

The effect of trait-based diversity on productivity results mainly from intraspecific trait variability in the macrophyte community

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Abstract

1. Trait-based methods are key to understanding the biodiversity–productivity relationship (BPR) of macrophyte communities. Community-weighted mean traits (i.e., community trait structure) have been proven to have more influence on macrophyte community productivity than species richness. However, the underlying mechanism by which community trait structure variation affects macrophyte community productivity along an environmental gradient is still not well understood.
2. A mesocosm experiment was used to investigate how community trait structure shapes macrophyte community productivity along the water depth gradient. Three submerged macrophyte species (*Myriophyllum spicatum*, *Vallisneria natans* and *Potamogeton malaiianus*) were assembled into all possible combinations (one, two and three species per community) at three different water depths (1, 2.5 and 4 m). We fitted the relationships between community-weighted mean traits and community productivity, and between species richness and community productivity as a comparison. We compared functional traits under different water depths and species composition at the species and community levels and disentangled the community trait structure into species turnover and intraspecific trait variability effects.
3. The results showed that community trait structure had various influences on macrophyte community productivity, which was based on traits *per se*. However, species richness had a non-significant impact on macrophyte community productivity. Water depth had a significant impact on most traits of the three species at the species level, whereas both water depth and species composition had significant impacts on community trait structure which was mainly affected by intraspecific trait variability along the water depth gradient.
4. Our findings highlight the importance of considering intraspecific trait variability and species turnover under water depth gradients to understand the relationship between trait-based biodiversity and productivity.

KEYWORDS

biodiversity–productivity relationships, community-weighted mean traits, functional traits, species composition, water depth

1 | INTRODUCTION

Biodiversity is declining rapidly as a consequence of the intensification of human activity (Balvanera et al., 2006). An increasing number of studies are focusing on the effects of biodiversity on ecosystem function and ecosystem services (Duffy et al., 2017). Most of our understanding of how biodiversity affects productivity comes from terrestrial ecosystems such as grasslands and forests (Duffy et al., 2017). However, little research has been carried out on aquatic ecosystems, especially for aquatic macrophytes (Gustafsson & Boström, 2011; Li et al., 2020). Aquatic macrophytes provide numerous ecological and economic services, such as offering habitat and food to aquatic animals and birds and supplying raw materials for social production (Costanza et al., 1997; Jeppesen et al., 2012). Therefore, exploration of the biodiversity–productivity relationship (BPR) of aquatic macrophyte communities is critical to our understanding of aquatic ecosystem functions (Alahuhta et al., 2017).

The effect of biodiversity on productivity generally occurs through a combination of niche complementarity (i.e., complementarity effect) and contributions from high-functioning or high-fitness species (i.e., selection effect) (Cadotte, 2017; Gustafsson & Boström, 2011; Loreau & Hector, 2001). Recently, Gustafsson and Boström (2011) demonstrated that both positive complementarity and selection effects caused enhancement of macrophyte production with increased diversity, whereas Riis et al. (2018) found no clear effects of diversity on production owing to the lack of a complementarity effect. Further work is needed to identify the underlying mechanism of the BPR pattern in the macrophyte community.

The existing studies of BPR patterns are based mainly on species richness. However, the investigation of the functional traits of species also is important for understanding the biodiversity of macrophyte ecosystems because traits characterise the ecological strategy (e.g., life history strategy or resource use strategy) of species and affect the fitness of individuals under certain environmental conditions (Dalla Vecchia et al., 2020; Liu & Wang, 2018; Mori, 2016). The alteration of productivity has been demonstrated to be caused mainly by the varying performance of vegetation functional traits (Cui et al., 2019; Jing et al., 2019). Community-weighted mean traits (CWM), which represent the functional composition of a community (Garnier et al., 2004), are the overall reflection of the ecological strategy of a community to its environment (Mason et al., 2003; Reich et al., 2001; Vileger et al., 2008). Fu, Zhong, Yuan, Ni, et al. (2014) indicated that CWM showed high explanatory power in determining variations in community productivity. Generally, changes in CWM result from transformations in species turnover and intraspecific trait variability (Lepš et al., 2011). Species turnover is a result of changes in species occurrence and abundance, whereas intraspecific trait variability relates to plastic responses of plants to environmental

changes (Niu et al., 2016). However, previous studies of macrophyte ecosystems have focused on the importance of specific traits or whole community trait structures in affecting ecosystem function (Cadotte, 2017; Gustafsson et al., 2019). The relative importance of the effects of species turnover and intraspecific trait variability in changing macrophyte ecosystem function remains largely unstudied.

Currently, an increasing number of studies have indicated that species composition has an important impact on community productivity (Hector et al., 1999, 2011; Sandau et al., 2017). On the one hand, both species identity and species richness influence ecosystem function (Stachowicz et al., 2007), and the effects of species on community structure are expected to increase with the magnitude of the differences among species (Tilman et al., 1997), which reveals that compositional differences are expected to have large effects on BPR patterns. On the other, species composition may result in intraspecific trait variability, which indirectly shapes the BPR pattern. Therefore, exploring the underlying mechanisms of different species compositions is key to understanding how biodiversity influences ecosystem function.

In addition, water depth is a major factor that influences the traits of aquatic plants mainly through controlling the light that plants require for growth (Bai et al., 2014; Dong et al., 2014; Strand & Weisner, 2001). Previous studies have shown that water depth has a significant impact on individual shoot length, specific leaf area and leaf chlorophyll content (Fu et al., 2012; Fu, Zhong, Yuan, Ni, et al., 2014; Fu, Zhong, Yuan, Xie, et al., 2014). Therefore, investigation of the influence of water depth on species traits and community trait structure also is critical for understanding the BPR pattern and the mechanisms underlying it within the macrophyte community.

In order to explore the mechanism underlying how macrophyte community productivity along a water depth gradient is shaped by community trait structure, we used three submerged macrophyte species (*Myriophyllum spicatum*, *Vallisneria spiralis* and *Potamogeton malaianus*) in a manipulative mesocosm experiment. These species dominate the middle and lower reaches of the Yangtze River. We created all possible combinations (one, two and three species per community) of these three species at different water depths. Firstly, we examined the BPR pattern of the macrophyte community by fitting the relationship between productivity and CWM as well as species richness to explore how these indices shape community productivity. In addition, we compared the biodiversity effects under different water depths and species compositions. Secondly we compared the functional traits of the three species under different water depths and species compositions to test their trait responses. Finally, we evaluated the community trait structure (i.e., CWM) under different conditions and disentangled species turnover and intraspecific trait variability effects to determine how interspecific and intraspecific variances in traits modify community-level performance.

2 | MATERIALS AND METHODS

2.1 | Plant materials

Three submerged macrophytes, *Myriophyllum spicatum*, *Vallisneria natans* and *Potamogeton malaianus*, were used in this study because they are distributed widely in China and across the world (Cook et al., 1974; Li et al., 2013), and they dominate the middle and lower reaches of the Yangtze River (Su et al., 2019). We collected 300 seedlings of *V. natans* (3.3 ± 1.0 g fresh biomass; 9.8 ± 0.8 cm length) and *P. malaianus* (2.5 ± 0.7 g fresh biomass; 10.3 ± 1.1 cm length), and 300 apical shoots (10 cm length) of *M. spicatum* (3.2 ± 1.0 g fresh biomass) from Liangzi Lake. Seedlings or apical shoots of each species were healthy in appearance and without branches. All seedlings or shoots were pre-cultured in nine aquariums ($L \times W \times H$: 1.00 m \times 0.50 m \times 0.70 m, three aquariums for each species) with an 0.08-m-thick layer of sand and 0.40 m water depth (mean \pm SE: total N content of the water column 0.75 ± 0.06 mg/L, total P content of the water column 0.02 ± 0.007 mg/L) for 2 weeks. Then, we selected 210 individuals from each species (4.37 ± 0.78 g initial fresh biomass) for this experiment.

2.2 | Experimental design

The experiment was carried out from 9 June to 1 September 2019 (12 weeks in total) at the National Field Station of the Freshwater Ecosystem of Liangzi Lake, Hubei Province, China ($30^{\circ}05' - 30^{\circ}18'N$, $114^{\circ}21' - 114^{\circ}39'E$). A replacement design using a standardised initial individual density (following Harper (1977)) was used. The starting density was six individuals in total, with equal numbers of individuals per species, that is, six individuals in monocultures, three individuals of each species in bicultures and two individuals in tricultures. Seven species composition treatments were designed, including three monocultures (*M. spicatum* [M], *V. natans* [V] and *P. malaianus* [P]), three bicultures (*M. spicatum* + *V. natans* [MV], *M. spicatum* + *P. malaianus* [MP], *V. natans* + *P. malaianus* [VP]) and one triculture (*M. spicatum* + *V. natans* + *P. malaianus* [MVP]) (Figure 1b). Three water depth treatments were designed: 1.00, 2.50 and 4.00 m for

each species composition treatment, respectively (Figure 1a). The experiment was replicated in five outdoor cement pools ($L \times W \times H$: 4.00 m \times 4.00 m \times 4.50 m) based on a randomised block design, each containing 21 treatments (7 species compositions \times 3 water depths). Each treatment was planted in a plastic pot (0.30 m diameter, 0.50 m height), and a total of 105 pots were used. Each pot was filled with a 0.10-m-thick layer of mud (mean \pm SE: total N content 0.57 ± 0.03 mg/g, total P content 0.27 ± 0.02 mg/g), which then was covered with a 0.02-m-thick layer of sand to prevent suspension of mud. The pots with the plants were tied by ropes and fastened to steel tubes fixed evenly in the cement pools. All treatments were immersed at a 0.50 m water depth for acclimation for 2 weeks at the beginning of the experiment and then kept at three water depths. At the end of this experiment, all aboveground and belowground plant materials of each species in every treatment were harvested and washed carefully for later measurements. At the end of the experiment, the photosynthetically active radiation was measured at the air–water surface and different depths (1.00, 2.50, 4.00 m) in each cement pool using a Light Meter LI-250A (LI-COR). Physical and chemical variables including water temperature (T), dissolved oxygen (DO), conductivity (Cond), total dissolved solids (TDS), salinity (SAL) and pH also were measured at different depths (1.00, 2.50, 4.00 m) in each cement pool using a portable water quality monitor (PROPLUS, YSI) (Table S1).

2.3 | Functional trait measurements

We measured six functional traits of each species in each pot: two physiological traits, including total chlorophyll content (mg/g) and the ratio of chlorophyll *a* and chlorophyll *b* (chlorophyll *a/b*) of plant leaves, and four morphological traits, including specific leaf area (SLA [cm^2/g]), shoot length (cm), root length (cm) and the number of branches or ramets. Chlorophyll, the molecular basis for the function of photosystems (Zhang et al., 2020), is closely related to vegetation productivity (Croft et al., 2015). Among these traits, chlorophyll *b* absorbs light and funnels energy, and chlorophyll *a* is responsible for light-induced charge translocation (Zhang et al., 2020). Thus, chlorophyll *a/b* reveals light-use efficiency

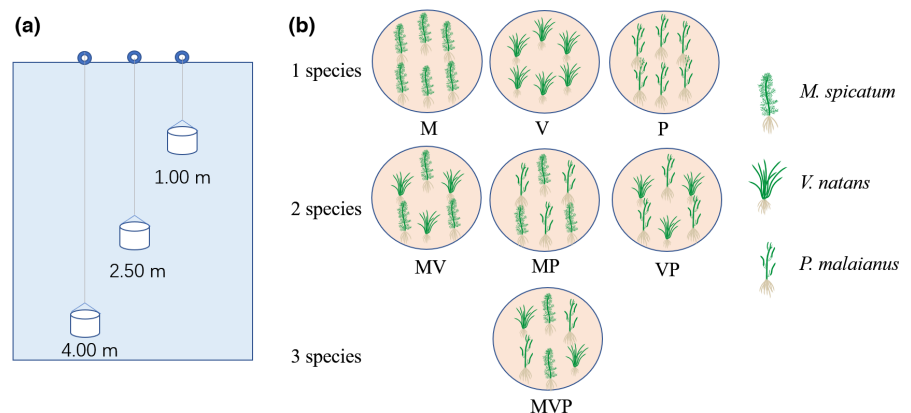


FIGURE 1 Schematic diagram of the experimental design. All treatments of species composition (b) were planted at three different water depths (a)

(LUE) (Croft et al., 2017). SLA, part of the leaf economic spectrum, is closely related to photosynthetic capacity (Wright et al., 2004). Shoot length is an indication of space occupied vertically and competitiveness for light (Fu, Zhong, Yuan, Xie, et al., 2014), whereas root length is a symbol of competition for nutrition in the substrate (Barko & Smart, 1981).

The chlorophyll content of leaves was measured according to the method described by Lichtenthaler and Wellburn (1983). At harvest, 0.1 g fresh, intact and healthy leaves growing at the same place below the top of shoots of each species in each treatment were selected and cut into pieces, and then chlorophyll was extracted with 80% acetone solution for 48 hr. A spectrophotometer (UV-1800; Shimadzu) was used to measure the absorbance values at 645 and 663 nm. The chlorophyll *a* and *b* contents were calculated as $12.7 \times A_{663} - 2.69 \times A_{645}$ and $22.9 \times A_{645} - 4.68 \times A_{663}$, respectively. The chlorophyll content was the sum of chlorophyll *a* and chlorophyll *b* content, and chlorophyll *a/b* was the ratio of chlorophyll *a* to chlorophyll *b* content.

The shoot and root length of each species were measured, and the number of branches or ramets was counted and recorded. In order to measure SLA, intact, healthy and mature leaves ($n = 10$, *P. malaianus*; $n = 20$, *M. spicatum*; $n = 5$, *V. natans*) were selected. The leaves of each species were scanned (Epson V850 Perfection Pro, Seiko Epson Corp.) to measure leaf area (*A*) using WinRHIZO Pro 2009 software (Regent Instruments Inc.). Then, these leaves were dried at 70°C for 72 hr and weighed individually to obtain biomass (*M*), and the SLA was calculated as *A/M*.

2.4 | Measurements of productivity and biodiversity

The individual plants of each species in each treatment were divided into aboveground (leaves and stems) and belowground (roots of *M. spicatum*, roots and rhizomes of *P. malaianus* or *V. natans*) parts, dried at 70°C for 72 hr and weighed to measure the aboveground and belowground biomass (g) of the species. The total biomass of the species was the sum of the aboveground and belowground biomass of each species, while the root/shoot ratio (*R/S*) was calculated as the belowground biomass/aboveground biomass. Community productivity was the sum of species biomass after subtracting the initial biomass within each treatment.

We selected species richness and CWM as biodiversity indices. For each pot, species richness was calculated as the number of species. The CWM is used to explain the functional composition of each pot.

The CWM is defined as:

$$CWM_t = \sum T_i \times P_i$$

where P_i is the proportional biomass of species *i* in the community, T_i is the value of trait *t* of species *i* (Fu, Zhong, Yuan, Ni, et al., 2014).

2.5 | Biodiversity effects

We used the additive partitioning method (Loreau & Hector, 2001) to statistically partition the net biodiversity effect (NE) into complementarity (CE) and selection effects (SE). The net biodiversity effect was the overyielding section of species in the mixture compared with the monoculture, calculated as the difference between the observed yield (community productivity of the mixture) and the expected yield (weighted average yield of the monocultures). The complementarity effect was valued as $N \times \overline{\Delta RY} \times \overline{M}$, and the selection effect was estimated as $N \times \text{cov}(\Delta RY, M)$. Here, *N* is the species richness, $\overline{\Delta RY}$ is the mean change in the relative yield for all species in the mixture, \overline{M} is the mean monoculture yield for each species in the mixture, ΔRY is the change in relative yield of a species in the mixture (i.e., the yield of a species in a mixture divided by the yield of the species in monoculture) and *M* is the monoculture biomass of a species. NE, CE and SE were calculated for each replicate of mixtures.

2.6 | Disentangling changes in community functional trait structure

The changes in community functional traits can be disaggregated into two parts: species turnover and intraspecific trait variability. To distinguish the relative contribution of intraspecific variability and species turnover to changes in the CWM for each trait, we used a sum of squares decomposition modified from Lepš et al. (2011).

Firstly, we calculated three types of community-weighted mean parameters: (1) specific average traits, using trait values of each species within each pot; (2) fixed trait values, using mean trait values of each species along the water depth gradient, whose variation is attributable only to changes in species turnover; and (3) intraspecific variability trait values, calculated from the differences between specific and fixed average traits, as an estimate of the pure effects of intraspecific variability.

Secondly, we partitioned the effects of species turnover into two components, that is, species occurrence and species abundance (de la Riva et al., 2016): (1) unweighted trait values, calculated by the species presence/absence data and fixed trait values to estimate the pure species occurrence effect; and (2) species-abundance trait values, which were calculated from differences between fixed and unweighted trait values to estimate the pure effects of species abundance.

Finally, we explored the effect of water depth on community-weighted mean traits for the five types of community parameters mentioned above. To quantify how much variability accounted for each component (species occurrence, abundance, and intraspecific variability), we used the method based on the sum of squares (SS) decomposition since SS corresponds to the variability of each component (Lepš et al., 2011). Since the effects of these community parameters do not always vary independently, we also calculated the

FIGURE 2 The effects of species richness on community productivity at 1.00 m (a), 2.50 m (b) and 4.00 m (c) water depth. The treatment of 1 for richness is the mean of three monocultures and 2 for richness is the mean of three bicultures. ns, non-significant

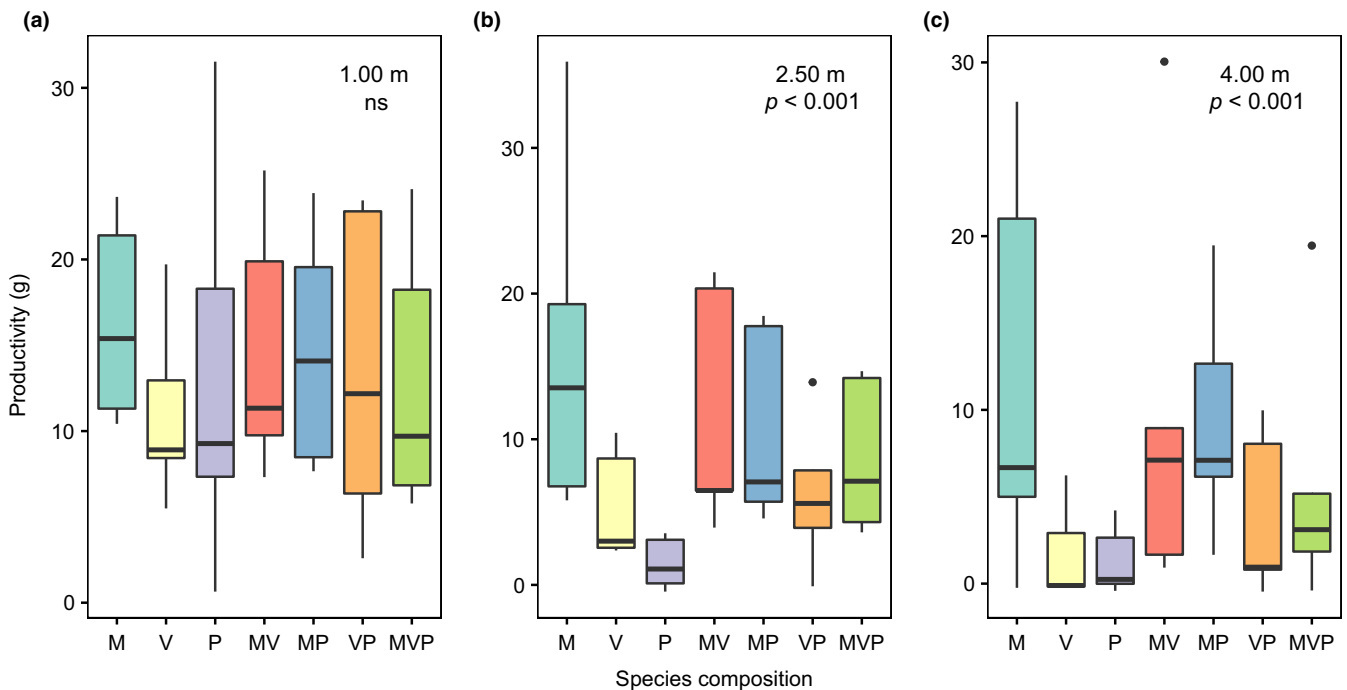
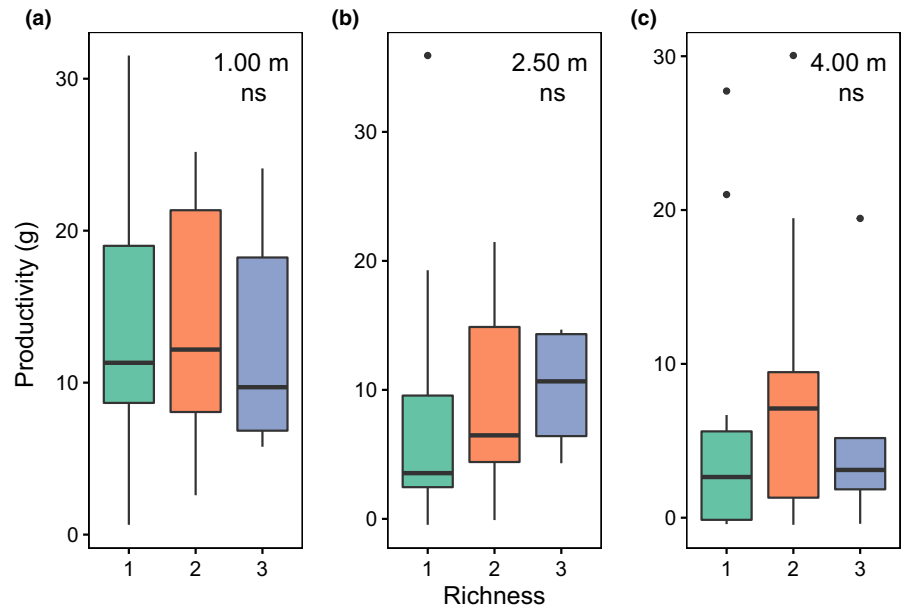


FIGURE 3 The effects of species composition on community productivity at 1.00 m (a), 2.50 m (b) and 4.00 m (c) water depth. ns, non-significant

effect of their covariation. In this approach, the covariation is partitioned into two different components: the covariation between intraspecific variability and species turnover (Covariation I = $SS_{\text{specific}} - SS_{\text{fixed}} - SS_{\text{intraspecific variability}}$) and covariation between species occurrence and abundance (Covariation II = $SS_{\text{fixed}} - SS_{\text{species occurrence}} - SS_{\text{species abundance}}$). The SS_{specific} will be higher if two effects are positively correlated than when the two effects are independent. For example, species will be taller when growing with tall species, leading to an increase in SS_{specific} .

2.7 | Data analysis

In order to investigate the effects of species richness, species composition and functional diversity on community productivity, linear mixed models using Gaussian distributions with 'identity' link functions were applied (block as a random effect) using the 'lmer' function in the lme4 package in R 4.0.2 (R Core Team, 2020). For each model, residual plots were inspected visually using the 'check_model' function in the 'performance' package (Lüdtke et al., 2021).

We calculated marginal r^2 (accounting only for fixed effects) and conditional r^2 (accounting for random and fixed effects) values using R/MuMIn (Barton, 2018).

In order to analyze the effects of water depth and species composition on species and communities, we fitted linear mixed effects models in R/lme4 (Bates et al., 2015). Water depth, species composition and their interaction were set as fixed effects, and the block was set as a random effect. At the species level, we tested the effects of water depth and species composition on six functional traits and biomass allocation (total biomass and R/S) of three species separately. At the community level, we assessed the effects of water depth and species composition on CWM and community biomass allocation. Multiple comparisons were performed using Tukey–Kramer post hoc tests (refer to Tables S2 and S3 for the results at the species level and community level, respectively) in R/emmeans (Lenth & Lenth, 2018).

With the aim of disentangling changes in community-weighted mean traits along a water depth gradient into intraspecific trait variability versus species occurrence and abundance, we first used one-way ANOVAs to estimate the variance (SS) of five types of community parameters (specific, fixed, intraspecific variability, unweighted and species-abundance trait values) explained by water depth. Then, the SS was decomposed into community-weighted mean variance components to quantify the relative contribution of intraspecific variability and change in species occurrence and abundance, and their covariance (Lepš et al., 2011).

3 | RESULTS

3.1 | The relationship between diversity/species composition and productivity

Species richness had a non-significant effect on community productivity at all three water depths (Figure 2). Likewise, there were no differences in community productivity among seven species compositions at 1.00 m water depth (Figure 3a). However, community productivity did differ between the three monocultures at 2.50 m and 4.00 m water depth, and species composition containing *M. spicatum* had higher productivity than other species compositions (Figure 3b, c). The additive partitioning analysis demonstrated that both net effects and complementarity effects were positive at all water depths and species compositions (Figure 4). Complementarity effects increased with water depth; however, selection effects changed from positive at 1.00 m to negative at 2.50 m and 4.00 m (Figure 4a). For species composition, the net effects and selection effects of MP and VP composition were higher than the net effects and selection effects of MV and MVP composition (Figure 4b). Moreover, the selection effects were positive for MP and VP composition and negative for MV and MVP composition (Figure 4b).

The community-weighted mean traits showed a changeable relationship with community productivity. Community-weighted mean traits such as the number of branches/ramets, root length and leaf chlorophyll *a/b* improved community productivity (Figure 5c, d, f), whereas the community-weighted mean SLA and chlorophyll content decreased community productivity (Figure 5a, e).

Community-weighted mean shoot length had a non-significant relationship with community productivity (Figure 5b). Among these community-weighted mean traits, SLA and the number of branches/ramets had the strongest relationships with community productivity ($R^2 = 0.22, 0.55$, respectively), while others had a weaker predictive ability for community productivity ($R^2 < 0.1$).

3.2 | The effect of water depth and species composition on species and community

At the species level, water depth significantly increased the SLA and shoot length of *M. spicatum*, and its root length was longest at 2.50 m water depth (Tables 1 and S2). Water depth significantly increased the shoot length of *V. natans* but decreased its number of ramets and total biomass, and its root length and R/S were largest at 2.50 m water depth (Tables 1 and S2). Water depth significantly decreased the number of branches, R/S and total biomass of *P. malaianus* (Tables 1 and S2). Most properties of the three species showed no significant difference among the four species compositions except for root length of *M. spicatum* and *P. malaianus* and shoot length and biomass of *V. natans* (Tables 1 and S2). Water depth and species composition had no interactive effect on the properties of the three species except for the shoot length of *P. malaianus* (Tables 1). At the community level, water depth significantly affected all community-weighted mean traits as well as community biomass allocation (Tables 1 and S3). Species composition also had a significant effect on community properties except for R/S (Tables 2 and S3). Water depth and species composition had an interaction effect on community-level shoot length (Table 2).

3.3 | Intraspecific variability versus species turnover

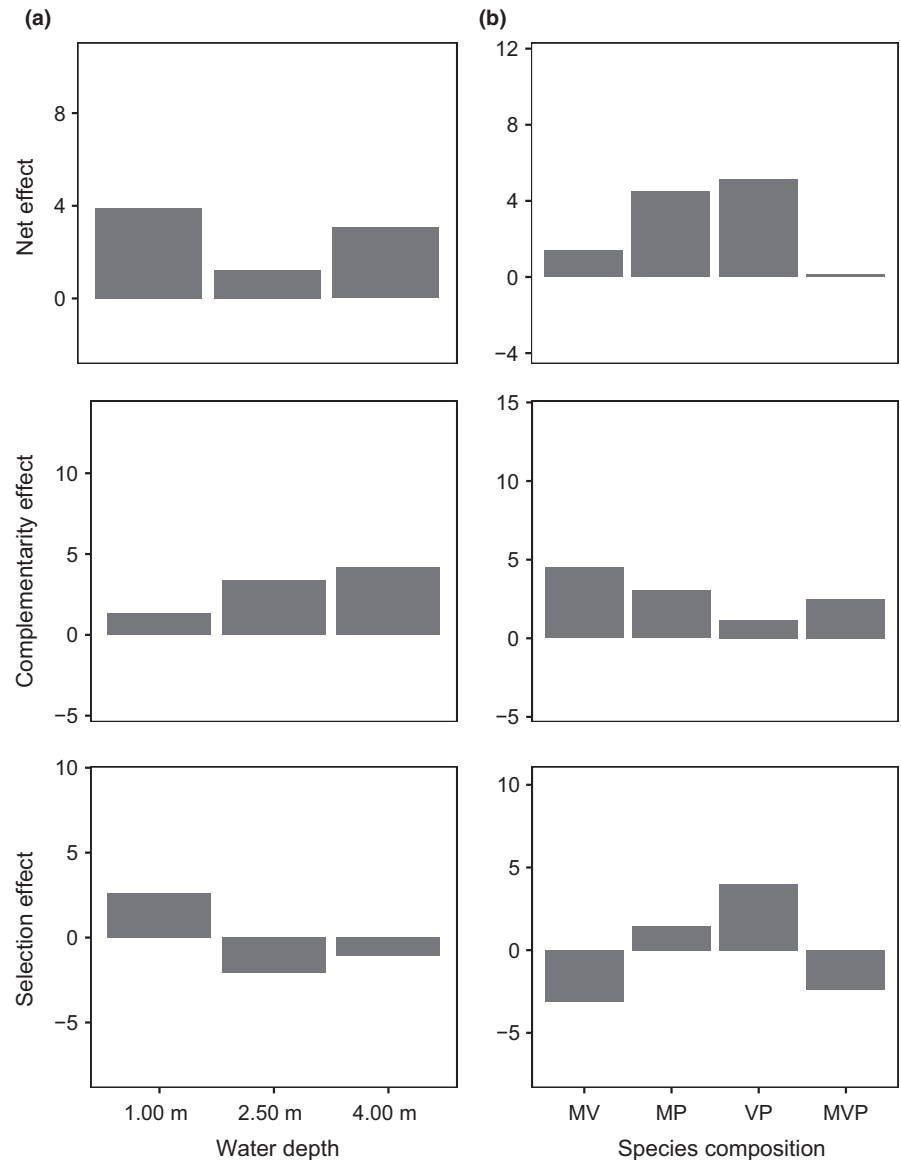
The results from partitioning the total variability in each functional traits demonstrated that changes in community functional structure along the water depth gradient were mainly promoted by intraspecific trait variability except for chlorophyll *a/b* (Figure 6). The total variation was decreased by a highly negative covariation between species turnover and intraspecific variability in SLA, root length, and number of branches or ramets. However, the positive covariation between species turnover and intraspecific variability in shoot length increased the total variation (Figure 6). Covariation between species occurrence and abundance contributed little to the total variation.

4 | DISCUSSION

4.1 | BPR pattern

In our study, species richness showed a non-significant effect on community productivity, which was in accordance with some previous studies showing no association between species richness and productivity

FIGURE 4 Net, complementarity and selection effects under different water depths (a) and species compositions (b)



(Fu, Zhong, Yuan, Ni, et al., 2014; Riis et al., 2018). However, mixtures exhibited positive complementarity effects at deeper water depth, especially at 2.50 m. The possible reason for the positive complementarity effect is the difference in species used in this research. The plants used in our experiment included both the rosette-type species *V. natans* and the canopy-forming species *M. spicatum* and *P. malaianus*, and they differ in many characteristics such as leaf type and reproduction strategy (Cook et al., 1974). The difference in many characteristics among the three species might result in a positive diversity and complementarity effect (Abonyi et al., 2018). The higher variation in functional traits increases the functional diversity of communities, enabling them to make full use of various resources (Choudhury et al., 2018). For example, the higher variations in shoot length and the total number of branches or ramets indicated that the ability of different species to use light resources is quite different, which effectively reduces competition among species and makes plants occupy the most space in the vertical direction of the water column to achieve a positive complementarity effect (Fu, Zhong, Yuan, Xie, et al., 2014). The selection

effect is positive in shallow water in our study because all species are able to establish and grow well, and community performance is determined by highly competitive species (Fargione et al., 2007). However, the selection effect in deep water becomes negative since competition among species is weakened and replaced by the complementarity of species (Fu, Zhong, Yuan, Xie, et al., 2014). Biodiversity effects are dissimilar among different species compositions in this study, demonstrating that the underlying mechanisms modifying productivity are different not only depending on water depth, but also on the plant community (Gustafsson et al., 2019). Community productivity comprises the contribution of each species within a community and is closely related to their traits and trait dissimilarities. The species identity effect occurs when communities with equal richness but different compositions perform variably (Stachowicz et al., 2007). Cadotte (2017) indicated that plant assemblages with low trait dissimilarity are inclined to affect productivity mainly through selection effects, whereas communities with high trait dissimilarity primarily shape production through niche complementarity.

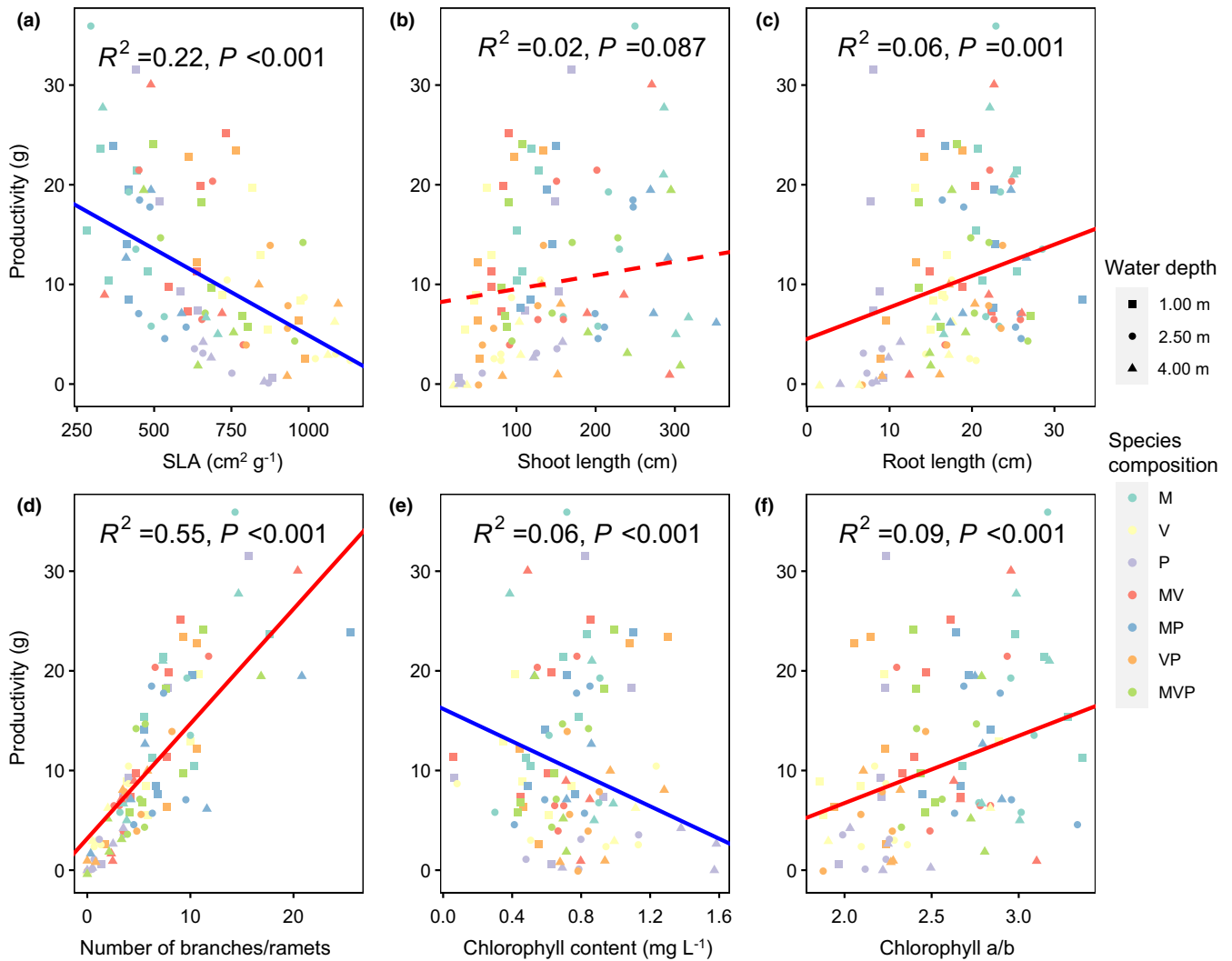


FIGURE 5 Relationships between productivity and community-weighted mean traits. Red line, positive relationship; blue line, negative relationship. The solid line indicates a significant relationship, and the dashed line indicates a non-significant relationship ($p > 0.05$)

There are different impacts of CWMs on community productivity. The community-level number of branches or ramets and shoot length facilitate macrophyte community productivity since tall or ramulose competitive aquatic plants, which are related to light interception (Pérez-Harguindeguy et al., 2013), can have rapid nutrient uptake and, thus, high primary production (Gustafsson et al., 2019). Root length signifies the rooting depth and potential nutrient acquisition of species; therefore, community-level root length also is positively correlated with the productivity of the macrophyte community (Hughes et al., 2009). However, our results indicate a negative correlation between the community-level SLA and productivity, which is different from previous studies that showed a weak correlation between the two parameters (Garnier et al., 2016; Gustafsson et al., 2019). Spence et al. (1973) reported that sun-adapted leaves have a small leaf area per unit leaf dry weight, whereas shade-adapted leaves possess a large leaf area per unit leaf dry weight. Sun-adapted leaves such as leaves of *M. spicatum*, can use more light to produce, which explains the negative correlation between community-level SLA and productivity in our study. Interestingly,

chlorophyll content at the community level had a negative influence on community productivity, whereas chlorophyll *a/b* had a positive relationship with production, because communities with high chlorophyll content consisted mainly of *V. natans*, which has a low biomass level. However, communities with high chlorophyll *a/b* are dominated by *M. spicatum*, which facilitates greater community productivity compared with the other two species. This difference also reveals the close relationship between productivity and LUE (Croft et al., 2017). Overall, the difference in the impact of community-level traits on productivity indicates that different traits have different extents of influence on the process of determining productivity.

4.2 | Disentangling species turnover and intraspecific trait variability

Our results showed that water depth affects the functional traits of each species directly and community trait structure indirectly by moderating species turnover and changing functional traits within

TABLE 1 *F*-values and significance of linear mixed effect models of the effects of water depth and species composition on functional traits and biomass allocation of three species

	Species	Water depth (W)		Composition (C)		W × C	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
SLA	M	13.251	<0.001	0.148	0.931	0.635	0.702
	V	2.349	0.111	2.619	0.067	0.667	0.677
	P	1.355	0.27	0.518	0.673	0.274	0.946
Shoot length	M	104.115	<0.001	2.588	0.065	0.687	0.661
	V	20.048	<0.001	3.95	0.015	0.86	0.112
	P	0.994	0.379	1.487	0.233	2.402	0.045
Root length	M	6.018	0.005	3.187	0.033	1.023	0.423
	V	3.764	0.032	0.614	0.61	0.444	0.845
	P	0.099	0.906	4.128	0.012	0.927	0.486
TB	M	0.815	0.449	2.765	0.053	0.847	0.541
	V	59.377	<0.001	2.135	0.109	0.325	0.92
	P	31.739	<0.001	0.156	0.925	0.43	0.855
Chlorophyll content	M	2.383	0.104	0.815	0.493	0.781	0.59
	V	6.395	0.004	0.833	0.484	0.66	0.682
	P	1.031	0.366	0.195	0.899	1.383	0.247
Chlorophyll a/b	M	0.758	0.475	0.675	0.572	0.615	0.717
	V	1.757	0.186	0.716	0.549	0.299	0.934
	P	2.939	0.065	1.721	0.179	0.624	0.71
R/S	M	0.592	0.558	0.456	0.715	1.16	0.345
	V	16.343	<0.001	0.543	0.655	0.46	0.834
	P	9.172	<0.001	2.57	0.066	0.982	0.449
Total biomass	M	0.28	0.757	1.081	0.367	0.394	0.879
	V	32.124	<0.001	5.056	0.004	0.201	0.975
	P	21.102	<0.001	0.873	0.463	0.986	0.447

Note: Block was included as a random effect in all models; significant effects were marked in bold; TB, number of branches or ramets.

TABLE 2 *F*-values and significance of linear mixed effect models of the effects of water depth and species composition on community species diversity, community-weighted mean functional traits and community biomass allocation

	Water depth (W)		Composition (C)		W × C	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
SLA	7.172	.002	32.101	<.001	1.399	.191
Shoot length	73.521	<.001	42.473	<.001	9.336	<.001
Root length	4.348	.016	18.996	<.001	0.898	.553
Chlorophyll content	3.991	.023	2.365	.039	1.077	.393
Chlorophyll a/b	3.817	.027	31.21	<.001	0.783	.666
TB	13.121	<.001	6.305	<.001	0.801	.648
R/S	3.662	.03	1.374	.235	0.953	.5
Total biomass	29.245	<.001	10.285	<.001	1.119	.357

Note: Block was included as a random effect in all models; significant effects were marked in bold. TB for number of branches or ramets.

species. The relative proportion of variability decomposition differs among traits, which reveals the importance of traits *per se* in determining community trait structure (Carlucci et al., 2015). In our study, shoot length had the largest variability in community trait structure as a result of the largest contribution of intraspecific trait variability

and positive covariation between species turnover and intraspecific trait variability. He et al. (2019) found that stem elongation was a major response strategy of canopy-forming species to low light conditions, whereas rosette-type species generated more chlorophyll to remedy the loss of production caused by light attenuation. These

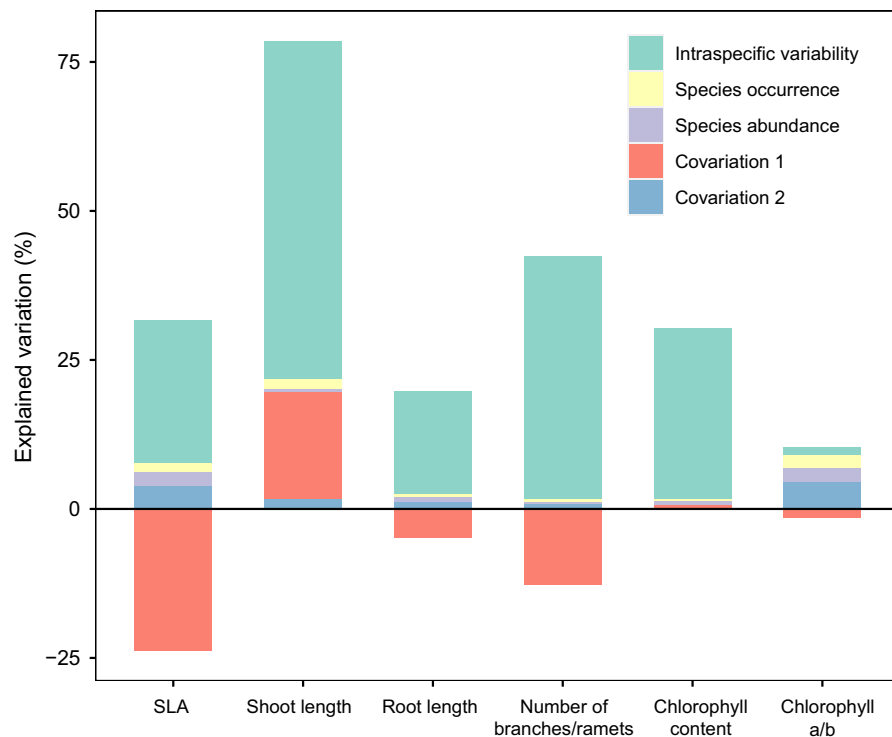


FIGURE 6 Disentangling the relative importance of intraspecific trait variability versus changes in species occurrence and abundance along water depth gradient in determining the water depth effect on variation in community weighted traits (CWM). Covariation I was the covariation between species turnover and intraspecific variability. Covariation II was the covariation between changes in species occurrence and abundance

findings are partly consistent with our result that the chlorophyll content of *V. natans* and shoot length of *M. spicatum* increase significantly with water depth. However, another canopy-forming species, *P. malaianus*, does not fit this relationship, mainly as a result of the flat-leaved *P. malaianus* having a lower tolerance to deep water than the needle-leaved species *M. spicatum* (Liu et al., 2021). These contrasting performances suggest that complex traits determine the species distribution together even though one specific trait dominates the growth of species along certain environmental gradients (Banares-de-Dios et al., 2020).

However, variations in community functional traits were explained mainly by strong intraspecific trait variability rather than by changes in species turnover in our study. Intraspecific trait adaptability has been demonstrated to be a vital factor of trait variation that determines plant community structures (Fu, Zhong, Yuan, Xie, et al., 2014). This is because intraspecific trait adaptability can make plants change themselves to occupy extra niches produced by increasing water depth and thus use resources more efficiently (Bolnick et al., 2011). For example, plants increase shoot length to get more available light in deep water. This plasticity also can assist species to adapt to stressed conditions and relieve population declines (Thuiller et al., 2008). This result is in accordance with some previous forest and grassland studies which demonstrate a relatively higher contribution of intraspecific trait variability compared with species turnover (Carlucci et al., 2015; Jung et al., 2014), but contrasts with others that discovered strong relative importance of species turnover as a driver of variation in community trait structure (de la Riva et al., 2016; Niu et al., 2016), mainly because the relative importance of the two components can be affected by many abiotic and biotic factors such as ecosystem types, habitats, spatial scales

or traits *per se* (Carlucci et al., 2015; de la Riva et al., 2016). For example, de la Riva et al. (2016) demonstrated that changes in forest community functional structure along soil water storage gradients were advanced mainly by species turnover rather than by intraspecific variability, whereas Jung et al. (2014) found that intraspecific trait variability mediated the response of grassland communities to extreme drought events. Therefore, considering the environmental context is of great importance in exploring the assemblage rules of community trait structure.

It is essential to understand how species turnover and intraspecific trait variability effects correlate in macrophyte communities because covariation of both components also can contribute to variation in community trait structure (Lepš et al., 2011). In our study, photosynthetically active radiation (i.e., light availability) decreased with water depth. Thus, under a limited light-available environment, the large positive covariation between species turnover and intraspecific trait variability in shoot length suggests that competition for light is expected to prevail, leading to the dominance of tall species, and plants that are able to grow taller will be selected (Lepš et al., 2011), where species turnover and intraspecific trait variability effects reinforce each other in shoot length. The opposite effects in SLA and the number of branches or ramets implied that the effects of species turnover and intraspecific variability of these two traits are likely to compensate for each other. The combination of these phenomena may explain the selection of dominant species of the macrophyte community under a certain environment; in our study this species was *M. spicatum*. Water depth reduced the number of branches or ramets of *P. malaianus* and *V. natans*; however, the presence of *M. spicatum* within communities notably alleviated the reduction of the number of branches or ramets at the community level,

illustrating the importance of species with good adaptability to low light stress to community performance (Wang et al., 2016, 2020). In the communities with *M. spicatum*, their community-weighted mean shoot length, root length, number of branches/ramets, chlorophyll *a/b*, and community biomass showed growth advantages in comparison with other species compositions, especially in deep water (2.50 m, 4.00 m), indicating that dominant species play a key role in forming community structures (Frieswyk et al., 2007).

In conclusion, mixtures exhibited positive complementarity effects at deeper water depth owing to the complementarity in growth form and characteristics of species. In addition, the various complementarity and selection effects under changing conditions demonstrate that the underlying mechanisms modifying productivity are different. However, variations in community trait structures have variable trait-based effects on community productivity. Water depth affects the functional traits of species directly and community trait structure indirectly by moderating species turnover and changing the functional traits of species. Moreover, variations in community functional traits along the water depth gradient are explained mainly by strong intraspecific trait variability because this upgrades divergent trait distribution to occupy new niches (that exist with increasing depth) and thus make better use of resources. Our results suggest the importance of considering intraspecific trait variability across habitats in exploring the underlying mechanism of how trait-based biodiversity influences community productivity.

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AUTHOR CONTRIBUTIONS

FM designed the experiment, collected and analysed the data and wrote the manuscript. ZZ and LY helped design the experiment, collected the data and contributed to the manuscript. DL, HW and FL collected the data and contributed to the manuscript. SF, CL and DY designed the experiment, revised this manuscript, and provided fund support. All authors contributed to the article and approved the submitted version.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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SUPPORTING INFORMATION

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