

Article

Invasive *Eichhornia crassipes* Affects the Capacity of Submerged Macrophytes to Utilize Nutrients

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Academic Editors: Lalit Kumar and Onesimo Mutanga

Received: 2 March 2017; Accepted: 3 April 2017; Published: 7 April 2017

Abstract: Invasion by free-floating species, such as *Eichhornia crassipes*, is one of the most critical threats to the biodiversity and sustainability of wetland ecosystems, where all plants experience spatial heterogeneity in substrate nutrients. However, few studies have focused on the effects of free-floating invaders on the capacity of submerged plants to utilize substrate nutrients. A 10-week greenhouse experiment was conducted to test the effects of free-floating invasive *E. crassipes* (presence or absence) on the growth of *Ceratophyllum demersum* and *Myriophyllum spicatum*, and their capacity to use heterogeneous and homogeneous substrate nutrients. We found that the invasion of *E. crassipes* could significantly decrease the growth of both submerged *C. demersum* and *M. spicatum* and that substrate nutrient heterogeneity increased the growth of *C. demersum* (approximately 30% in total biomass and 40% in the number of nodes) but not of *M. spicatum*. The two submerged species have different strategies to address invasion by *E. crassipes*. These results indicate that *E. crassipes* can prevent the growth of submerged plants even if the submerged plants can effectively use heterogeneous nutrients. For the effective conservation of submerged macrophytes in wetlands, measures should be taken to restrict the spread of invasive free-floating species.

Keywords: biodiversity; sustainability; biological invasion; wetland ecology; resource heterogeneity; water; *Ceratophyllum demersum*; *Myriophyllum spicatum*

1. Introduction

Biological invasions have seriously threatened the stability and sustainability of both terrestrial and aquatic ecosystems on a global scale [1–3]. Invasive free-floating plants, such as *Eichhornia crassipes*, are known to cause significant ecological damage by altering water quality [4,5], reducing the abundance and richness of wetland plant communities [6], and even affecting bacteria and algae [7]. Moreover, dense mats of free-floating invaders can reduce submerged macrophyte biomass and diversity [8,9], mostly because they generate dark conditions, secrete allelochemicals and compete fiercely with other species for nutrients and space [10,11].

Free-floating species can only acquire essential nutrients from the water column, whereas rooted macrophytes obtain most of their required nutrients from the sediment and a small amount of nutrients from the water column, even in eutrophic ecosystems [12,13]. Therefore, rooted submerged plants are expected to be limited by the availability of substrate nutrients. Some studies found that increased levels of sediment nutrients (e.g., nitrogen, phosphorus and organic matter) can increase the accumulation of submerged macrophyte biomass at both the individual [14] and community scales [15]. High nutrient levels could be related to anoxic sediment conditions, a greater proportion

of clay with more organic matter and greater pore water nutrient concentrations [16], which may contribute to submerged species gaining advantages in interspecific competition with their free-floating invasive neighbours.

All natural environments are characterized by patchy distributions of both competitors, such as invaders [13,17], and essential resources, such as nutrients, light and water [18]. Wetland substrates are always affected by human activities, elevation and tidal flooding, which results in a heterogeneous distribution of substrate nutrients. In response to substrate nutrient heterogeneity, many species show variation in how their roots are arranged in the substrate where nutrient levels are relatively high. Many studies have found that the effects of substrate nutrient heterogeneity may increase plant performance across all growth parameters [19–22]. Substrate nutrient heterogeneity may work as a modulator by changing plant growth at the individual and community levels. Moreover, one species with easy access to nutrients may obtain a competitive advantage over others for which nutrients are less accessible [18,23]. As a consequence, increased substrate nutrient levels may shift dominance from free-floating invaders to submerged species. However, few studies have focused on the effects of free-floating plants, particularly invasive species, on the capacity of submerged macrophytes to use heterogeneous substrate nutrients.

To better understand the effects of substrate nutrient heterogeneity on interspecific interactions between submerged macrophytes and free-floating plants, we addressed the following question: Could invasive floating *E. crassipes* affect the capacity of submerged macrophytes to utilize heterogeneous substrate nutrients? We conducted a greenhouse experiment testing the effects of substrate nutrient heterogeneity (heterogeneous or homogeneous substrate) and floating invasive *E. crassipes* (presence or absence) on two common submerged macrophytes, *Ceratophyllum demersum* and *Myriophyllum spicatum*.

2. Materials and Methods

2.1. Species and Sampling

The experiment was constructed using three co-occurring wetland species widely distributed in China. *Eichhornia crassipes* (Mart.) Solms, which is native to South America and commonly known as water hyacinth, is one of the world's most prevalent invasive free-floating perennial vascular species [1,24]. The invasiveness of *E. crassipes* is related to its ability to clone itself, and large patches are likely to all be part of the same genetic form [25]. Both *Ceratophyllum demersum* L. (Ceratophyllaceae) and *Myriophyllum spicatum* L. (Haloragaceae) are submerged macrophytes that grow in static or slow-moving water, such as that found in wetlands [26].

All the plants used in the experiment were collected from Luoma Lake (34°05′05.64″N, 118°11′16.29″E), located in Suqian, Jiangsu Province, China. The area of the freshwater lake is 375 km², in which both *C. demersum* and *M. spicatum* are regionally dominant species, and invaded by the *E. crassipes*. All the plants were then preincubated in a greenhouse at the Wildlife Rescue and Rehabilitation Center, Beijing, China, in early March of 2016.

2.2. Experimental Design

For each submerged species, the mesocosm experiment took a factorial design and had two factors: substrate nutrient heterogeneity (homogeneous or heterogeneous substrate nutrients) and interspecific interaction (with or without *Eichhornia crassipes*); see Figure 1 for the experimental design. Each treatment had eight replicates.

Before the experiment, we selected 32 apical shoots (20 cm length, without lateral shoots, initial dry biomass of 0.20 ± 0.01 g for *C. demersum* and 0.24 ± 0.02 g for *M. spicatum*, $N = 5$) of each submerged macrophyte and planted them in individual plastic pots (10 cm diameter and 11 cm high), which were filled with 10 cm of heterogeneous or homogeneous substrate. For the heterogeneous substrate treatment, the pots were half filled with sand that had been collected from the bank of an artificial lake located at the Wildlife Rescue and Rehabilitation Center, Beijing, China, and was low in total N, total P and organic matter [0.183 (0.022) mg total N (mean [SE]; $N = 3$), 0.643 (0.064) mg total P and

1.401 (0.069) mg organic matter g⁻¹ dry mass of substrate] and half with commercial potting soil purchased from Heroda Fertilizer Technology Co. Ltd, which was high in total N, total P and organic matter [4.311 (0.112) mg total N, 5.253 (0.631) mg total P and 38.663 (2.708) mg organic matter g⁻¹ dry mass of substrate]; we have two patches of each kind of substrate, and a total of four patches in the heterogeneous substrate treatment, see Figure 1. For the homogeneous substrate treatment, each pot was filled with a 1:1 (v/v) mixture of the sand and commercial potting soil described above. The total amounts of substrate nutrients were thus the same in both the heterogeneous and homogeneous treatments. The four pots (two heterogeneity treatments × two species) were then placed in a glass tank (50 cm long × 50 cm wide × 40 cm high) with the sides covered by black shade cloth to prevent light penetration. A total of 16 tanks (eight with *E. crassipes* and eight without *E. crassipes*) were established and filled to a level of 40 cm with tap water.

After allowing the submerged plants to become established for one week, we randomly placed *E. crassipes* on the water surface of eight tanks (four similar ramets in each tank). During the experiment, we (1) added tap water to the tanks each week to compensate for loss via evaporation and maintained the water level at 40 cm; and we (2) sprayed insecticide to reduce the damage caused by insects every two weeks. The mean temperature was 20.1 °C in the greenhouse during the experiment.

2.3. Measurements and Data Analysis

After 10 weeks, both *C. demersum* and *M. spicatum* were harvested, measured for the total number of nodes and total shoot length, dried at 70 °C for 72 h, and weighed. Before analysis, we calculated two growth indices to better describe the effects of invasion on the growth of the submerged plants: (1) the internode length (IL), which was calculated as

$$IL = SL/NN \quad (1)$$

where SL is the total shoot length and NN is the total number of nodes; and (2) the relative growth rate (RGR) of submerged plants during the 10 weeks, which was calculated based on the total dry biomass and initial biomass [12] using the following formula:

$$RGR = (\ln DB_t - \ln DB_0)/t \quad (2)$$

where DB_t is the dry biomass at time t, DW₀ is the initial dry biomass, and t is the experimental duration, which was 70 days (10 weeks, from 7 April to 16 June 2016) in our study.

To better measure the intensity of interspecific interactions between the invasive species and native submerged plants, we calculated a log response ratio (LnRR) [27,28], which is widely used to quantify plant–plant interactions. This is partly because it can compare the performance of each species when grown in mixed culture to its performance in monoculture and often meets the assumptions for statistical analysis better than other interaction models [27,29]. The formula is

$$\text{LnRR} = \ln (B_{\text{with}}/B_{\text{without}}) \quad (3)$$

where B_{with} is the biomass of the plants in the presence of invasive neighbours and B_{without} is the mean biomass of the plants in the absence of *E. crassipes* across eight replicates. LnRR = 0 indicates that there is no significant effect of the presence of *E. crassipes* on submerged plant growth; higher positive values indicate that the interaction is more facilitative, while lower negative values indicate stronger negative effects of competition.

All analyses were conducted using SPSS 20.0 (version 20.0; SPSS Inc., Chicago, IL, USA). We conducted a two-way ANOVA to test the effects of substrate nutrient heterogeneity (heterogeneous or homogeneous) and interspecific interaction (with or without *E. crassipes*) on total biomass, number of nodes, total shoot length, IL and RGR. Substrate nutrient heterogeneity and interspecific interaction were treated as fixed effects in the ANOVA models. Data on the total biomass and number of nodes of *C. demersum* and the number of nodes and shoot length of *M. spicatum* were natural log transformed before analysis to meet the requirements of homoscedasticity and normality. Differences between the heterogeneous and homogeneous substrates within each treatment were tested via

paired *t*-tests. Then, we used a one-way ANOVA to test the effects of substrate nutrient heterogeneity on the LnRR. Effects were considered significant at $P < 0.05$.

3. Results

3.1. Growth of Two Submerged Species

As predicted, the invasion of *E. crassipes* significantly reduced the total biomass, number of nodes and RGR, but not the IL, of both *C. demersum* and *M. spicatum* (Table 1; Figures 2 and 3). This interspecific interaction also reduced the total shoot length by 50% for *C. demersum* but not for *M. spicatum* ($P = 0.528$ in Table 1).

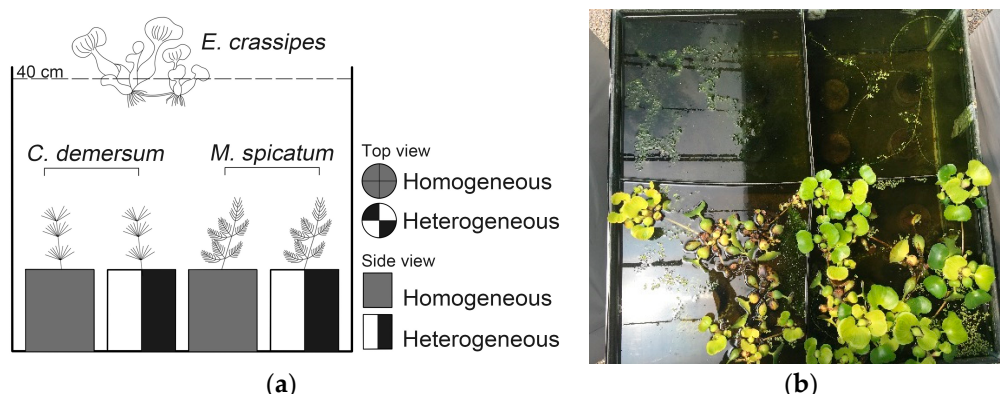


Figure 1. Experimental design. (a) 2D schematic showing the two submerged species crossed with two substrate treatments (homogeneous and heterogeneous), treated with *Eichhornia crassipes*; (b) Photograph of the experiment taken in the fourth week (5 May 2016).

Table 1. Effects of *Eichhornia crassipes* and nutrient heterogeneity on growth and morphological data for *C. demersum* and *M. spicatum*.

Trait	<i>Eichhornia crassipes</i> (E)		Heterogeneity (H)		I × H	
	<i>F</i> _{1,28}	<i>P</i>	<i>F</i> _{1,28}	<i>P</i>	<i>F</i> _{1,28}	<i>P</i>
<i>Ceratophyllum demersum</i>						
Total biomass	108.61	<0.001	7.34	0.011	6.63	0.016
No. of nodes ¹	68.73	<0.001	5.03	0.033	0.56	0.460
Shoot length ¹	132.23	<0.001	3.36	0.078	2.27	0.143
IL	2.37	0.135	1.14	0.295	0.03	0.865
RGR	113.05	<0.001	3.29	0.081	3.74	0.063
<i>Myriophyllum spicatum</i>						
Total biomass ¹	7.89	0.009	2.31	0.140	0.01	0.941
No. of nodes ¹	13.65	0.001	0.13	0.718	0.10	0.757
Shoot length	0.41	0.528	0.85	0.364	0.27	0.609
IL	1.77	0.194	0.30	0.588	0.02	0.900
RGR	16.41	<0.001	0.78	0.386	0.50	0.484

¹ indicates that these data were natural logarithm-transformed to meet the requirements of homoscedasticity and normality. Bold text indicates a significant difference ($P < 0.05$), and italics indicate $0.05 < P < 0.1$.

Across the *E. crassipes* treatment, the heterogeneous substrate nutrient treatment obviously increased the total biomass, number of nodes, total shoot length and RGR ($0.05 < P < 0.1$), but not the IL ($P = 0.295$ in Table 1), of *C. demersum* (Figure 2). The substrate treatment did not affect the growth of *M. spicatum* (Table 1; Figure 3).

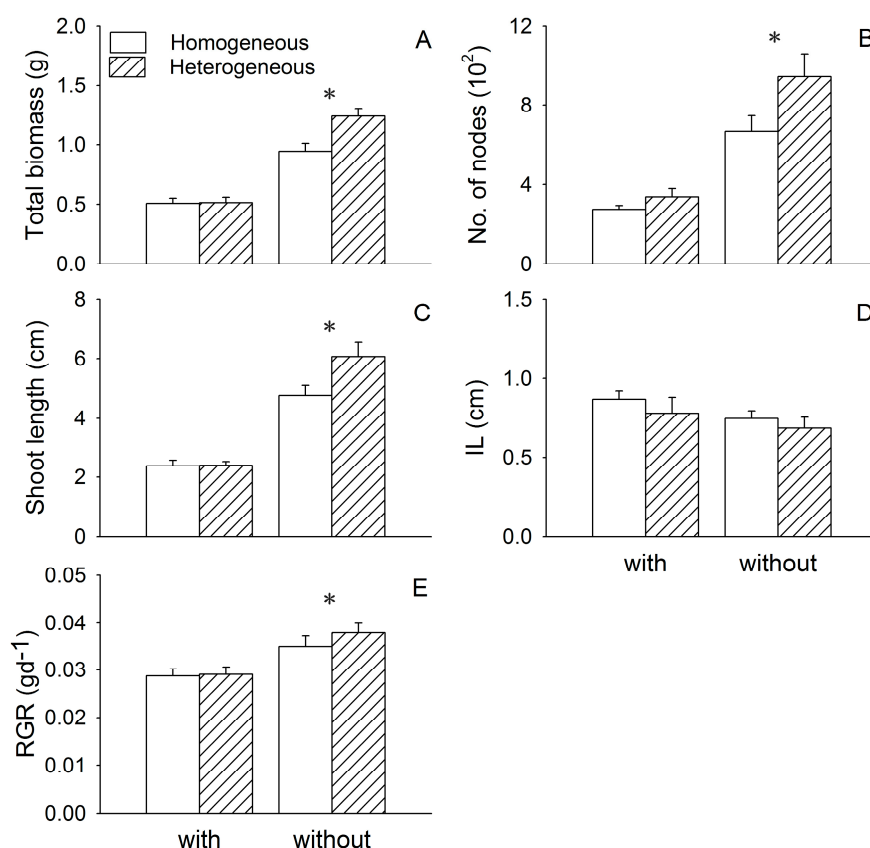


Figure 2. Effects of heterogeneous substrate nutrients and interspecific competition (with and without *E. crassipes*) on the (A) total biomass; (B) number of nodes; (C) total shoot length; (D) average internode length (IL); and (E) relative growth rate (RGR) of *C. demersum*. Symbols (*): indicates difference between the two substrate treatments (paired *t*-tests, $P < 0.05$); no symbol: $P > 0.05$. Means $\pm$ SE are given. See Table 1 for ANOVA results.

The interaction between substrate heterogeneity and the presence of *E. crassipes* was statistically significant for the total biomass of *C. demersum* ($F_{1,28} = 6.63$, $P = 0.016$ in Table 1), but the interaction term was never statistically significant for *M. spicatum*. *C. demersum* accumulated approximately 30% more biomass in the heterogeneous treatment than in the homogenous treatment, but only when *E. crassipes* was not present (Figure 2A).

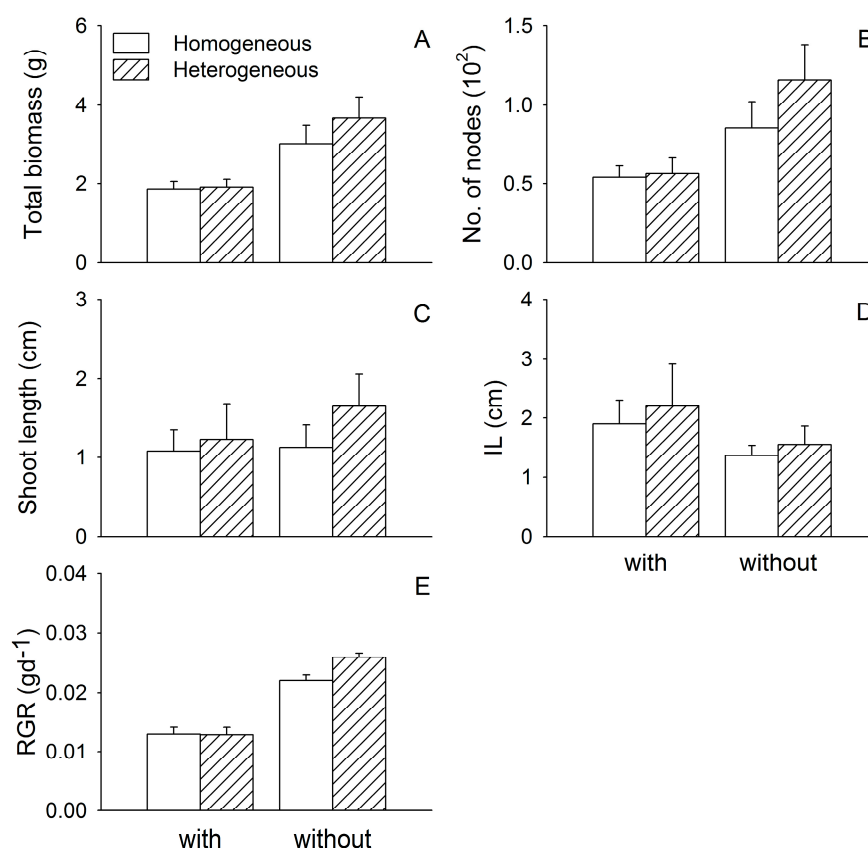


Figure 3. Effects of heterogeneous substrate nutrients and interspecific competition (with and without *E. crassipes*) on the (A) total biomass; (B) number of nodes; (C) total shoot length; (D) average internode length (IL); and (E) relative growth rate (RGR) of *M. spicatum*. Means $\pm$ SE are given. See Table 1 for ANOVA results.

3.2. Results of LnRR

The LnRRs of both species were all negative. More negative values of LnRR indicate greater competitive intensity between species. Heterogeneous substrate nutrients increased the interspecific interaction between *C. demersum* and *E. crassipes* ($P = 0.073$, Figure 4A) as measured by the LnRR. LnRRs for *M. spicatum* were not significantly different between the two substrate treatments ($P = 0.539$, Figure 4B).

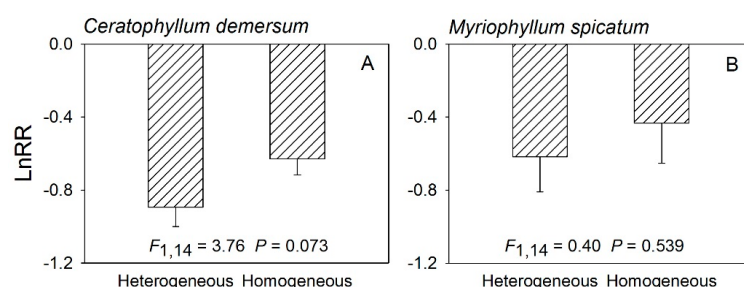


Figure 4. Log response ratio (LnRR) of (A) *C. demersum* and (B) *M. spicatum* with or without *E. crassipes* under heterogeneous and homogeneous treatments. Means $\pm$ SE are given. One-way ANOVA followed by Dunnett's test.

4. Discussion

Nutrient uptake and light availability are two major environmental factors determining the growth of submerged macrophytes [30,31]. The results show that the floating invader, such as *E.*

crassipes significantly reduced the growth of both species, suggesting that invasion by free-floating species has significant effects in aquatic ecosystems. These effects occur mainly because the free-floating invader has primacy in competition for light and can attenuate most of the incoming light, secretes allelochemicals and immobilizes water-borne nutrients [8,32]. In nature, water hyacinth often establishes in areas where there is a lack of significant aquatic phytoplankton and vegetation, but it is also able to out-compete submersed species, especially in eutrophic water [1,9].

Our research found that the heterogeneous substrate significantly increased the total biomass, number of nodes, shoot length and RGR of *C. demersum* under the no-invasion treatment, but it had no significant effects on *M. spicatum* (Table 1). Moreover, our study also found that these two submerged species showed different GRG when faced with the invasion of *E. crassipes* (Figures 2 and 3). Recent studies found that increased substrate nutrients could significantly increase the accumulation of submerged macrophyte biomass [30,33]. Compared with the homogeneous substrate, patches of pure commercial potting soil in the heterogeneous substrate provided a high level of nutrients, which resulted in better growth of *C. demersum*. You et al. [34] also found that clonal integration significantly increased the photosynthetic performance of daughter ramets of submerged macrophytes, which increases plant performance in heterogeneous habitats. Therefore, another possible explanation may be that the clonal integration of *C. demersum* allowed it to accumulate more biomass in our study, because clonal integration can facilitate the colonization and growth of ramets under both eutrophic and stressful conditions.

Some studies found that there may be a nutrient level threshold at which significant effects on the growth of individual submerged macrophytes occurs [10,15], which means that high levels of substrate nutrients may not increase or may even restrict growth. The nutrient level in the substrate may be higher than the necessary nutrient demand threshold for *M. spicatum*. In addition, *M. spicatum* may be insensitive to the effects of the heterogeneous substrate at this mesoscale. Previous studies illustrated that inappropriate sizes of heterogeneous patches may not affect the growth of plants [35–37], because inappropriate patch sizes cause plants to meet only one type of patch and the effects will thus be small. The positive effect of environmental heterogeneity on submerged macrophytes may be transitory; a previous study reported that nutrient heterogeneity could increase the growth of an annual herb species only at the early stage of growth (first month), but not in the long run (second month) [23]. Due to the 10-week experimental cycle, the nutrient-rich patches might gradually decline to the same low level as the nutrient-poor patches. These effects may limit the growth of *M. spicatum* in this study.

In the case of *E. crassipes* invasion, none of the measured growth data showed a difference between the heterogeneous and homogeneous substrate treatments for either species (Figures 2 and 3). This result indicates that the invasive free-floating *E. crassipes* reduced the capacity of *C. demersum* to utilize heterogeneous nutrients. Free-floating plants can monopolize light, which prevents the submerged vegetation from obtaining sufficient resources for photosynthesis [1,38]. In this case, light resources become more important than the substrate nutrients in limiting the growth of submerged macrophytes.

The LnRR of *C. demersum* in the heterogeneous substrate was much more negative than that for plants in the homogeneous substrate ($P = 0.073$, Figure 4), indicating that the intensity of the interspecific interaction between *C. demersum* and *E. crassipes* was much greater in the heterogeneous treatment than in the homogeneous treatment, but it had no significant effects on the interaction between *M. spicatum* and invasive *E. crassipes*. These results indicate that aquatic environmental factors can change the interaction between submerged and free-floating species, and these effects are determined by species, which is consistent with previous studies in terrestrial ecosystems [39–41]. Because floating and submerged plants have different positions in the water column, the competition for both light and nutrients in the substrate becomes asymmetric [13]. Van Gerven et al. [42] found that floating plants always outcompete submerged plants when there is an adequate supply of light and nutrients. Moreover, an increasing nutrient level leads to an advance of free-floating species in competition with submerged macrophytes; this effect is also found in both field and mesocosm

studies [43,44]. Therefore, the presence of sufficient light and nutrients may explain why the floating *E. crassipes* dominates the micro-ecosystem in this study.

5. Conclusions

Our study demonstrated that (1) the invasion of *E. crassipes* could significantly decrease the growth of both submerged *C. demersum* and *M. spicatum*; (2) substrate nutrient heterogeneity increased the growth of *C. demersum* but not of *M. spicatum*; and (3) invasive *E. crassipes* reduces the capacity of *C. demersum* to utilize heterogeneous nutrients. These results indicate that water hyacinth can prevent the growth of submerged plants even if the submerged plants can effectively use heterogeneous nutrients. Submerged macrophytes provide food and habitat for other biotas. Changes in the primary-production base of the wetland can resonate throughout the whole ecosystem, affecting multiple trophic levels directly through changes in habitat availability.

Although our results are short-term, they may have important implications considering that controlling the growth of invasive free-floating plants is key to the restoration of submerged macrophytes and the sustainable conservation of aquatic ecosystems and that increasing substrate nutrient heterogeneity may not be effective.

Acknowledgments: We thank Meng-Jie Li and Yun-Mei Ping for collecting plants and harvest, and the Beijing Wildlife Rescue and Rehabilitation Center for providing the experimental space. We are grateful to three anonymous reviewers for their valuable comments. The research is financially supported by the Special Forestry Project of Public Interests (201404305).

Author Contributions: Jian Zhou and Li-Juan Cui conceived and designed the experiments; Jian Zhou, Xu Pan and Hai-Ting Xu executed the experiments and measured the data; Jian Zhou and Hai-Ting Xu analyzed the data, and made the figures; Li-Juan Cui, Xu Pan and Qi Wang contributed to writing and editing the manuscript; Jian Zhou wrote the paper; Jian Zhou, Hai-Ting Xu and Qi Wang revised the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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