Snail communities improve submerged macrophytes growth by graze epiphytic algae and phytoplankton in a mesocosm experiment

Abstract

The relationship between producers (e.g., macrophyte, phytoplankton and epiphytic algae) and snails plays an important role in maintaining the function and stability of the shallow ecosystems. A complex relationship exists among macrophytes, epiphytic algae, phytoplankton and snails. An outdoor mesocosm experiment with two-way factorials was carried out, three species submerged macrophytes (*Hydrilla verticillate*, *Vallisneria natans* or one exotic submerged plant *Elodea nuttallii*) and two grazing treatments (4 snail species present or absent) to elucidate those relationships. The results showed that the snail communities reducing the biomass of phytoplankton and epiphytic algae indirect then enhanced the growth of the submerged macrophytes. The macrophyte with complex architecture supported more snail and epiphytic algae, and snails preferred to feed on native plants. Competition drove snails change the grazing preferences to achieve coexistence, so that led to the assembling of snail communities towards the direction of highest resource utilization.

Keywords: snail-macrophyte-algae relationship; exotic macrophyte; grazing preferences; coexisting

1 Introduction

Submerged macrophytes, phytoplankton, epiphytic algae and aquatic snails are important biological groups in freshwater ecosystems and are widely distributed in various water bodies (Carpenter & Lodge, 1986; Underwood, Thomas, & Baker, 1992; Zhu, Lu, & Liu, 2013). The relationship between producers (e.g., macrophyte, phytoplankton and epiphytic algae) and snails plays important roles in maintaining the function and stability of the shallow ecosystems (Scheffer, 1999; Underwood et al., 1992; Yang et al., 2020). Previous studies have shown that a complex relationship exists among macrophytes, epiphytic algae, phytoplankton and snails (Brönmark, 1989; Y. Cao, Li, & Jeppesen, 2014; Underwood et al., 1992).

Submerged macrophytes play significant roles in maintaining good water quality and high biodiversity in shallow ecosystems (Jeppesen, Søndergaard, Søndergaard, & Christoffersen, 1998; Kuiper et al., 2017). Submerged macrophytes inhibit epiphytic algae and phytoplankton through the reduction of nutrients, allelopathy and shading (Casartelli & Ferragut, 2018; Hilta & Grossb, 2008; Mohamed & Shehri, 2010; Sand-Jensen & Borum, 1991). On the other hand, macrophytes can also provide habitats for epiphytic algae (Celewicz-Gołdyn & Kuczyńska-Kippen, 2017; Lv, He, Hong, Liu, & Yu, 2019; Toporowska, Pawlikskowron´Ska, & Wojtal, 2008). Submerged macrophytes are also important foods and habitats provide for aquatic animals (Brix, 1994; Zhi, Liu, Li, & Cao, 2020). The heterogeneity of macrophytes with distinct structures can affect periphyton (Hao et al., 2017; Santos, Ferragut, & Bicudo, 2013) and therefore food availability of the invertebrate community (Mason & Underwood, 2010; Thomaz, Dibble, Evangelista, Higuti, & Bini, 2008). On the other hand, the relationship

between epiphytic algae, phytoplankton and snails with macrophytes are affected by history. Snails consumed more biomass of native than exotic plants when tested across 20 native and seven exotic species found growing in Liangzi Lake (Xiong, Yu, Wang, Liu, & Wang, 2008). The snail and algae have generally adapted to the defense methods of native plants in the long co-evolution, while they are lack of the defense strategy of exotic plants (Keane & Crawley, 2002; Xiong et al., 2008).

Phytoplankton and epiphytic algae play significant roles in the functioning of shallow ecosystems, contributing to material circulation, energy flow and the maintenance of food webs (Sánchez, Pizarro, Tell, & Izaguirre, 2010; Sand-Jensen & Borum, 1991; Song, Wang, & Gao, 2017; Vadeboncoeur & Steinman, 2002). Epiphytic algae and phytoplankton are considered the key factors in the transformation between clear and turbid state of shallow ecosystem (Phillips, Willby, & Moss, 2016; Qin et al., 2013). In the turbid state, the establishment and growth of submerged macrophytes may be restricted due to light attenuation induced by high phytoplankton and epiphytic algae biomass (Arthaud et al., 2012; Hidding, Bakker, Hootsmans, & Hilt, 2016). In contrast, in the clear-water state, a high grazing pressure from predators reduces the biomass of phytoplankton and epiphytic algae, which then increases light availability and promotes macrophyte growth (Hilt, 2015; Sánchez et al., 2010).

Freshwater snails filter phytoplankton in the water and scrape organic detritus and periphyton, and sometimes also feed on macrophytes (Y. Cao et al., 2014; Kuan Yi Li, Liu, Hu, & Yang, 2009; Yang et al., 2020). Snails can release nutrients in the water in the process of metabolism (Kuan Yi Li et al., 2009; Parr, Vaughn, & Gido, 2019), which maybe affect the growth of macrophytes and algae. The snail-algae interactions may thus be of great importance for submerged macrophytes, grazing

on epiphytic algae and phytoplankton increases the growth rates of macrophytes, potentially by reducing competition for light and/or nutrients (Brönmark, 1989; Yang et al., 2020). The above phenomenon is called snail-macrophyte mutualistic relationship (Carpenter & Lodge, 1986; K. Li, Wen, Yang, Li, & Zhengwen, 2007). Macrophyte, however, also be grazed by snails that may impose a significant impact on macrophyte growth (Elger & Lemoine, 2005; Kuan Yi Li et al., 2009; Xiong et al., 2008). Such as, *Radix swinhoei* belong to Lymnaeidae, which not only scrape organic detritus and periphyton, but also feed on macrophytes (K. Y. Li, Liu, & Hu, 2006). Therefore, the relationship between snails and macrophytes is still controversial. On the other hand, snail exhibit complex and flexible behaviors when coexisting with other snails (Lombardo & Cooke, 2004). The food sources of freshwater snail are overlap maybe lead to competition (Holomuzki & Hemphill, 1996), changes in resource utilization by coexisting snail species may impact the whole food web and community assembling (Estebenet, Cazzaniga, & Pizani, 2002). Yet, the studies of interspecific interactions among freshwater snails are uncommon.

However, ecological mechanisms by the snail communities affect macrophytes growth, phytoplankton biomass, epiphytic algal community, and nutrient cycling and transformation are unclear. We hypothesized that snail community grazing both epiphytic algae and phytoplankton indirectly improve the growth of submerged macrophytes. We further hypothesized that the food resource composition determines the structure and composition of snail communities. In order to test our hypotheses, we conducted an outdoor mesocosm experiment to elucidate the effects of snail communities on aquatic ecosystem.

2 Material and Methods

2.1. Experimental design

An outdoor mesocosm experiment was conducted from at National Field Station of Freshwater Ecosystem of Liangzi Lake (Hereinafter referred to as Liangzi Lake Station), Hubei Province, China. Thirty-six glass fiber reinforced polymer (GFRP) aquariums (inner diameter: 40 cm, height: 70 cm) were placed on a cement platform (50m long, 20m wide). The sediment used in our experiment was collected from Liangzi Lake. To ensure homogeneity and remove benthic animals (especially snails) before the experiment began, the sediment was air-dried under natural conditions, ground, sieved (0.6 mm mesh size) and mixed before being added to the aquarium. To each aquarium, we added 10 cm depth of above sediment (Nitrogen content 0.56 ± 0.05 $mg \cdot g^{-1}$, means±SD; Phosphorus content 1.63 ± 0.02 $mg \cdot g^{-1}$, means±SD; Organic matter content 0.068 ± 0.003 $mg \cdot g^{-1}$, means±SD). We added 70 L groundwater (TN,0.52 $mg \cdot L^{-1}$ and TP, 0.03$mg \cdot L^{-1}$), subsequently.

H. verticillate and *V. natans* was the dominant species in Liangzi Lake (Wang, Han, Yu, Fan, & Liu, 2019; Xu, Yang, Huang, Li, & Yu, 2018), and *E. nuttallii* belong to the invasion species in China (Xiong et al., 2008). On August 21 2017, 72 specimens of the submerged macrophyte *H. verticillate*, *V. natans* and *E. nuttallii* were collected from a homogeneous population in the nursery ponds of the Liangzi Lake Station, respectively. Each macrophyte species had similar biomass and length (*H. verticillate*: 0.53±0.12g and 20±2cm, mean±SD; *V. natans*: 1.08±0.99g and 15±2cm, mean±SD; *E. nuttallii*: 0.41±0.09g and 18±2cm, mean±SD). All plants were carefully washed to remove snail eggs and periphyton, and planted 8 specimens of each macrophyte species to each aquarium.

A large number of vigorous and sexually mature *Radix swinhoei*, *Hippeutis cantori*, *Bellamya aeruginosa* and *Parafossarulus striatulus* were collected from macrophyte profile in the nursery ponds of Liangzi Lake Station. The snails were kept without food for 24 h before being added to the aquarium. Subsequently, four snail species were selected 360 individuals with the homogeneous size and age, respectively. *R. swinhoei* and *H. cantori* are hermaphrodite and allogeneic fertilization； *B. aeruginosa* and *P. striatulus* are dioecism (Kuan Yi Li et al., 2009). So, the rate of female and male is 1 to 1 that we selected to *B. aeruginosa* and *P. striatulus* in this study. Among them, the fresh mass of *R. swinhoei* was 0.38±0.04 g/ind., *H. cantori* was 0.04±0.01 g·ind.$^{-1}$, *B. aeruginosa* was 2.33±0.15 g·ind.$^{-1}$, and *P. striatulus* was 0.16±0.01 g·ind.$^{-1}$. After the submerged plants grew over one month (on September 21), 80 individuals (20 individuals of each snail species) were added to each aquarium which was covered by a nylon net (1.0 mm mesh size) to prevent escape of snails. The aquariums were regularly topped up to the initial level with groundwater during the experiment.

A two-way factorials experiment was carried out in three species submerged macrophytes (*H. verticillate*, *V. natans* or *E. nuttallii*) and two grazing treatments (snails present or absent), with 6 replicates of each treatment, resulting in a total of 36 aquariums. The experiment ended on December 21, 2017.

2.2. Sample analyses

2.2.1. Water physical and chemical characteristics

In each aquarium, water temperature (T), dissolved oxygen (DO), conductivity (Cond) and pH of water samples were measured with a portable water quality monitor (PROPLUS, YSI, United States), and chlorophyll a (Chl-a) was measured with a handheld probe of chlorophyll fluorometer (HYDROLAB DS5, HACH,

United States) in the field tests. We collected 1 L water samples with depth-integrated (under water 30cm) for chemical analysis from each aquarium, and stored on ice. Then, total nitrogen (TN), total phosphorus (TP) and ammonia nitrogen (NH_3-N) were analyzed by flow injection analyzer (QC8500, LACHAT, USA). Chemical oxygen demand (COD) was analyzed with a digestion solution for each corresponding parameter and landscape photometry (DR900, HACH, USA).

2.2.2. Epiphytic algae

50 leaves of *H. verticillata*, 50 leaves of *E. nuttallii* and 5 leaves of *V. natans* were carefully selected to ensure uniformity in growth state and size before putting each into wide-mouth plastic bottle with 200ml of pure water in respective pot. Periphyton were removed by banister brush in water (Foerster & Jr, 1965) and preserved in a well labeled plastic container, with 2ml Lugol's solution to fix the periphyton sample. The area of selected leaves was measured by area meter (LI-3100C, LI-COR, USA). The species and quantity of epiphytic algae were counted by microscope, using the blood count plate method (Effiong & Inyang, 2015; Hu & Wei, 2006; Qian, Liu, & Chen, 2015). The richness (S) of each sample was the species quantity of the sample. The abundance (N, cells) of each sample was sum of all individual quantity and calculated as the follow formulation:

$$N = \frac{total\ leaf\ number}{seleted\ leaf\ number} \times \sum_{i=1}^{S} n_i$$

Where, n_i was the quantity of i species; S was the number of species.

2.2.3. Macrophyte

The macrophyte samples were carefully washed with distilled water at least three times. Then, the leaf number of each sample were counted (including the

selected leaf for area measuring and algae collection). After that, all samples were dried to a constant weight in a drying oven at 60°C. The dry weight of biomass of the submerged macrophytes was measured using electronic scale.

2.2.4. Snail

All snail species (adults and offspring) were collected from the aquarium and the number of individuals and their fresh mass was determined. Before weighing, the snails were drained on absorbent paper for 5 min, then gently blotted until surface dry to ensure consistency of samples.

2.3. Data analyses

Environmental factors (i.e., T, DO, Cond, pH, TN, TP, NH_3-N and COD), phytoplankton biomass (Chl-a concentrations), macrophyte biomass and epiphytic algae numeral traits (richness and abundance) were statistically tested for the effect of macrophyte and grazing treatment and their interaction were compared using the analysis of Two-way ANOVA by *post hoc* LSD tests for multiple comparisons.

The relative growth rate (RGR) of Macrophytes and snails were calculated by the equation: RGR ($mg \cdot g^{-1} \cdot d^{-1}$) = 1000ln ($W_f/W_i$)/days, where W_f (g) and W_i (g) were the average final and initial fresh mass of stock plants in each tank, respectively (Gu et al., 2018).

The data describing of snail characteristics (i.e., number and biomass, on the overall level) from macrophyte were compered using One-way ANOVA by *post hoc* LSD tests for multiple comparisons. The Two-way ANOVA was used compared macrophyte and snail species effect on snail characteristics (i.e., number and biomass, on species level), and *post hoc* LSD tests were conducted for multiple comparisons.

To determine the relative importance of direct vs. indirect effects of snail driving macrophyte, we built a structural equation model (SEM) including snail biomass, epiphytic algae biomass (abundance), and phytoplankton biomass (Chl-a) with macrophyte biomass (Oberski, Grün, Pebesma, & Zeileis, 2014). By performing a principal component analysis (PCA), the nutrient factors (i.e., TN, TP, NH_3-N and COD) were reduced to the first principal components (proportion variance of PC1 = 0.97) as explanatory variables reflecting Nutrient. Consequently, we also quantified and visualized changes in composition of snail to the biotic factors (i.e., macrophyte biomass, epiphytic algae abundance and phytoplankton Chl-a content) and abiotic factors (i.e., water temperature, dissolved oxygen and Nutrient) manipulations with redundancy analysis (RDA; using species-level biomass, Hellinger distance).

To ensure that the data conform to a normal distribution or homogeneity of variance, some parameters were log10-transformed before performing ANOVA, SEM, PCA and RDA. Statistics were performed using R version 3.6.3 with the packages of agricolae (Mendiburu, 2009), vegan (Jari Oksanen et.al., 2019) lavaan (Oberski, 2014) and the significance level was set to $P < 0.05$.

3 Results

3.1 Variations of water environmental factors

During the experiment, the concentrations of DO, Cond, Turb, TN, TP, NH_3-N and COD were notably affected by both submerged macrophyte species and snail presence ($P < 0.05$, Table1). There were significant interactions between macrophyte species and snail presence observed for DO and Cond ($P < 0.05$, Table

1), but not observed for Turb, TN, TP, NH_3-N and COD ($P > 0.05$, Table 1). The presence of snails led to significantly lower concentrations of nutrients (i.e., TN, TP, NH_3-N and COD) in three species macrophyte scenarios, consistently ($P < 0.001$, Table 2). The concentrations of nutrients (i.e., TN, TP, NH_3-N and COD) in the scenarios of *H. verticillate* were lowest both in snail present and absent (Table 2). Water temperature was not affected by submerged macrophyte species or snail presence (Table 1, $P = 1.000$). pH was only affected by submerged macrophyte species (Table 1, $P = 0.006$).

Table 1. Effect of macrophyte species and snail grazing on the water environmental factors during the experiment using Two-way ANOVA analysis (values in bold are below significance level 0.05).

		Macrophyte	Snail	Macrophyte × Snail
T	*Df*	2	1	2
	F	0.00	0.00	0.00
	P	1.000	1.000	1.000
Do	*Df*	2	1	2
	F	287.89	138.46	4.53
	P	**<0.001**	**<0.001**	**0.019**
Cond	*Df*	2	1	2
	F	366.75	8.33	4.08
	P	**<0.001**	**0.007**	**0.027**
pH	*Df*	2	1	2
	F	6.15	1.63	0.01
	P	**0.006**	0.211	0.99
Turb	*Df*	2	1	2
	F	35.06	18.99	2.6
	P	**<0.001**	**<0.001**	0.09
TN	*Df*	2	1	2
	F	51.3	46.93	0.73
	P	**<0.001**	**<0.001**	0.496
TP	*Df*	2	1	2
	F	71.59	30.1	0.34
	P	**<0.001**	**<0.001**	0.715
NH_3-N	*Df*	2	1	2
	F	27.65	30.12	0.87
	P	**<0.001**	**<0.001**	0.43
COD	*Df*	2	1	2
	F	21.19	14.56	0.06
	P	**<0.001**	**<0.001**	0.945

Table 2. Comparison of environmental factors in the different treatment scenarios of macrophyte and snail grazing during the experiment, with water temperature (T), dissolved oxygen (DO), turbidity, total nitrogen (TN), total phosphorus (TP), ammonia nitrogen (NH_3-N) and chemical oxygen demand (COD). Values represent mean ± SD, means with the different letters are significantly different at $P < 0.05$ (LSD test).

	Snail-absent			Snail-present		
	E. nattalii	*V. natans*	*H. verticillata*	*E. nattalii*	*V. natans*	*H. verticillata*
T (°C)	16.2±0.06a	16.2±0.063a	16.2±0.06a	16.2±0.06a	16.2±0.06a	16.2±0.06a
DO ($mg \cdot L^{-1}$)	8.88±0.01d	8.94±0.02c	9.02±0.01b	8.92±0.01c	9.01±0.02b	9.11±0.02a

Conductivity (μS·cm^{-1})	110.6±0.1a	110.2±0.1b	109.5±0.2cd	110.6±0.1a	110.2±0.1b	109.2±0.1d
pH	7.74±0.01a	7.74±0.11a	7.66±0.02a	7.77±0.06a	7.77±0.06a	7.68±0.08a
Turbidity (NTU)	6.62±0.11ab	6.71±0.12a	5.65±0.71c	6.14±0.61bc	6.32±0.07ab	4.46±0.67d
TN (mg·L^{-1})	0.38±0.007a	0.37±0.014a	0.34±0.008c	0.36±0.011b	0.35±0.008bc	0.31±0.012d
TP (mg·L^{-1})	0.018±0.002a	0.017±0.001b	0.014±0.001c	0.017±0.001b	0.015±0.001c	0.011±0.001d
NH_3-N (mg·L^{-1})	0.011±0.001a	0.011±0.001a	0.009±0.001c	0.01±0.001b	0.009±0.001bc	0.007±0.001d
COD (mg·L^{-1})	6.5±0.84a	6.2±0.75ab	4.8±0.41d	5.7±0.82bc	5.3±0.52cd	3.8±0.75e

3.2 Macrophyte

The biomass and relative growth rate of three species macrophytes were marked affected by their species and snail presence (Table 3, $P < 0.05$)，but there were nonsignificant interactions between macrophytes species and snails. Snails significantly increased the biomass (dry mass) and relative growth rate of the *H. verticillate*, *V. natans* and *E. nuttallii*, (Figure 1). The *H. verticillate* were with the largest biomass and relative growth rate among the three submerged macrophytes in the scenario of snail presence (Figure 1).

Table 3. Effect of snail grazing on the three submerged macrophytes biomass during the experiment using Two-way ANOVA analysis (values in bold are below significance level 0.05).

	Biomass			RGR		
	Df	*F*	*P*	*Df*	*F*	*P*
Macrophyte	2	698.71	< **0.001**	2	8.65	**0.001**
Snail	1	34.64	<**0.001**	1	39.29	< **0.001**
Macrophyte × Snail	2	2.49	0.10	2	0.29	0.75

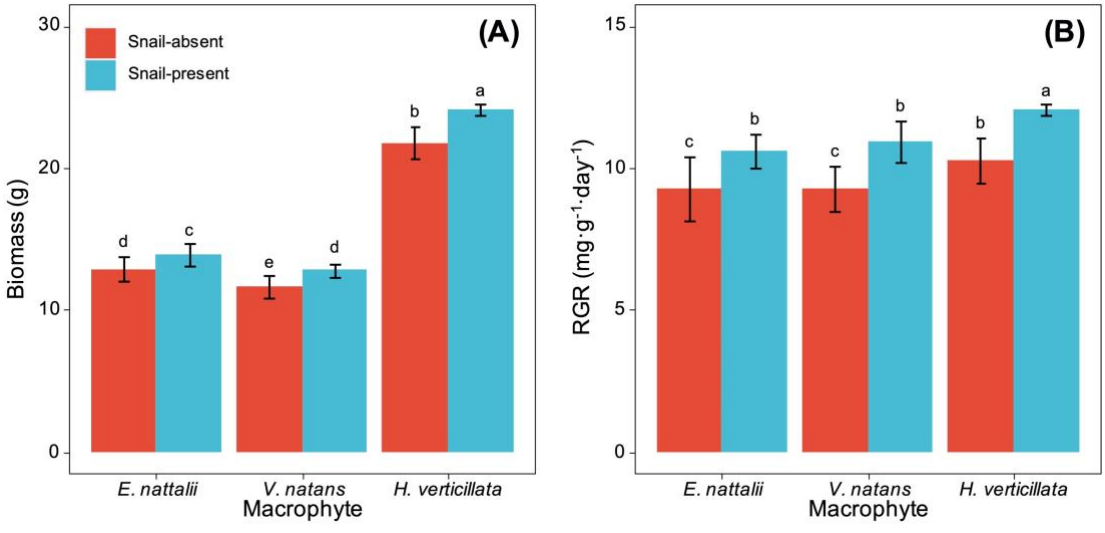

Figure 1. Comparison of three macrophytes biomass and relative growth rate (RGR) in the different treatment scenarios of snail grazing during the experiment, with *E. nuttallii*, *H. verticillata* and *V. natans*. Values represent mean ± SD, means with the different letters are significantly different at $P < 0.05$ (LSD test).

3.3 Snail

The total biomass (fresh mass), number (individual) and relative growth rate of snail communities were marked affected by macrophytes species (Table 4, $P < 0.001$). The snail total biomass, number and relative growth rate was largest in the scenario of *H. verticillata* during the experiment (Figure 2 A - C).

During the experiment, the biomass and number of four species snails (i.e., *B. aeruginosa*, *H. cantori*, *P. striatulus* and *R. swinhoei*) were notably affected by macrophyte and snail species (Table 5, $P < 0.001$). Significant interactions between macrophyte and snail species were observed for four species snails (Table 5, $P < 0.001$). *R. swinhoei* and *B. aeruginosa* was with the maximum number and biomass in all scenarios, respectively, and the maximum value were both in the scenario of *H. verticillata* (Figure 2 D & E).

Table 4. Effect of macrophyte on snail number, biomass and relative growth rate (RGR) during the experiment using one-way ANOVA analysis (values in bold are below significance level 0.05).

	Biomass		Number		RGR	
	$F_{(2,15)}$	*P*	$F_{(2,15)}$	*P*	$F_{(2,15)}$	*P*
Macrophyte	109.4	**<0.0001**	293.4	**<0.001**	103.1	**<0.0001**

Table 5. Effects of macrophytes on number and biomass of four snail species during the experiment using Two-way ANOVA analysis (values in bold are below significance level 0.05).

	Biomass			Number		
	Df	*F*	*P*	*Df*	*F*	*P*
Macrophyte	2	132.92	**< 0.001**	2	172.22	**< 0.001**
Species	3	8258.96	**<0.001**	3	2631.18	**<0.001**
Macrophyte × Species	6	15.47	**<0.001**	6	19.69	**<0.001**

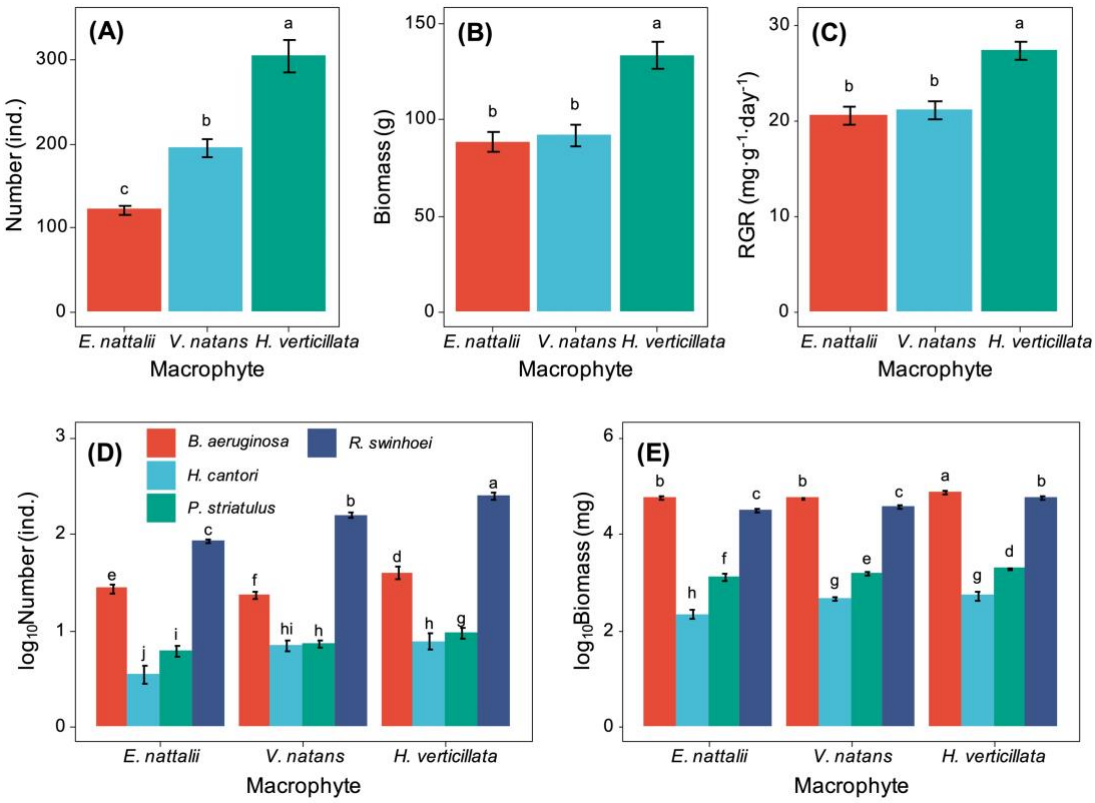

Figure 2. Comparison of total snail number **(A)**, total snail biomass **(B),** total snail relative growth rate **(C)** and four speciessnail's (i.e., *B. aeruginosa*, *H. cantori*, *P. striatulus* and *R. swinhoei*) number **(D)** and biomass **(E)** in the different treatment scenarios of macrophyte during the experiment. Values represent mean ± SD, means with the different letters are significantly different at $P < 0.05$ (LSD test).

3.4 Phytoplankton and epiphytic algae

Phytoplankton biomass was usually replaced by chlorophyll a of water. The Chl-a concentration was marked affected by submerged macrophyte species and snail presence (Table 5, $P < 0.001$). Significant interactions between macrophyte species and snail presence were observed for Chl-a concentrations (Table 5, $P = 0.001$). Snail grazing decreased the Chl-a concentrations significantly, and presence of snails led to significantly lower Chl-a concentrations in three species macrophyte scenarios, consistently (Figure 3 A).

Snails had significant decreased on the richness and abundance of epiphytic algae (Table 5, $P < 0.001$; Figure 3 B & C), and the species of macrophytes marked

effects on the richness and abundance of epiphytic algae (Table 5, $P < 0.001$). Macrophyte species and snail treatments made significant interaction effects on the epiphytic algal richness and abundance (Table 5, $P < 0.001$). The epiphytic algal richness in the scenario of *H. verticillate* were significantly larger than the scenario of *E. nuttallii* and *V. natans* both in snail present and snail absent (Figure 3 B). The epiphytic algal abundance in the scenario of *V. natans* were significantly lower than the scenario of *E. nuttallii* and *H. verticillate* both in snail present and snail absent (Figure 3 C). A total of 35 epiphytic algae species belonging to 6 phyla were identified on 3 submerged macrophyte in 36 aquariums. Eleven genera of diatoms, 17 genera of green algae, 4 genera of blue green algae, 1 genus of cryptomonad, euglenoid and dinoflagellate were identified (supplementary Table S1). Diatoms and green algae accounted for a mainly proportion in abundance of epiphytic algae (Figure 3 D). With the snail presented, the abundance of diatoms and green were on the decreased trend (Figure 3 D).

Table 6. Effect of macrophyte and snail grazing on chlorophyll a of water, epiphytic algal richness and abundance during the experiment using Two-way ANOVA analysis (values in bold are below significance level 0.05).

		Chl-a		Abundance		Richness	
	Df	*F*	*P*	*F*	*P*	*F*	*P*
Macrophyte	2	69.47	**<0.001**	441.1	**< 0.001**	110.53	**< 0.001**
Snail	1	150.28	**<0.001**	775.82	**<0.001**	553.47	**< 0.001**
Macrophyte × Snail	2	9.56	**0.001**	11.41	**<0.001**	20.18	**<0.001**

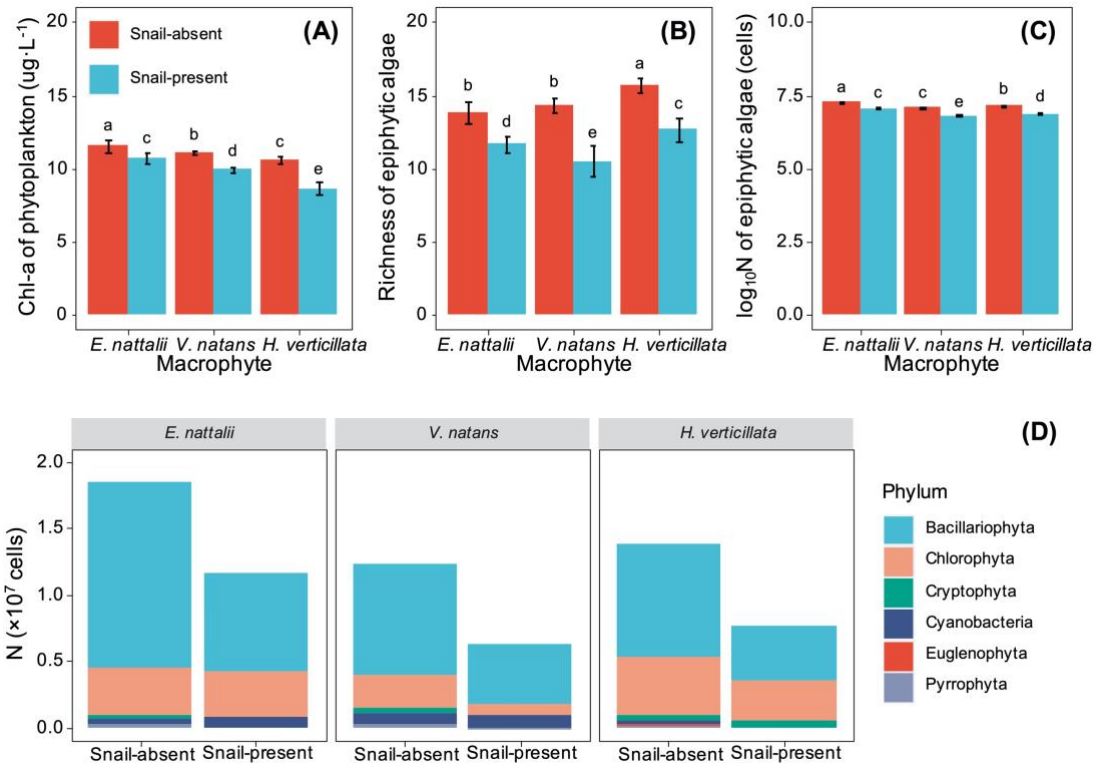

Figure 3. Comparison of water chlorophyll a concentration **(A)**, epiphytic algal richness **(B)**, epiphytic algal abundance **(C)** and 6 phyla abundance of epiphytic algae **(D)** in the different treatment scenarios of macrophyte and snail grazing during the experiment. Values represent mean ± SD, means with the different letters are significantly different at $P < 0.05$ (LSD test).

3.5 The relationship of snail-macrophyte-epiphytic algae

The snails (biomass) had a significant negative effect on epiphytic algae (abundance, $C = -0.43$, $P < 0.001$) and phytoplankton (Chl-a, $C = -0.48$, $P < 0.001$; Figure 4), and had a non-significant positive effect on the macrophyte (biomass, $C = 0.04$, $P = 0.06$; Figure 4). Epiphytic algae ($C = -0.20$, $P = 0.006$) and phytoplankton ($C = -0.45$, $P < 0.001$) both had significant negative effect on the macrophyte (Figure 7). Phytoplankton had a significant positive effect on the epiphytic algae (biomass, $C = 0.76$, $P < 0.001$; Figure 4). The model shows that Snail effects the macrophyte by reducing epiphytic algae and phytoplankton biomass to improve macrophytes (Figure 4).

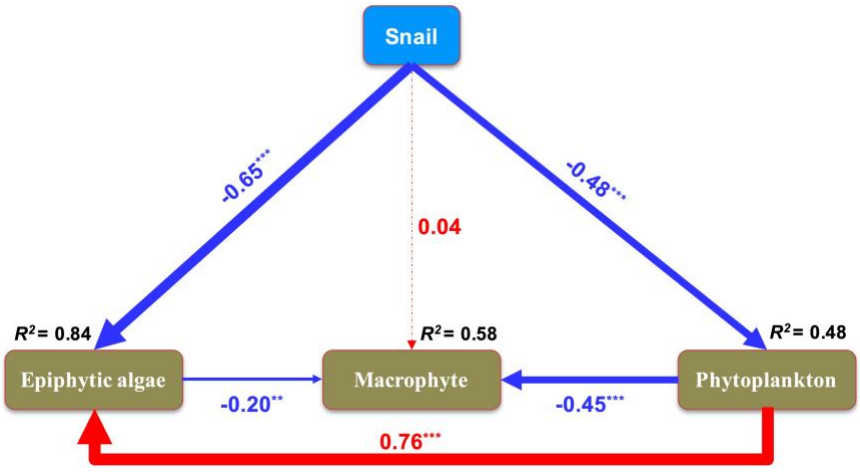

Figure 4. A structural equation model of the relationship between snail, macrophyte, epiphytic algae and phytoplankton. Red and blue arrows represent significant positive and negative pathways, respectively. Arrow width is proportional to the strength of the relationship, and solid and dotted lines represent significant and non-significant pathways, respectively. Numbers indicate the standard path coefficients (*C*). χ^2 = 45.80, *P* = 0.66; RMSEA = 0.07, AIC = 37.5. Significance levels are indicated by asterisks: *** *P* < 0.001, ** *P* < 0.01, * *P* < 0.05.

Two main axes of RDA indicate a significant relationship between environmental variables and 4 species snail biomasses (explaining 75.84% of the total variance, *P* = 0.001; Figure 8A). Snail community structure was significantly affected by DO (R^2 = 0.29, *P* < 0.001), nutrient (R^2 = 0.25, *P* < 0.001), epiphytic algae abundance (R^2 = 0.27, *P* < 0.001), phytoplankton biomass (R^2 = 0.26, *P* = 0.002) and macrophyte biomass (R^2 = 0.25, *P* = 0.002; Figure 5 B). The biomass of *B. aeruginosa* was significant positive correlated with Nutrients (*R* = 0.76, *P* < 0.001), epiphytic algae abundance (*R* = 0.75, *P* < 0.001) and Chl-a (*R* = 0.80, *P* < 0.001) and significant negative with macrophytes biomass (*R* = -0.67, *P* = 0.002; Figure 5 A & C). The biomass of *R. swinhoei* was significant positive correlated with the macrophyte biomass (*R* = 0.69, *P* = 0.001) and negative with nutrients (*R* = -0.78, *P* < 0.001), epiphytic algae abundance (*R* = -0.74, *P* < 0.001) and Chl-a (*R* = -0.81, *P* < 0.001; Figure 5 A & C). The biomass of *H. cantori* was significant negative correlated with epiphytic algae abundance (*R* = -0.66, *P* = 0.003; Figure 5

A & C). There was no significant correlation between *P. striatulus* and all environmental factors ($P > 0.05$, Figure 5 A & C).

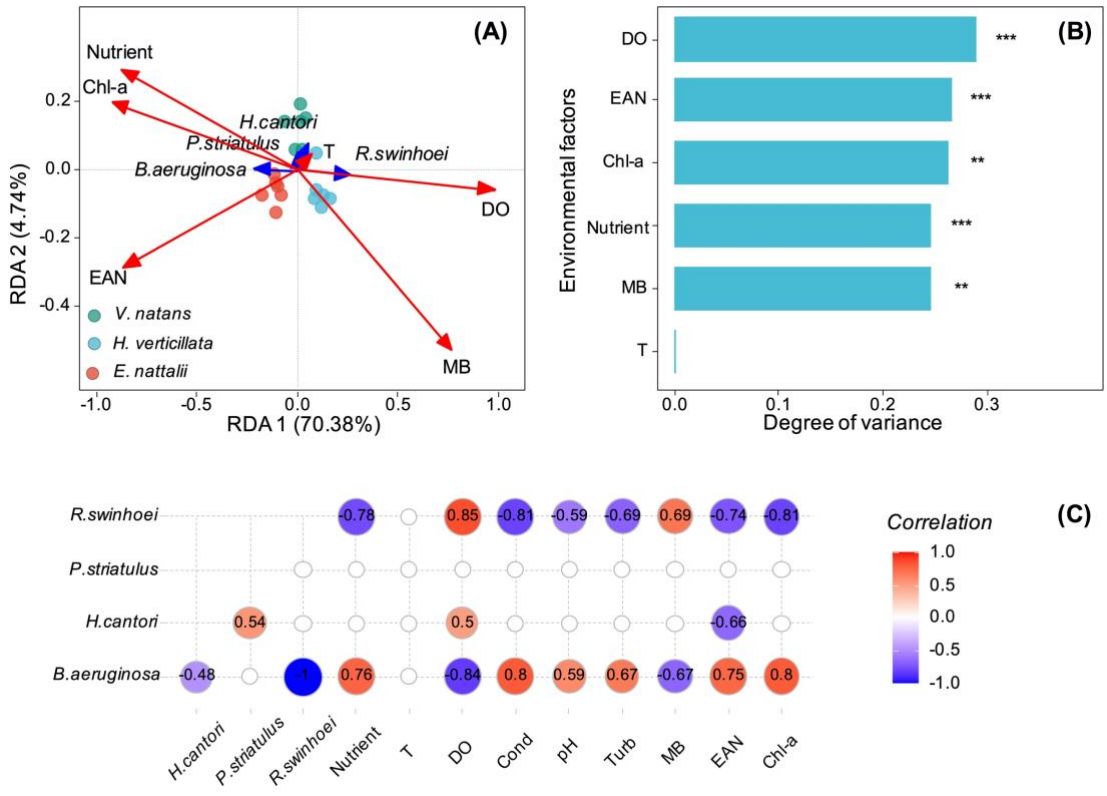

Figure 5. Relationships among snail's species and environment factors based on RDA. Figure was based by the data of snail biomass and environment factors (i.e., macrophyte biomass-MB, epiphytic algae abundance-EAN, T, DO, Nutrient and Chl-a). **(A)** shows the RDA plot of the snail species, environmental factors and samples. Environmental variables are represented with red arrows; 4 species snail vectors are represented with blue arrows; samples were represented with a symbol of filled dot. **(B)** shows the effects of the environmental factors on the snail community's structure. Significance levels are indicated by asterisks: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. **(C)** shows the correlation among four snail species and environmental factors. The snail species data is based on the Hellinger-transformation of biomass. The correlation coefficient with *P*-value below 0.05 were shown.

4 Discussion

Snail positively affected the submerged macrophytes growth and development by increasing biomass both in simulation experiments and field investigations were demonstrated (K. Li, Liu, & Gu, 2008; Mormul, Ahlgren, & Bronmark, 2018; Yang

et al., 2020). The snail communities could reduce the phytoplankton and epiphytic algae in a system and thereby enhance the growth of the submerged macrophyte in this study. We found that the presence of snail significantly reduced biomasses of epiphytic algae and phytoplankton (Figure 3). Earlier studies showed that shading by epiphytic algae and phytoplankton might limit the growth of submerged macrophytes (Arthaud et al., 2012; Song et al., 2017; Tóth, 2013) and, hence, grazing by snails should favor macrophyte growth by decreasing the competition for light between epiphytic algae, phytoplankton with submerged macrophytes (Hidding et al., 2016; Yang et al., 2020). When the snail biomass increases, the biomass of epiphytic algae decreased significantly (C = -0.43, P < 0.001), and improved the biomass of submerged biomass (C = -0.29, P < 0.001), as shown by the pathway from snail to macrophyte via epiphytic algae in the SEM (Figure 4). However, the direct effect of snail communities on submerged macrophytes was nonsignificant (C = 0.09, P = 0.06). These results further evidenced the snail communities have indirect positive effects on submerged macrophyte growth by removed epiphytic algae (Mormul et al., 2018).

On the other hand, in the snail-present treatments, the nutrients of water body were significantly lower than which in snail-absent treatments (Table 2). Due to the snail communities eliminated the competition between epiphytic algae and phytoplankton with macrophyte for resources (light and nutrients), as result, a large amount of nutrients in the water column were absorbed for macrophyte growth and reproduction (X. Cao et al., 2018; Kuiper et al., 2017; W. Li et al., 2019). Furthermore, the increasing of macrophyte biomass could inhibit the epiphytic algae and phytoplankton by the enhancing competition and allelopathically (Jones, Moss, Eaton, & Young, 2000; Mohamed & Shehri, 2010). In addition, we also found increasing macrophyte biomass could increase the species richness of epiphytic

algae which might by providing more diverse and heterogeneous habitats for epiphytic algae, or decreasing the intraspecific competition in the epiphytic algal community (Celewicz-Gołdyn & Kuczyńska-Kippen, 2017; Lv et al., 2019; Toporowska et al., 2008).

Macrophytes were important foods and refuges for aquatic animals (Krecker, 1939), and the heterogeneity architecture might affect the species composition and distribution of snail communities (Ferreiro, Feijoó, Giorgi, & Leggieri, 2011; Thomaz et al., 2008). In this experiment, both the number and biomass of snail communities on *H. verticillata* were the largest (Figure 2). The architecture complexity of *H. verticillata* and *E. nuttallii* was greater than *V. natans*. Which suggested that more complex architecture macrophyte (*H. verticillata*) might provide more habitats and spatial niches for snail communities (Mcabendroth, Ramsay, Rundle, & Bilton, 2010). Although, *H verticillata* and *E. nuttallii* belong to Hydrocharitaceae and had similar leaf shapes, furthermore, the structure of *E. nuttallii* was more complex than *V. natans*, while, the number and biomass of snail communities on *E. nuttallii* were less than *H. verticillata* and *V. natans* in this study (Figure 2). It was possible to because of *E. nuttallii* belonging to exotic species (Xie, Yu, Yu, & Liu, 2010; Xiong et al., 2008). Native predators have gradually adapted to the defense methods of native plants in the long co-evolution with native plants, while they were lack of the defense strategy of foreign plants, so they prefer to feed on native plants (Keane & Crawley, 2002; Xiong et al., 2008). Native macrophyte has a long history of co-evolution with native snails which could help snail quickly adapt to habitat with native macrophyte. On the other hand, the richness and abundance of epiphytic algae on *H. verticillata* (native) was significantly greater than which on *E. nuttallii* (exotic), accordingly, *H. verticillata* could provide more source of foods for snails.

The dominate species of snail communities was *B. aeruginosa* (58.95% of biomass on average) or *R. swinhoei* (78.84% of number on average) in biomass or number, respectively (Figure 2). On biomass level, *B. aeruginosa* and *R. swinhoei* contributed 98.09% biomass on average. The biomass of *B. aeruginosa* was significant positive correlated with epiphytic algae and phytoplankton (Figure 6), namely, the epiphytic algae and phytoplankton was the main food source for *B. aeruginosa* (Han et al., 2010; K. Li, Liu, & Gu, 2008; Zhu et al., 2013). The biomass of *R. swinhoei* was significant positive correlated with the macrophyte in this study (Figure 6), which indicate that *R. swinhoei* mainly fed on submerged macrophytes (K. Y. Li et al., 2006; Kuan Yi Li et al., 2009; Yang et al., 2020). Furthermore, in the treatment aquariums, we did observe the major of *R. swinhoei* was on the surface of the submerged macrophytes, which also indicated that the food of *R. swinhoei* might be submerged macrophytes. While, there were previous studies shown that *R. swinhoei* also fed on macrophytes, but the periphytons were the main food source for them (K. Li, Liu, Li, Li, & Wen, 2008). In this study, the correlation between *B. aeruginosa* and *R. swinhoei* was negative (Figure 5 A&C), which indicated that the feeding preference of the two snails had diverged, that was, *B. aeruginosa* preferred to graze epiphytic algae and phytoplankton, while, *R. swinhoei* tended to feed on macrophytes. Competition leaded to the niche differentiation (Hardin, 1960), predators with the same niche and multiple food sources, competition drove them change the grazing preferences to achieve coexistence (Kolsch & Kubiak, 2011; Zaret & Rand, 1971). Consequently, the assembling of snail communities would be toward the direction of highest resource utilization in this study.

5 Conclusion

The snail communities can reduce the biomass of phytoplankton, epiphytic algae and thereby enhance the growth of the submerged macrophytes. The macrophyte with complex architecture supports more snail and epiphytic algae, and snails prefer to feed on native plants. Competition drives snails change the grazing preferences to achieve coexistence, so that led to the assembling of snail communities towards the direction of highest resource utilization.

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