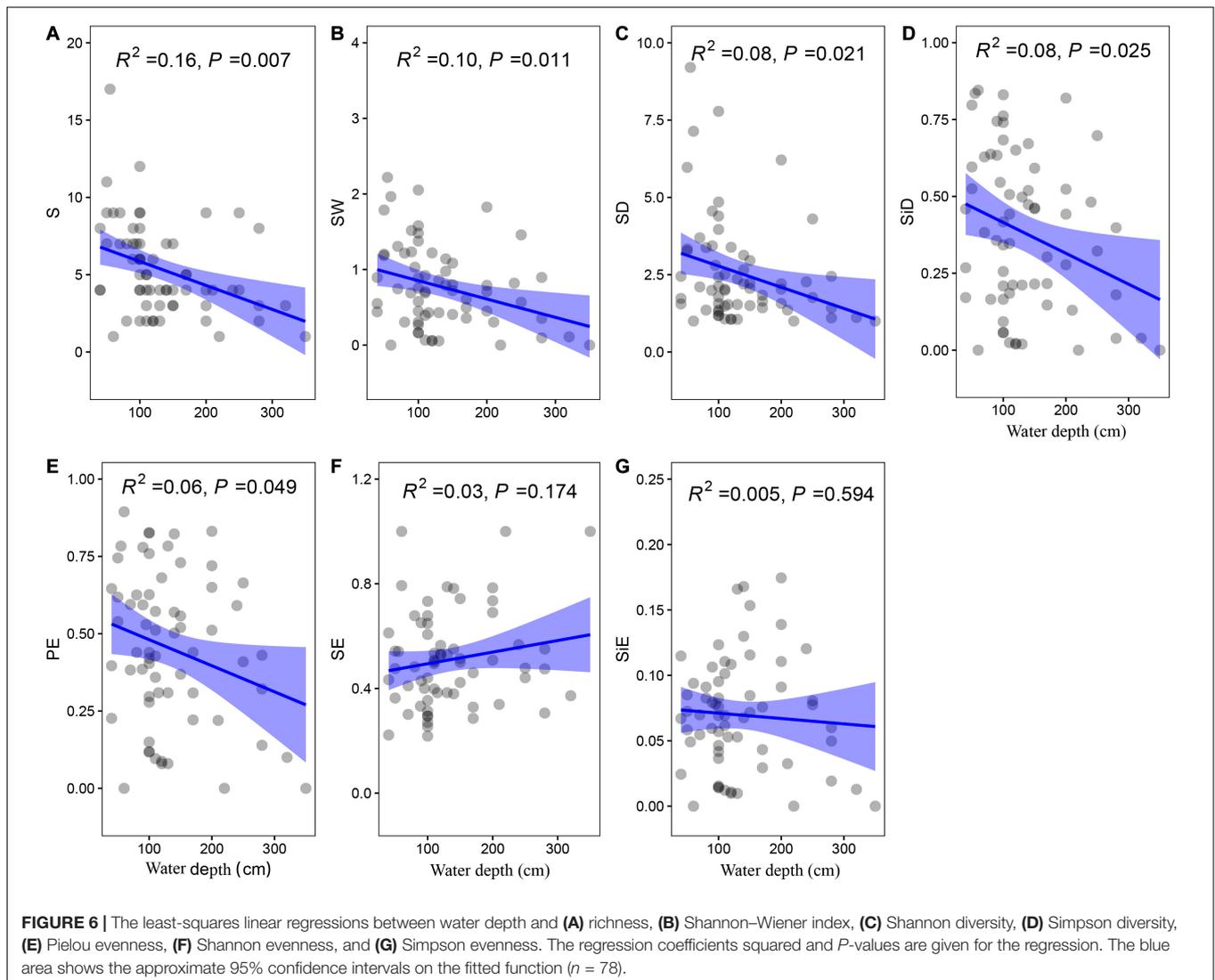
Our results demonstrate unimodal relationships between biomass and some biodiversity indices, such as richness,





Shannon-Wiener index, Shannon diversity, and Simpson diversity (Figure 2). Although this result supports our hypothesis of a unimodal biodiversity–biomass pattern in the macrophyte community, the unimodal pattern in our study is relatively weaker compared with other studies that found an apparent unimodal BPR pattern (Dodson et al., 2000; Leduc et al., 2012; Fei et al., 2018). A previous study about the biomass richness relationship of six taxa (i.e., phytoplankton, rotifers, cladocerans, copepods, macrophytes, and fish) in lakes from Dodson et al. (2000) states that the increasing richness at low biomass is caused by more available energy supporting additional species and trophic levels, and the decreasing richness at high biomass is due to competition between species. In addition, Chase and Leibold (2002) point out that interspecific interactions might have a prominent effect on the BPR pattern at the local scale. However, our results from the DI models indicate that species identity plays a decisive role in the biodiversity–biomass pattern of the macrophyte community rather than interspecific interaction, which contributes barely to the biodiversity–biomass pattern. Different species often have dissimilar impacts on community biomass (Slade et al., 2017), which is proved by the varying direction and magnitude of the estimates each

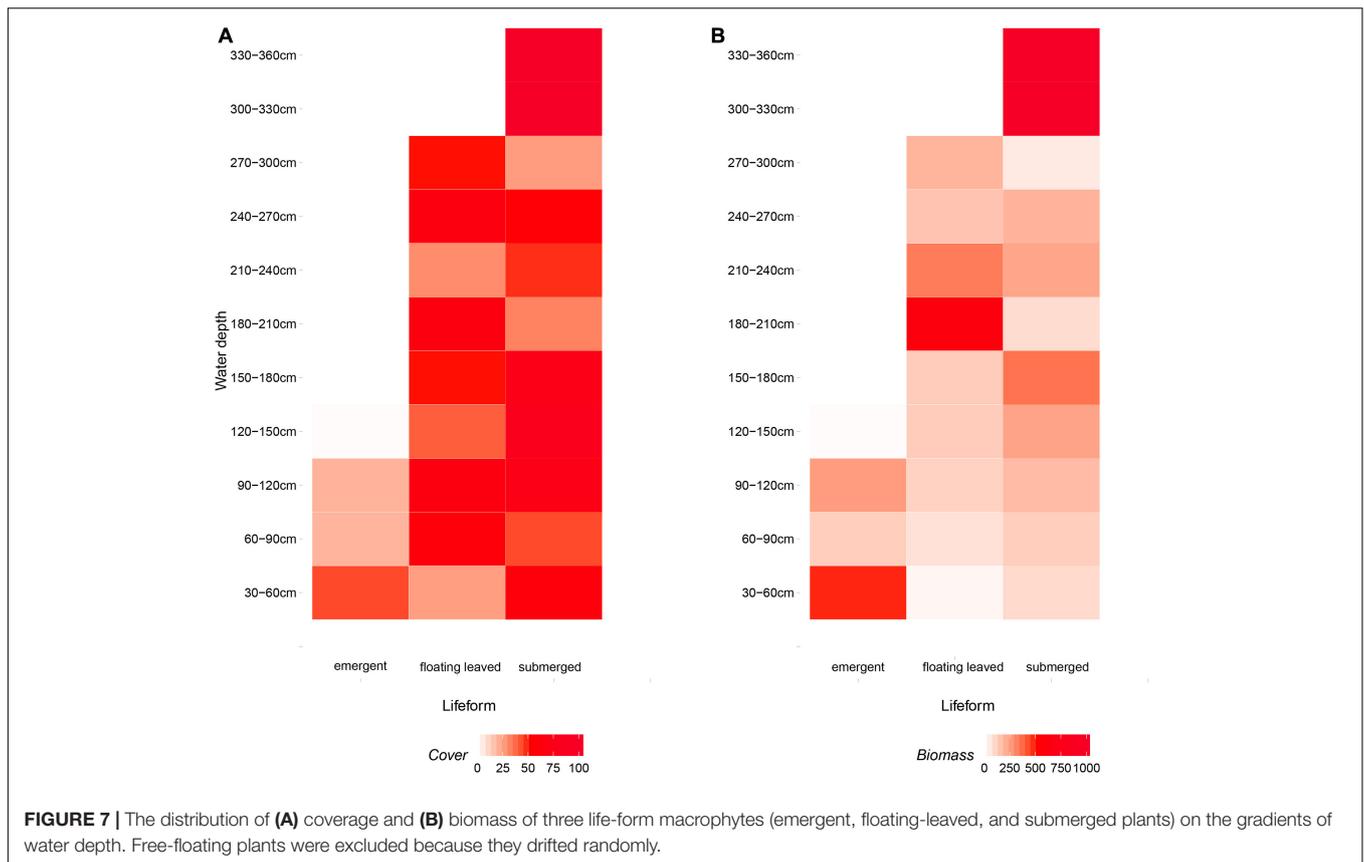
species loads in our study (Supplementary Method). Submerged species *V. natans* and *Najas minor*, which have significant negative estimates, contribute little to community biomass. On the contrary, emergent species (e.g., *Typha orientalis*, *Zizania latifolia*, and *Polygonum* sp.), floating-leaved species (e.g., *Nelumbo* sp.), and free-floating species (e.g., *Eichhornia crassipes*) have great contribution indicated by significant positive estimates. Besides this, community structure largely depends on the dominant species according to our results (Figure 3). Communities dominated by emergent species, such as *Polygonum* sp., *Z. latifolia*, and *T. orientalis* tend to be at a high level of diversity and biomass, and communities with dominant species, such as *C. demersum* are prone to have low diversity and high biomass. This further illustrates the importance of species identity in regulating the biodiversity–biomass pattern of the macrophyte community. The large difference of species composition among communities might dilute the correlation between community biomass and biodiversity, which is proved by the weak unimodal patterns in our study. Therefore, considering specific species within community is of great importance when studying the BPR pattern (Slade et al., 2017).



However, both species identity and distribution, which decorates community composition (Nsor et al., 2019) are affected by the environmental condition (Fu et al., 2014). Moreover, species of different life-forms are affected by dissimilar environmental factors (Garcia-Giron et al., 2019). Our results show that the growth of emergent plants is inhibited significantly by water depth (**Supplementary Figure 1**), which is widely proved by previous studies (Spence, 1967; Hudon et al., 2000; Seabloom et al., 2001; Middleton et al., 2015). Floating-leaved plants in our study are mainly promoted by the TN of the water and have a negative correlation with SS (**Supplementary Figure 1**) due to reduced wind exposure through leaves covering the water (Bornette and Puijalon, 2011). Generally, submerged plants are negatively related to SS (Nurminen and Horppila, 2009; Pan et al., 2017). Surprisingly, our results present a positive relationship between SS and the growth of submerged plants (**Supplementary Figure 1**), which might be caused by species identity. To be specific, communities dominated by *C. demersum* have a high biomass level; however, *C. demersum*

has strong growth ability and tends to be more tolerant of slightly turbid waters (Vanausdall and Dinsmore, 2019). On the contrary, low-biomass species, such as *V. natans* and *N. minor*, have higher water quality requirements (Su et al., 2019). The effect of the environment on the growth of macrophyte species emphasizes the critical role of environmental filtering, which points out that few species in the local pool can adapt to extreme conditions, such as insufficient light in deep water (Dodson et al., 2000). In addition, environmental filtering also depends on the trophic state of lakes, which can regulate turbidity and thus macrophyte distribution patterns (Azzella et al., 2014, 2016). In summary, environmental condition may be the crucial factor that profiles the BPR pattern through the effect of species identity and distribution.

The importance of the various biodiversity indices should be addressed in the test of relationships with biomass. In our study, species richness, Shannon diversity, Shannon–Wiener index, and Simpson diversity have significant correlations with biomass (**Figure 2**). However, evenness indices have no significant



correlations with biomass in our study (Figure 2). This is consistent with some previous studies that found no relationship between community evenness and biomass (Wilsey and Polley, 2004; Morris et al., 2014). Wilsey and Polley (2004) state that evenness itself does not alter the BPR pattern. Similarly, Morris et al. (2014) also prove that diversity indices composed of species richness and abundance are more reliable when evaluating the community process compared with evenness indices. Our results reveal that not all diversity indices have a connection with community biomass and emphasize the limited value of community evenness *per se* in the prediction of BPR pattern and the importance of considering both the species richness and the abundance of each species when exploring the underlying mechanism of the community BPR pattern. Our results also demonstrate that considering multiple diversity indices can provide deeper insight into the community process (Morris et al., 2014).

### The Mechanism of Water Depth Driving the Biodiversity–Biomass Pattern

The most explanatory power of water depth proves that the relationship between biodiversity and biomass is depth-dependent. Our study shows that water depth affects the macrophyte BPR pattern mainly through shaping community structure (both biomass and biodiversity) (Figures 5, 6). Submerged and emergent plants occupy aquatic communities

together, which results in high diversity in a shallow water area. However, the number of submerged species almost remains constant with the gradual increase in water depth, but emergent plants gradually drop out from the community due to limitations in gas exchange (Sorrell et al., 2012), and this causes the reduction of diversity. This is because water depth primarily correlates with light availability (Su et al., 2019) and impedes gas exchange (Armstrong et al., 1994), and few species can adapt to the low light availability in deep water (Li et al., 2017). The community biomass increases gradually along the water depth gradient as a result of superimposed effects of decreasing biomass of emergent plants and increasing biomass of floating-leaved and submerged plants (Figure 5). The differentiation in distribution and maximum yields of emergent, floating-leaved, and submerged plants along the water depth gradient is due to the dissimilarity of species identity. Recent studies report that emergent plants had a physiological flooding tolerance to water depth (Middleton et al., 2015), and internal oxygen concentrations in deeper water limit the growth of emergent plants (Sorrell et al., 2012). For submerged macrophytes, the positive correlation between water depth and biomass indicates that the positive effect of water depth on the biomass of submerged plants is primarily due to the larger growth space (Hudon et al., 2000) and beneficial adaptation to water depth of some submerged species (e.g., *C. demersum*), which also can be proved by the largest biomass of communities dominated by *C. demersum* in our study. With regard to floating-leaved plants,

biomass allocation patterns in the different plant organs and stem density contribute to the changes in biomass of floating-leaved plants in varying water depth (Nohara and Kimura, 1997; Paillisson and Marion, 2006). As a whole, water depth is the crucial factor adjusting the BPR pattern of the aquatic macrophyte ecosystem as a result of the effect on species identity and distribution. In other words, the BPR pattern is the reflection of performance of species with different life-forms and identities distributing along the water depth gradient on the axis of biomass and diversity.

Our study is carried out in a macrophyte-dominated shallow lake with a mesotrophic level and may only represent the mesotrophic or oligotrophic shallow lakes in the middle and lower reaches of the Yangtze River because these lakes have a similar macrophyte community structure with Liangzi Lake (Su et al., 2019). Eutrophic lakes may perform different community structures (Penning et al., 2008; Brothers et al., 2013), and investigation of the macrophyte BPR pattern in eutrophic lakes could provide a more general underlying mechanism for how biomass and biodiversity interact with each other generally. Moreover, macrophyte degradation in a deep water area caused by flood in 2016 resulted in the lack of vegetation data in the deep water area, which might also have a non-negligible influence on the generalization of our work. In addition, many studies demonstrate that spatial scale dictates the BPR pattern (Chase and Leibold, 2002; Chase and Ryberg, 2004), and it is of great importance to explore the BPR pattern of the macrophyte community at different scales. Our work may be useful for exploring the biodiversity–biomass pattern and its underlying mechanism at a larger scale. Our study may reveal the BPR to some extent in the macrophyte community due to the close correlation between productivity and biomass production (Carr et al., 1997; Hillebrand and Cardinale, 2010).

## CONCLUSION

Overall, we show weak unimodal patterns between biomass and diversity indices, such as Shannon–Wiener index, Shannon diversity, Simpson diversity, and species richness, and evenness indices have no significant correlation with the community biomass. This reveals that not all biodiversity indices have a connection with the community biomass. Our results illustrate the limited value of community evenness *per se* in the prediction of biodiversity–biomass patterns and the importance of considering both the species richness and the abundance of each species when exploring the underlying mechanism of community BPR pattern. Species identity rather than

interspecific interaction plays a decisive role in the biodiversity–biomass pattern of the macrophyte community. However, species identity within the community is mainly regulated by water depth, which shapes the BPR pattern of the macrophyte community ultimately as a result of effects on species identity and species distribution of the macrophyte community. These results suggest that it may be possible to improve aquatic ecosystem function by adjusting the water level of shallow lakes.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

FM collected and analyzed the data and wrote the manuscript. LY, ZZ, and HZ collected the data and contributed to the manuscript. TL calibrated this manuscript and improved the figures. DY, CL, and SF designed the experiment, revised this manuscript, and provided fund support. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.650001/full#supplementary-material>

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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