



# Effects of disturbance on functional diversity-productivity relationships of aquatic plant communities depend on nutrients and life-forms

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**Abstract** Numerous studies note the overwhelming influence of functional diversity on ecosystem functioning. It remains unclear how functional diversity affects the productivity of aquatic plant communities with different life-forms. We constructed free-floating plant communities dominated by *Salvinia natans* and submerged plant communities dominated by *Valisneria natans* to explore the effects of disturbance (clonal fragmentation) on functional diversity-productivity relationships under different nutrient availability. Results showed that, in free-floating plant communities, disturbance had significant impacts on three community-weighted means traits (average leaf length, average leaf width and average root length), functional evenness (FEve) and productivity under high nutrient conditions. Three single-trait indices and FEve showed reverse correlations with productivity. In submerged plant communities, disturbance-induced considerable variations of single- and multi-trait indices and inapparent variation of productivity.

Functional evenness was negatively related to community productivity under low nutrient conditions. Our results suggest that mechanisms of mass ratio and niche complementarity can simultaneously explain variations in free-floating plant community productivity under high nutrient conditions. Niche complementarity had a weak explanatory power for variations in submerged plant community productivity under low nutrient conditions. Our study provides the first evidence for the non-negligible role of nutrients and life-forms in functional diversity-productivity relationships of aquatic plant communities.

**Keywords** Free-floating plants · Submerged plants · Nutrient availability · Functional traits · Community productivity

## Introduction

In the past few decades, global climate change and the increasing disturbance due to human activities have led to a dramatic decline in biodiversity (Cardinale, 2012; Naeem et al., 2012; Li et al., 2020; Caro et al., 2022; Manhaes et al., 2022). The relationship between biodiversity and ecosystem functioning has also become a research hotspot for community ecologists (Brophy et al., 2017; Jing & He, 2021). Productivity, one of the most fundamental properties representing ecosystem function, is often used to evaluate biodiversity effects (Duffy et al., 2017). Most studies

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investigating the relationships between biodiversity and productivity have largely focused on terrestrial ecosystems such as grasslands and forests (Liu et al., 2018; Xu et al., 2018; Gao et al., 2021). However, aquatic ecosystems providing numerous ecological and economic services are often neglected. Aquatic macrophytes impact many processes in aquatic ecosystems, such as nutrient cycling and foodweb dynamics (Rejmankova, 2011). Therefore, investigating the biodiversity-productivity relationships of aquatic macrophyte communities can contribute to our understanding of aquatic ecosystem functions (Alahuhta et al., 2017; Ma et al., 2022).

Most previous studies have mainly focused on species diversity (e.g., species richness) as a measure of biodiversity related to productivity (vanandel, 1998; Petchey, 2000; Hooper et al., 2005). Recent studies have shown that community functional diversity based on functional traits could better explain ecosystem functions and processes than species diversity based on the taxonomical composition of communities (Butterfield & Suding, 2013; Roscher et al., 2013; Zhan et al., 2019). Functional diversity can be quantified by two main components: single trait indices (community-weighted means (CWM)) and multi-trait indices (functional richness, functional evenness, and functional dispersion) (Villéger et al., 2008; Vandewalle et al., 2010). CWM (i.e., the average trait value of plants for a single trait in the community), which reflects dominant species' influences on ecosystem function, is frequently assumed to be more related to the mass ratio hypothesis (Garnier et al., 2004; Roscher et al., 2012). Multi-trait indices (i.e., the distribution of trait values), representing the degree of overlap in trait values within the community, are often associated with the niche complementarity hypothesis (Petchey & Gaston, 2002; Cadotte, 2017). Only a few studies have compared the explanatory power of the mass ratio hypothesis and the niche complementarity hypothesis on ecosystem processes (Mokany et al., 2008; Carreño-Rocabado et al., 2012; Xu et al., 2018). Nevertheless, the results were diverse and these studies are all from terrestrial ecosystems. In aquatic macrophyte communities, there is limited knowledge about how functional diversity affects productivity.

In aquatic habitats, most aquatic plants are characterized by clonal growth and play important roles in many aquatic ecosystems (Schmid, 1990; Wang

et al., 2016). Stolons between ramets of aquatic clonal plants tend to be fragile due to low levels of lignification (Barratsegretain, 1996). Moreover, aquatic habitats are frequently disturbed by flooding, transportation, fish-farming and other human activities (Lin et al., 2012; Huber et al., 2014), so connections between clonal ramets are more prone to breakage. However, few studies have attempted to measure the effects of this disturbance (clonal fragmentation) on functional diversity and productivity of aquatic clonal plant community. In addition, frequent human activities also strengthen N and P deposition, resulting in increased nutrient availability in the water body and sediment (Gao et al., 2019, 2020). It is well-known that nutrient availability is a key factor affecting the growth and development of aquatic clonal plants (Krouk et al., 2011). For instance, high nutrient availability significantly increased the total biomass and ramet number of floating clonal plants, *Salvinia natans* (Zhang et al., 2020b). Submerged plants like *Vallisneria spiralis* exhibited greater compensatory growth responses to partial leaf removal in high nutrient sediments (Li et al., 2010). It is recognized that sediment nutrient availability is closely coupled with aquatic macrophyte productivity and species composition (Barko et al., 1991). Therefore, it would be better to take nutrient availability into account when exploring the effects of disturbance on aquatic plant communities.

In this study, we constructed two aquatic plant communities (free-floating plant communities and submerged plant communities) dominated by *S. natans* and *V. natans*, respectively, to investigate the effects of clonal fragmentation on the functional diversity and functional diversity-productivity relationships of free-floating and submerged plant communities under different nutrient availability. Both *S. natans* and *V. natans* are typical stoloniferous clonal plants. In the experiment, clones of *S. natans* and *V. natans* were periodically disturbed (stolons were severed or remained connected). Our study aimed to answer two questions. First, in different life-form plant communities, how does fragmentation affect the different components (single trait indices and multi-trait indices) of functional diversity and community productivity under different nutrient availability? Second, what are functional diversity-productivity relationships under different nutrient availability?

## Materials and methods

### Plant species

*Salvinia natans* is a free-floating, fast-growing, clonal pteridophyte. Its stem nodes are whorled with three leaves; two oval leaves that float on the water, and the third is split into linear segments covered with hairs, which functions like a root (referred to as the root in this study) (Gałka & Szmeja, 2012). New whorls, which can be regarded as ramets, can develop within several days. The other two coexisting species were *Lemna perpusilla* and *Spirodela polyrhiza*. *Lemna perpusilla* is a floating clonal plant of the Lemnaceae and its frond is green on both sides, nearly flat, obliquely obovate or obovate-oblong (Tang et al., 2011). *Spirodela polyrhiza* is also a floating clonal plant of Lemnaceae and its frond is flat and obovate, with the purple back towards the water and the green surface towards the air (Zhang et al., 2020a). The combination of one frond and some roots is treated as a ramet in *L. perpusilla* and *S. polyrhiza*. All three of them are often found in slow moving water associated with ditches, shallow pools, and eutrophic lakes. Plants of the three species were collected on July 28, 2020 from a pond located in the National Field Station of the Freshwater Ecosystem of Liangzi Lake (hereafter referred to as the National Field Station of Liangzi Lake), Wuhan University, China. Then, they were thoroughly cleaned and cultivated in containers (35 cm in diameter and 15 cm in height) filled with lake water (TN 1 mg l<sup>-1</sup> and TP 0.03 mg l<sup>-1</sup>) at the experimental outdoor platform.

*Vallisneria natans*, a submerged macrophyte with a wide geographical range, is a dominant native species in many freshwater habitats in China (Lowden, 1982). It usually spreads horizontally above ground by producing stolons and forming clonal ramets, and is often used for the restoration of aquatic vegetation (Zhu et al., 2018). The other two coexisting species were *Potamogeton malaianus* and *Myriophyllum spicatum*. *Potamogeton malaianus* is a submerged perennial herb with developed underground rhizomes system (Liu et al., 2007). *Myriophyllum spicatum* is a common submerged macrophyte that has a high rate of survival, and strong resistance to pollution (Sun et al., 2021). These three species are extensively dispersed throughout the world and are usually found in the same habitat. We used the seeds from a

population of *V. natans* cultivated the previous year to obtain seedlings of *V. natans*. Seedlings of *V. natans* and shoots of *P. malaianus* and *M. spicatum* were collected and cultivated on May 10, 2021 in aquariums in the greenhouse at the National Field Station of Liangzi Lake.

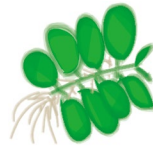
## Experimental design

### Free-floating plant community experiment

The free-floating plant community experiment started on August 3, 2020. In a fully factorial design with five replicates each, two levels of nutrient (low or high) and two levels of fragmentation (no fragmentation or with fragmentation) were applied. Nutrient levels were 1 mg N l<sup>-1</sup> and 0.03 mg P l<sup>-1</sup> in the low nutrient treatment (lake water) and 4 mg N l<sup>-1</sup> and 0.2 mg P l<sup>-1</sup> in the high nutrient treatment. The concentration of N and P solutions in high nutrient treatments was supplied by adding NH<sub>4</sub>NO<sub>3</sub> and NaH<sub>2</sub>PO<sub>4</sub>·2H<sub>2</sub>O (Yu et al., 2019). Among nutrients, nitrogen and phosphorus especially control the abundance of free-floating plants (Smith, 2014). Based on fresh weight and coverage of species, we put 20 clonal fragments of *S. natans* (9.682 ± 0.192 g fresh weight, mean ± SE; about 75% coverage in the community) that were similar in morphology and size into each experimental container (28 cm in diameter and 10 cm in height). Each clonal fragment of *S. natans* consisted of four connected ramets (Fig. 1). 26 clones of *L. perpusilla* (0.500 ± 0.003 g fresh weight, mean ± SE; about 10% coverage in the community) and 26 clones of *S. polyrhiza* (0.946 ± 0.002 g fresh weight, mean ± SE; about 15% coverage in the community) were also evenly put into each experimental container. Each clone of *L. perpusilla* consisted of six connected fronds and each clone of *S. polyrhiza* consisted of four connected fronds (Fig. 1). Twenty experimental containers were placed completely randomly under a transparent canopy. After 3 days of growth (August 5), all connected stolons of *S. natans* in five experimental containers were severed at each nutrient level, and stolons of *S. natans* in the other five experimental containers remained connected. The experiment lasted for 4 weeks, and the mean air temperature was 27.1 °C. Every 7 days, nutrient solutions and lake water in containers were completely

**Fig. 1** Plant materials used in this study

### Free-floating plants



*Salvinia natans*

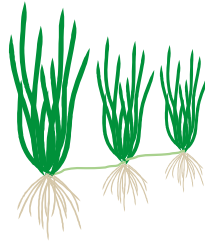


*Lemna perpusilla*



*Spirodela polyrhiza*

### Submerged plants



*Vallisneria natans*



*Potamogeton malaianus*



*Myriophyllum spicatum*

replaced, and disturbances (severing) were done once every 2 weeks.

### Submerged plant community experiment

The submerged plant community experiment started on May 20, 2021. 10 of the 20 containers were filled with lake clay (depth of 10 cm, TOC 30.869 mg g<sup>-1</sup>, TN 4.038 mg g<sup>-1</sup>, TP 0.50 mg g<sup>-1</sup>) for high nutrient conditions, and the other 10 were filled with mixed substrate (lake clay: sand=1:2) (depth of 10 cm) for low nutrient conditions. The lake clay was salvaged from Liangzi Lake with tools, and the sand was taken from the sand washed by the lake water to the lake shore. Two clonal fragments of *V. natans* with similar morphology and size, two apical shoots (15 cm in plant height) of *M. spicatum* and two apical shoots (15 cm in plant height) of *P. malaianus* were selected and evenly planted in the experimental container (80 cm in diameter and 80 cm in height) filled with lake water (TN 0.068 mg l<sup>-1</sup>, TP 0.019 mg l<sup>-1</sup>). Each clonal fragment (15–18 cm in length) of *V. natans* consisted of three connected ramets (Fig. 1). One week after the plants were planted, half of the stolons of *V. natans* at each nutrient level were severed (with fragmentation) and the other half remained connected (no fragmentation), with 5 replicates per treatment. Severing was repeated every 2 weeks during the experiment, and the experiment lasted for 8 weeks.

The experimental containers were placed at random on an outdoor cement platform and the mean air temperature was 24.3°C.

### Measurements

#### Free-floating plant community

At harvest, the free-floating plants covered the whole water surface in some containers. We counted the total ramet number of each species in each container. Three traits for light acquisition and utilization (average leaf length, average leaf width and specific leaf area), two traits for nutrients acquisition and utilization (average root length and specific root length) and a regenerative trait (ramet number) were used as functional trait measurements (Table 1). We randomly selected 20 ramets of *S. natans*, 50 ramets of *S. polyrhiza*, and 50 ramets of *L. perpusilla* in each container and measured the leaf (frond) length, leaf (frond) width, and longest root length (hereafter “root length”) of each ramet with waterproof digital calipers (MNT-200). Average leaf length, average leaf width and average root length were also calculated based on the data of these selected ramets in each container. These ramets were then separated into leaves, stems, and roots, dried in an oven at 70°C for 48 h, and weighed to obtain leaf biomass, stem

**Table 1** Single- and multi-trait indices of functional diversity used in this study

	Traits	Abbreviations	Functions
Single-trait	Average leaf length	CWM <sub>ALL</sub>	Light acquisition and utilization
	Average leaf width	CWM <sub>ALW</sub>	Light acquisition and utilization
	Specific leaf area	CWM <sub>SLA</sub>	Light acquisition and utilization
	Average shoot height	CWM <sub>ASH</sub>	Light acquisition and utilization
	Leaf N content	CWM <sub>LN</sub>	Light acquisition and utilization
	Average root length	CWM <sub>ARL</sub>	Nutrients acquisition and utilization
	Specific root length	CWM <sub>SRL</sub>	Nutrients acquisition and utilization
	Ramet number	CWM <sub>RN</sub>	Propagation
Multi-trait	Functional richness	FRic	Occupation of the potential niche
	Functional evenness	FEve	Degree of resource utilization
	Functional dispersion	FDis	Variation of trait values among species

biomass, root biomass, and total biomass of these ramets for each species separately. Before drying, the leaf areas of each species were measured using a leaf area meter (LI-COR, LI-3100 AREA METER, USA) to calculate the specific leaf area, which was calculated as leaf areas divided by the leaf biomass of these ramets of each species. Specific root length was calculated as total root length divided by the root biomass of these ramets of each species. The remaining plants of each species in each container were also harvested whole, and not separated into leaves and roots. They were dried in an oven at 70°C for 48 h, and weighed. The total biomass of each species in a container was the sum of the biomass of the selected ramets and the remaining ramets of each species in that container. The total biomass (dry weight, DW) of a community (community productivity) was the pooled total biomass of all species in a container.

Community-weighted mean (CWM) trait values were calculated as the sum across all species of the products of each species trait value and their relative abundance (Garnier et al., 2004). Functional richness was calculated as the convex hull volume in n-dimensional space, where n is the number of traits, and is analogous to the multidimensional range (Villéger et al., 2008). Functional evenness was calculated as the abundance-weighted nearest neighbour distances along the minimum spanning tree in n-dimensional trait space (Villéger et al., 2008). Functional dispersion was calculated as the weighted mean distance of individual species to the weighted centroid of all species in multidimensional trait space, where weights correspond to the relative abundances of the species (Laliberté & Legendre, 2010).

### Submerged plant community

At the end of the submerged plant community experiment, we counted the total ramet or branch number of each species in each container. In the calculation of community index, we collectively called them ramet number. Three traits for light acquisition and utilization (average shoot height, specific leaf area and leaf N content), two traits for nutrient acquisition and utilization (average root length and specific root length) and a regenerative trait (ramet number) were used as functional trait measurements. Six fully developed and healthy leaves for *V. natans* and *P. malaianus* severally and 20–25 fully developed and healthy leaves for *M. spicatum* were selected to measure the leaf areas using the leaf area meter, then oven-dried and weighed to calculate specific leaf area. The dried leaves were also fully ground to determine the leaf N content with the organic elemental analyzer (FLASH 2000, Thermo Fisher Scientific Inc., USA). We randomly selected 10 ramets of *V. natans* and *P. malaianus* in each container and measured the shoot height and root length of all species. Furthermore, average shoot height and average root length of all species were calculated. These ramets and plants of *M. spicatum* were then separated into shoots, roots, stolons or rhizomes, dried in an oven at 70 °C for 48 h, and weighed to obtain shoot biomass, root biomass, spacer biomass, and total biomass of these plants. Specific root length was calculated as total root length divided by the root biomass of these plants of each species. The remaining plants of each species in each container were also harvested in the same way. The total biomass of each species in a container was the

sum of the biomass of the selected plants and the remaining plants of each species in that container. The total biomass (dry weight, DW) of a community (community productivity) was the pooled total biomass of all species in a container.

Calculations of CWM trait values and functional diversity indices were the same as those in the free-floating plant community.

### Data analysis

Based on functional traits and abundance (biomass) of all species, community-weighted mean (CWM) trait values and multi-trait indices (functional richness, functional evenness, and functional dispersion) were calculated with the FD package (Laliberté et al., 2014) in R software. Two-way ANOVAs were used to evaluate the effects of clonal fragmentation and nutrient on single trait indices, multi-trait indices, and productivity of two plant communities. Further, we examined the differences between different treatments using Fisher’s least significant difference [LSD] test

at the 0.05 significance level. Then, we used simple linear regression to assess the capacity of each single trait indices and multi-trait indices to explain variation in productivity. Prior to the analyses, all data were normal and homoscedastic. All analyses were conducted in R 3.5.2.

## Results

### Free-floating plant community

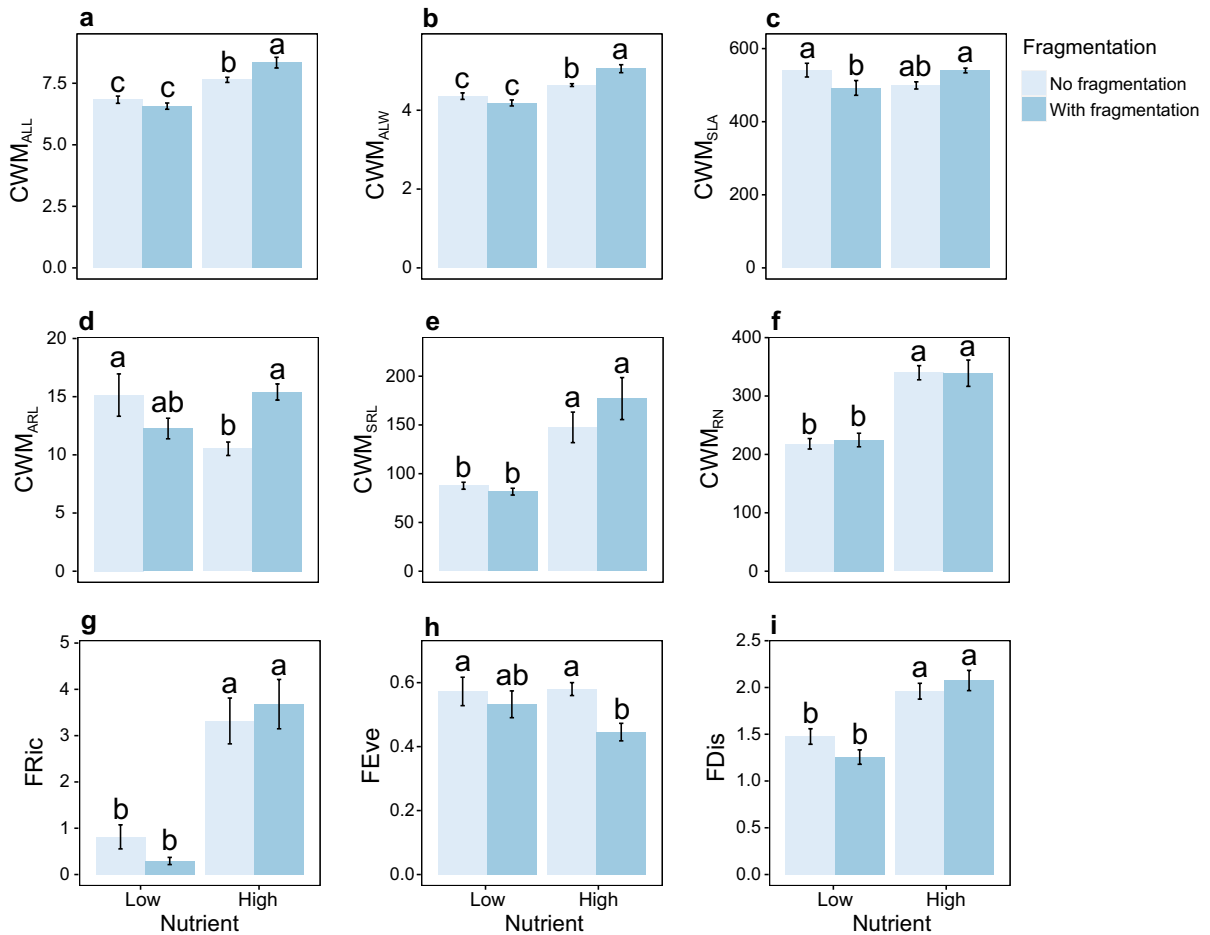
Nutrient and the interaction of nutrient and fragmentation significantly affected leaf morphology of free-floating plant communities (Table 2). Clonal fragmentation greatly increased CWM<sub>ALL</sub> and CWM<sub>ALW</sub> in high nutrient conditions, while there was no significant difference between fragmentation and non-fragmentation treatments in low nutrient conditions (Fig. 2a and b). CWM<sub>ALL</sub>, CWM<sub>ALW</sub>, CWM<sub>SRL</sub>, CWM<sub>RN</sub>, FRic and FDis in high nutrient conditions were strongly greater than those in low nutrient

**Table 2** Two-way ANOVAs for the effects of fragmentation, nutrient and their interaction on single- and multi-trait indices of functional diversity in free-floating plant communities and submerged plant communities

CWM<sub>ALL</sub> Average leaf length, CWM<sub>ALW</sub> Average leaf width, CWM<sub>SLA</sub> Specific leaf area, CWM<sub>ASH</sub> Average shoot height, CWM<sub>LN</sub> Leaf N content, CWM<sub>ARL</sub> Average root length, CWM<sub>SRL</sub> Specific root length, CWM<sub>RN</sub> Ramet number, FRic Functional richness, FEve Functional evenness, FDis Functional dispersion  
Significant *P*-values are presented in bold

Variables	Fragmentation (F)		Nutrient (N)		F × N	
	<i>F</i> <sub>1,16</sub>	<i>P</i>	<i>F</i> <sub>1,16</sub>	<i>P</i>	<i>F</i> <sub>1,16</sub>	<i>P</i>
Free-floating plant community						
CWM <sub>ALL</sub>	1.99	0.177	68.55	<0.001	9.53	<b>0.007</b>
CWM <sub>ALW</sub>	2.43	0.139	54.37	<0.001	14.24	<b>0.002</b>
CWM <sub>SLA</sub>	0.07	0.799	0.04	0.846	8.89	<b>0.009</b>
CWM <sub>ARL</sub>	0.82	0.379	0.44	0.515	12.22	<b>0.003</b>
CWM <sub>SRL</sub>	0.75	0.400	32.80	<0.001	1.72	0.208
CWM <sub>RN</sub>	0.04	0.849	63.83	<0.001	0.06	0.810
FRic	0.04	0.842	57.56	<0.001	1.30	0.270
FEve	6.23	<b>0.024</b>	1.29	0.273	1.82	0.197
FDis	0.35	0.564	53.29	<0.001	3.51	0.080
Productivity (g DW)	24.00	<0.001	48.70	<0.001	7.19	<b>0.016</b>
Submerged plant community						
CWM <sub>ASH</sub>	19.79	<0.001	265.83	<0.001	13.43	<b>0.002</b>
CWM <sub>SLA</sub>	10.21	<b>0.006</b>	4.74	<b>0.045</b>	3.79	0.069
CWM <sub>LN</sub>	0.58	0.459	32.76	<0.001	0.04	0.837
CWM <sub>ARL</sub>	1.36	0.261	123.62	<0.001	0.53	0.478
CWM <sub>SRL</sub>	9.39	<b>0.007</b>	8.42	<b>0.010</b>	19.90	<0.001
CWM <sub>RN</sub>	39.49	<0.001	64.75	<0.001	7.41	<b>0.015</b>
FRic	13.48	<b>0.002</b>	13.09	<b>0.002</b>	55.14	<0.001
FEve	274.82	<0.001	20.59	<0.001	0.38	0.548
FDis	2.30	0.149	11.28	<b>0.004</b>	0.38	0.548
Productivity (g DW)	1.51	0.238	152.45	<0.001	0.38	0.549





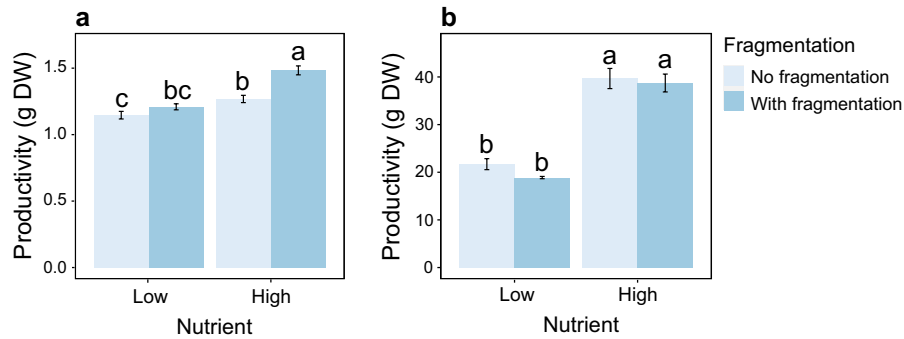
**Fig. 2** Effects of fragmentation and nutrient on single- and multi-trait indices of functional diversity in free-floating plant communities. Mean values ( $\pm$ SE;  $n=5$ ) of **a** Average leaf length ( $CWM_{ALL}$ ), **b** Average leaf width ( $CWM_{ALW}$ ), **c** Specific leaf area ( $CWM_{SLA}$ ), **d** Average root length ( $CWM_{ARL}$ ), **e**

Specific root length ( $CWM_{SRL}$ ), **f** Ramet number ( $CWM_{RN}$ ), **g** Functional richness (FRic), **h** Functional evenness (FEve) and **i** Functional dispersion (FDIs) are given. Different lowercase letters indicate significant differences ( $P < 0.05$ )

conditions (Table 2, Fig. 2a, b, e, f, g and i). Clonal fragmentation significantly decreased  $CWM_{SLA}$  in low nutrient conditions and increased  $CWM_{ARL}$  in high nutrient conditions (Table 2, Fig. 2c and d). Lower FEve was only found in fragmentation treatments under high nutrient conditions rather than low nutrient conditions (Fig. 2h). Productivity was greatly increased by clonal fragmentation under high nutrient conditions but not under low nutrient conditions (Fig. 3a).

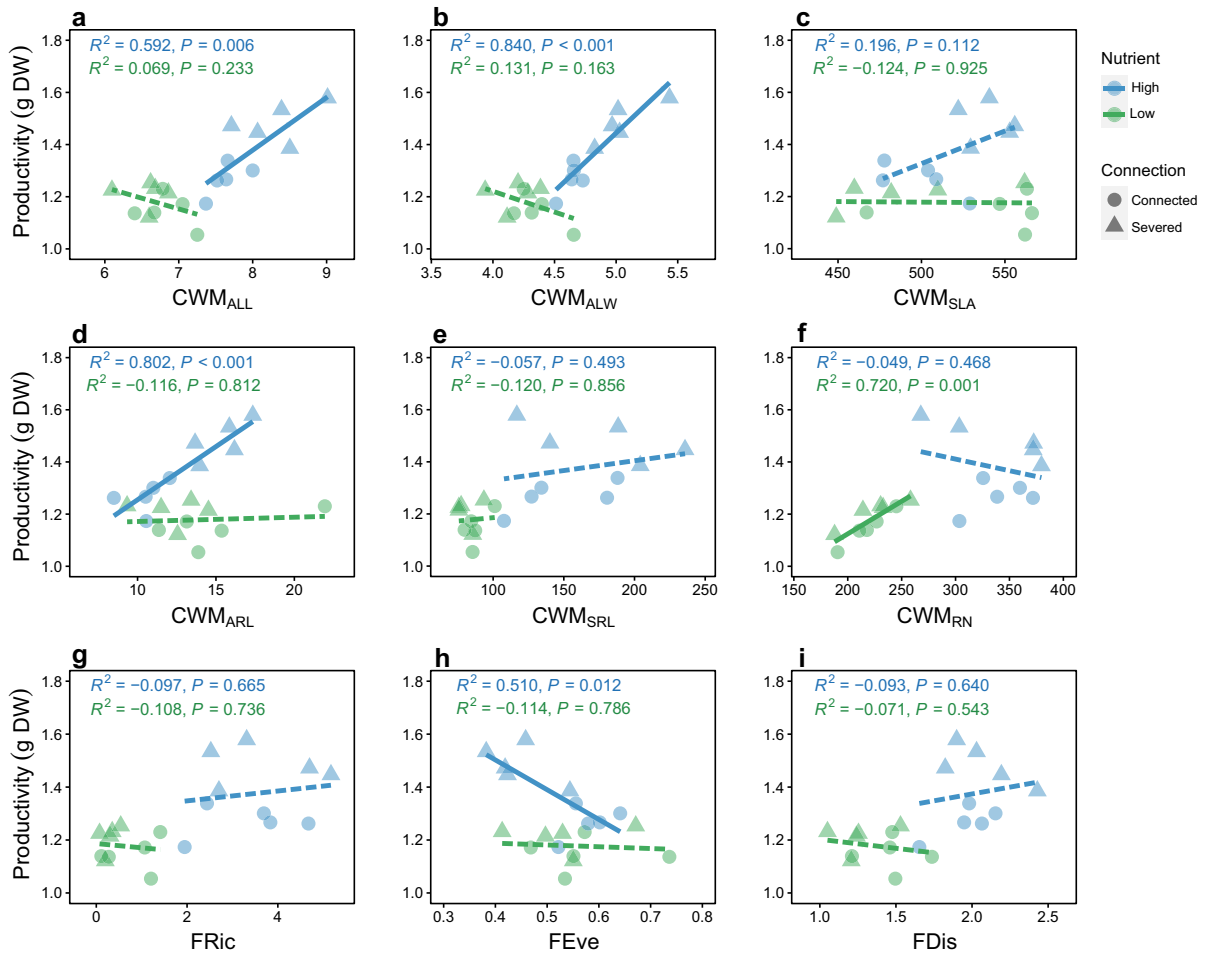
In single-trait indices of functional diversity,  $CWM_{ALL}$ ,  $CWM_{ALW}$ , and  $CWM_{ARL}$  showed significantly positive relationships with community

productivity under high nutrient conditions rather than low nutrient conditions (Fig. 4a, b, and d). Community productivity was not related to  $CWM_{SLA}$  and  $CWM_{SRL}$  under two nutrient conditions (Fig. 4c and e).  $CWM_{RN}$  showed significantly positive relationships with community productivity under low nutrient conditions (Fig. 4f). In multi-trait indices of functional diversity, only FEve showed significantly negative relationships with community productivity under high nutrient conditions (Fig. 4h). Both FRic and FEve had not significant relationships with productivity under two nutrient conditions (Fig. 4g and i).



**Fig. 3** Effects of fragmentation and nutrient on productivity (dry weight, DW) of free-floating plant communities and submerged plant communities. Mean values ( $\pm$ SE;  $n=5$ ) of

(a) productivity of free-floating plant communities and (b) productivity of submerged plant communities are given. Different lowercase letters indicate significant differences ( $P < 0.05$ )



**Fig. 4** Relationship between productivity and single- and multi-trait indices of functional diversity under different nutrient conditions in free-floating plant communities. The solid line indicates a significant relationship

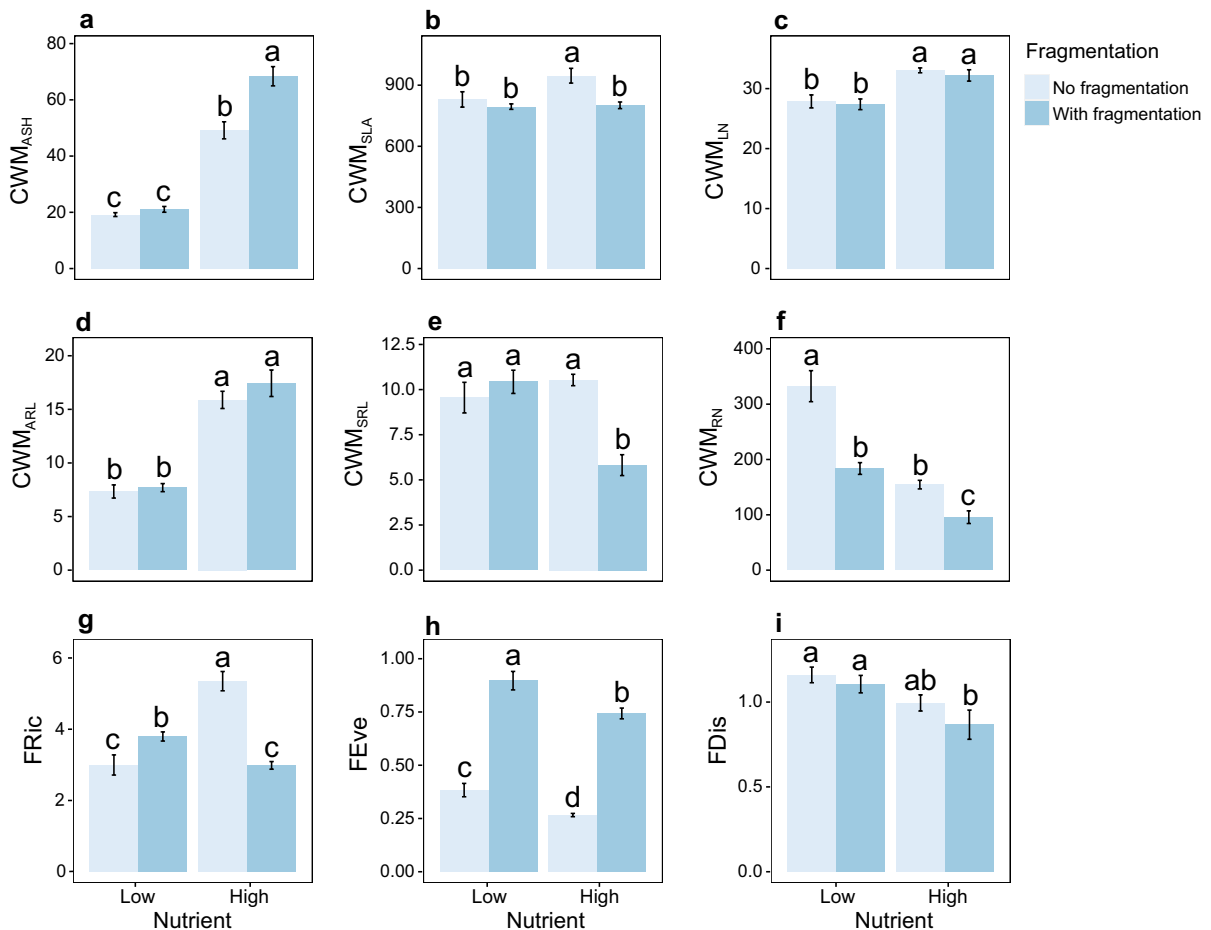


## Submerged plant community

Clonal fragmentation, nutrients and their interaction significantly affected  $CWM_{ASH}$ ,  $CWM_{SRL}$  and  $CWM_{RN}$  (Table 2). The positive effects of clonal fragmentation on  $CWM_{ASH}$  and the negative effects of clonal fragmentation on  $CWM_{SLA}$  and  $CWM_{SRL}$  were found under high nutrient conditions but not under low nutrient conditions (Fig. 5a, b, and e).  $CWM_{ASH}$ ,  $CWM_{LN}$  and  $CWM_{ARL}$  in high nutrient conditions were strongly greater than those in low nutrient conditions (Table 2, Fig. 5a, c, and d). There were no significant effects of clonal fragmentation and interaction effects of clonal fragmentation and nutrients on

$CWM_{LN}$ ,  $CWM_{ARL}$  and  $FD_{is}$  (Table 2, Fig. 5c, d and i). Clonal fragmentation markedly decreased  $CWM_{RN}$  under two nutrient conditions (Table 2, Fig. 5f).  $FRic$  was significantly increased by clonal fragmentation under low nutrient conditions, while  $FRic$  was significantly decreased by clonal fragmentation under high nutrient conditions. (Table 2, Fig. 5g).  $FEve$  was significantly increased by clonal fragmentation under two nutrient conditions (Table 2, Fig. 5h). Productivity was not affected by clonal fragmentation under two nutrient conditions (Fig. 3b).

All single-trait indices of functional diversity showed non-significant relationships with community productivity under two nutrient conditions



**Fig. 5** Effects of fragmentation and nutrient on single- and multi-trait indices of functional diversity in submerged plant communities. Mean values ( $\pm$  SE;  $n=5$ ) of **a** Average shoot height ( $CWM_{ASH}$ ), **b** Specific leaf area ( $CWM_{SLA}$ ), **c** Leaf N content ( $CWM_{LN}$ ), **d** Average root length ( $CWM_{ARL}$ ), **e** Spe-

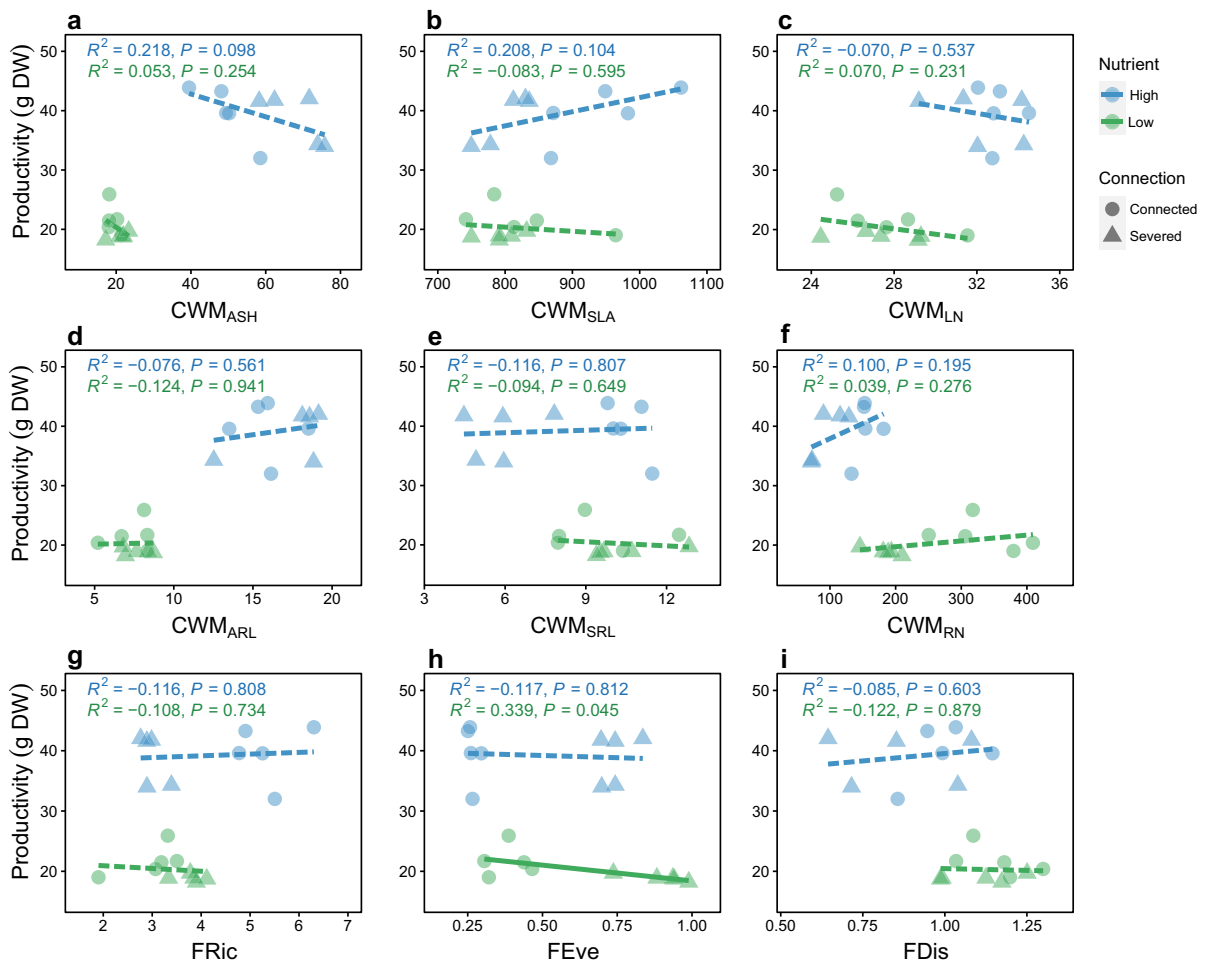
cific root length ( $CWM_{SRL}$ ), **f** Ramet number ( $CWM_{RN}$ ), **g** Functional richness ( $FRic$ ), **h** Functional evenness ( $FEve$ ) and **i** Functional dispersion ( $FD_{is}$ ) are given. Different lowercase letters indicate significant differences ( $P < 0.05$ )

(Fig. 6a–f). In multi-trait indices of functional diversity, only FEve showed significantly negative relationships with community productivity under low nutrient conditions (Fig. 6h). FRic and FDis did not exhibit strong correlations with productivity (Fig. 6g and i).

## Discussion

Clonal fragmentation positively affected resources acquisition and use characteristics of free-floating plant communities under high nutrient conditions. This phenomenon was likely due to increased intraspecific and interspecific competition of

free-floating plants *S. natans* caused by fragmentation under high nutrient conditions, which may further influence the functional responses of the plants. Under low nutrient conditions, the surface area of the water was sufficient for plant growth due to fewer ramets, which may have little effect on intraspecific and interspecific competition of free-floating plants (Si et al., 2019). Therefore, resources acquisition and use characteristics were not affected by fragmentation under low nutrient conditions, except for specific leaf area. Ramet numbers of communities were not greatly altered by fragmentation under two nutrient conditions, which may be because variations of ramet number in dominant species *S. natans* are covered by



**Fig. 6** Relationship between productivity and single- and multi-trait indices of functional diversity under different nutrient conditions in submerged plant communities. The solid line indicates a significant relationship

ramet number of two coexisting species with the rapid asexual reproduction ability. In submerged plant communities, fragmentation greatly decreased ramet number under two nutrient conditions, which may indicate different strategies for asexual reproduction in different plant life-forms. Furthermore, a recent study also showed that stolon connection could greatly improve the horizontal spreading ability of *V. natans* during the whole growth stage (Ma et al., 2021). The increasing of ramet number by non-fragmentation may lead to the intensification of interspecific competition, further stimulating the positive responses of functional traits. But this phenomenon was not obvious under low nutrient conditions, which may suggest that the functional trait variability of the submerged clonal plants was greater in the face of disturbance under high nutrient availability. Traditionally, morphological and/or physiological plasticity of plants require expensive cost (Hodge, 2006). High nutrient availability can provide more and accessible outlay for structure adjustments in plants. In addition, clonal fragmentation may eliminate the effects of mother ramets of *V. natans* on daughter ramets (such as resource transportation, metabolic costs, and apical dominance), resulting in individual development of mother ramets (observed greater average shoot height) (Pauliukonis & Gough, 2004; Zhang et al., 2016).

In free-floating plant communities, only functional evenness representing the degree of resource utilization was strongly decreased by fragmentation under high nutrient conditions, suggesting that disturbance increased niche overlap between free-floating plant species, especially between two functionally similar coexisting species (Prado-Junior et al., 2016). This response to disturbance is the opposite of that in most single-trait indices of functional diversity. In submerged plant communities, increased functional richness and functional evenness by fragmentation under low nutrient conditions may indicate the increased complementarity among submerged plant species (Mouillot et al., 2005). Different effects of fragmentation on functional richness and functional evenness under high nutrient conditions highlight the role of nutrients in the effect of disturbance on functional diversity of submerged plant community. For community productivity, fragmentation also showed different effects at nutrients and life-form levels: only the

productivity of free-floating plant communities under high nutrient conditions was significantly increased by fragmentation.

Among six traits of free-floating plant communities, three CWM traits showed significantly positive correlations with productivity under high nutrient conditions. This finding demonstrates that community productivity could be influenced by some traits' values of dominant species in communities (Enquist et al., 2015). Remarkably, under high nutrient conditions, the greatly negative relationships between functional evenness and productivity are impressive but not often reported by previous studies. This is most likely related to our selection of two morphologically and functionally similar species of Lemnaceae. Based on the study of Ali et al. (2018), we speculated that high productivity could be maintained or built up by dominant species through niche overlap of two coexisting species. These results imply that both mechanisms of mass ratio and niche complementarity can simultaneously affect community productivity, but their effects on productivity were opposite (Fu et al., 2014). Similarly, a previous study also found the opposite effects of community-weighted means and functional dispersion on grassland productivity (Xu et al., 2018). However, only a weak explanation (one CWM traits) of mass ratio hypothesis for productivity was observed under low nutrient conditions. These results suggest that nutrient plays an important role in the effects of disturbance on functional diversity-productivity relationships. In submerged plant communities, all single-trait indices of functional diversity had no significant relationships with productivity under two nutrient conditions, indicating that the functional traits of the dominant species are less important in influencing ecosystem function. Mokany et al. (2008) provide a striking contrast with our study, in which the traits of the dominant species most influenced the ecosystem processes. Under low nutrient conditions, FEve was negatively related to community productivity, which may be related to the non-random assembly of our experimental communities and was consistent with the result of a previous study (Ali et al., 2018). Though disturbance may promote the occupation of the potential niche by submerged plants (canopy-forming *P. malaianus* and *M. spicatum*), resulting in increased degree of resource utilization, the growth dominant species (rosette-forming *V. natans*) may be reduced by disturbance. Dominant species generally

occupies large biomass in community. Therefore, community productivity may reduce with the increasing occupation of the potential niche by coexisting species. However, inapparent variation of productivity indicates a weak explanatory power of niche complementarity.

For free-floating plant communities under high nutrient conditions, disturbance can not only directly influence community productivity but also indirectly influence community productivity through mechanisms of mass ratio and niche complementarity. These results suggest that the growth of free-floating plants may be more sensitive to disturbance in eutrophic water bodies (Zhang et al., 2019). Although disturbance changed single- and multi-trait indices of functional diversity in submerged plant communities, productivity was not affected. This phenomenon is probably due to the flexible morphological and functional plasticity of submerged clonal plants (Strand & Weisner, 2001; Chen et al., 2016, 2020). Another alternative explanation is that submerged plants can absorb nutrients not only from sediments through their roots but also from overlying water through their leaves compared with free-floating plants (Barko, 1982; Chambers et al., 1989) and further compensate for the effects of disturbance (Li et al., 2010). Therefore, submerged plants may have greater stability of ecosystem function than free-floating plants in the face of disturbance.

## Conclusions

Our results show that disturbance, accompanied by the effects of nutrients, directly and indirectly affected free-floating plant community productivity. In the indirect effect on productivity, single- or multi-trait indices of functional diversity showed opposite effects under high nutrient conditions. Significant effects of disturbance on functional diversity of submerged plant communities did not cause variations of productivity, while a weak explanatory power of the niche complementarity for functional diversity-productivity relationships was found under low nutrient conditions. Plants with different life-forms may have different survival strategies, especially in aquatic clonal plants. Therefore, it is better to take nutrient availability and plant life-form into account when studying biodiversity-productivity relationships.

Admittedly, our study has some limitations. The strength of disturbance is variable under natural conditions, but we applied only one level of fragmentation. In addition, our experimental period was not long enough. Performance of plant community may differ with different growth times and different levels of disturbance. Even so, our study suggests that studying the underlying mechanisms of productivity variations could more accurately quantify and predict the impact of disturbances on biodiversity patterns, thereby contributing to the formulation of strategies for biologically effective conservation and sustainable resource utilization.

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**Data availability** Upon request to authors.

## Declarations

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

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