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RESEARCH ARTICLE

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Invasion of water hyacinth and water lettuce inhibits the abundance of epiphytic algae

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Abstract

Aim: The invasion of exotic macrophytes causes native biodiversity loss in aquatic ecosystems of China. However, the influence of invasive free-floating macrophytes on epiphytic algal communities has rarely been reported, especially in comparison with those of native free-floating macrophytes.

Region: Southern China.

Methods: We investigated the interrelationship between epiphytic algal communities on the roots of three free-floating macrophytes [two invasive species (*Eichhornia crassipes* and *Pistia stratiotes*) and one native species (*Hydrocharis dubia*)] and environmental factors in 40 natural freshwater ecosystems throughout southern China. We also tested the relationship between allelochemicals from the macrophytes and epiphytic algae. A mesocosm experiment was conducted to verify the discoveries of the field investigation.

Results: The abundance of epiphytic algae on the invasive macrophytes was lower than that on the native species in the field investigation and mesocosm experiment. Macrophyte traits were the main factor explaining the epiphytic algal abundance in both the field investigation and mesocosm experiment. In linear models, the slopes of epiphytic algal abundance were lower across gradients of native macrophyte biomass and coverage than across gradients of invasive macrophyte biomass and coverage. The allelochemical contents secreted by the invasive macrophytes were significantly higher than those secreted by the native species. The composition of allelochemicals was another factor that drove the decrease in epiphytic algal abundance. Among the allelochemicals, organic acids and alkaloids were abundant.

Main Conclusions: The inhibitory effect of two invasive free-floating macrophytes on epiphytic algae is stronger than that of the native macrophyte *H. dubia*. The main reason for this finding is that the invasive macrophytes have greater biomass and occupied more space, resulting in greater limitations on spatial niches and resources. Moreover, invasive macrophytes release more allelochemicals than native macrophytes, leading to stronger inhibitory effects on epiphytic algae.

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KEYWORDS
allelochemicals, field investigation, freshwater ecosystems, inhibitory effect, mesocosm experiment, resource, spatial niche

1 | INTRODUCTION

Non-native species in invaded aquatic habitats are a global challenge with severe ecological consequences (Vilà et al., 2011). Invasive species increasingly affect aquatic life, ecosystem functioning and productivity, ecological and hydrological processes, and human livelihoods (Fleming & Dibble, 2015). Invasive aquatic plants have caused high levels of local species extinction and outcompete and exclude most native macrophytes and algae for space and resources (Emery-Butcher et al., 2020).

Invasion by free-floating plants is found to be a serious threat to freshwater ecosystems and generates considerable public concern (Wang et al., 2013, 2016). The large, dense mats formed by these species cover lakes and rivers, blocking waterways and interfering with the water transport of agricultural products, tourism activities, water power generation and irrigation of agricultural fields (Adebayo et al., 2011; Shanab et al., 2010; Thamaga & Dube, 2018). These dense mats monopolize light and absorb nutrients from the water column, minimizing the rate of photosynthesis by submerged plants and algae (Coetzee et al., 2011; Fileto-Perez et al., 2015; Khanna et al., 2012; Mengistu et al., 2017; Wang et al., 2012). In addition, low oxygen conditions cause increasing organic detritus to decrease clarity, which inhibits macrophyte and algal growth (Thamaga & Dube, 2018; Wang et al., 2016). Moreover, the novel weapons of non-native plants (for macrophytes, weapons are often manifested through allelopathic chemicals) can result in increased competitive ability and accelerate invasion (Callaway & Aschehoug, 2000). Chromatographic and spectroscopic analyses show that macrophytes release allelochemicals such as fatty acids, steroids, polyphenols and tannins (Shanab et al., 2010; Wu et al., 2015). Free-floating invasive macrophytes can also use their allelopathic substances to gain a competitive advantage over algae or other plants (Pei et al., 2018; Wu et al., 2015).

Epiphytic algae are the key primary producers in aquatic ecosystems (Vadeboncoeur & Steinman, 2002). Epiphytic algae adhere to and inhabit almost all macrophyte organs in water, and there are competitive and symbiotic relationships between these algae and macrophytes (Cattaneo et al., 1998; Li et al., 2017; Santos et al., 2013). Epiphytic algae in freshwater systems are influenced by a number of physical (Tóth & Palmer, 2016; Vadeboncoeur et al., 2003), chemical (Andrew et al., 2001; Trochine et al., 2014) and biological factors (Hao et al., 2017; Jones & Sayer, 2003; Tunca et al., 2014). Macrophytes can strongly influence the spatial and temporal variability in the epiphytic algal community, especially in areas with high macrophyte coverage (Chambers et al., 2008; Santos et al., 2013; Souza et al., 2015). Free-floating macrophytes can directly or indirectly modify the environmental conditions for epiphytic algae. For example, free-floating macrophytes participate in nutrient cycling, changing nutrient, oxygen and light conditions for epiphytic algae (Tesolín & Tell, 1996). Free-floating macrophytes provide surfaces for epiphytic algal development, but they may also decrease epiphytic algal growth through a reduction in light availability due to shading and allelochemical production (Effiong & Inyang, 2015). Therefore, the impacts of free-floating macrophytes on epiphytic algae are complex.

However, the effects of invasive free-floating macrophytes on the epiphytic algal community are rarely reported, especially compared with reports on the effects of native macrophytes. *Eichhornia crassipes* (Mart.) Solms and *Pistia stratiotes* L. are invasive free-floating macrophytes that have invaded China and caused severe harm, particularly in southern China (Qin et al., 2016; Wang et al., 2016). *Hydrocharis dubia* (Bl.) Backer is a native free-floating macrophyte in China (Huang et al., 2019). *Hydrocharis dubia* has a broad distribution and can coexist with *E. crassipes* and *P. stratiotes* in the open waters of southern China (Huang et al., 2019). Therefore, we investigated the interrelationship between the epiphytic algal community, specific water traits and free-floating macrophyte communities in various natural freshwater ecosystems throughout southern China. A mesocosm experiment was conducted to verify the field discoveries. Moreover, we measured the contents of allelochemicals from free-floating macrophytes and analysed the relationship between the allelochemicals and epiphytic algal abundance. We hypothesized that the invasive species had a stronger inhibitory effect than the native species on algae due to higher growth rates and greater allelochemical production.

2 | METHODS

2.1 | Field investigation

From June to September 2016, field surveys were conducted in various natural water ecosystems (40 inland water bodies) in southern China, and a total of 40 samples were collected (Figure 1). After selecting a sampling site, we recorded the habitat information: location (latitude, longitude and altitude) and habitat type.

Since free-floating macrophytes mainly expand their populations by clonal reproduction, *E. crassipes*, *P. stratiotes* and *H. dubia* often form monodominant communities (Yu et al., 2018). To eliminate the influence of other macrophytes in mixed communities on epiphytic algae, we sampled only monodominant communities. Six quadrats (1 × 1 m, quadrats were randomly placed without overlapping) with a monodominant free-floating macrophyte community were investigated at each site, and the coverage of each quadrat was visually estimated (Fang et al., 2009). The coverage of the macrophyte community (MC) at each sampling site

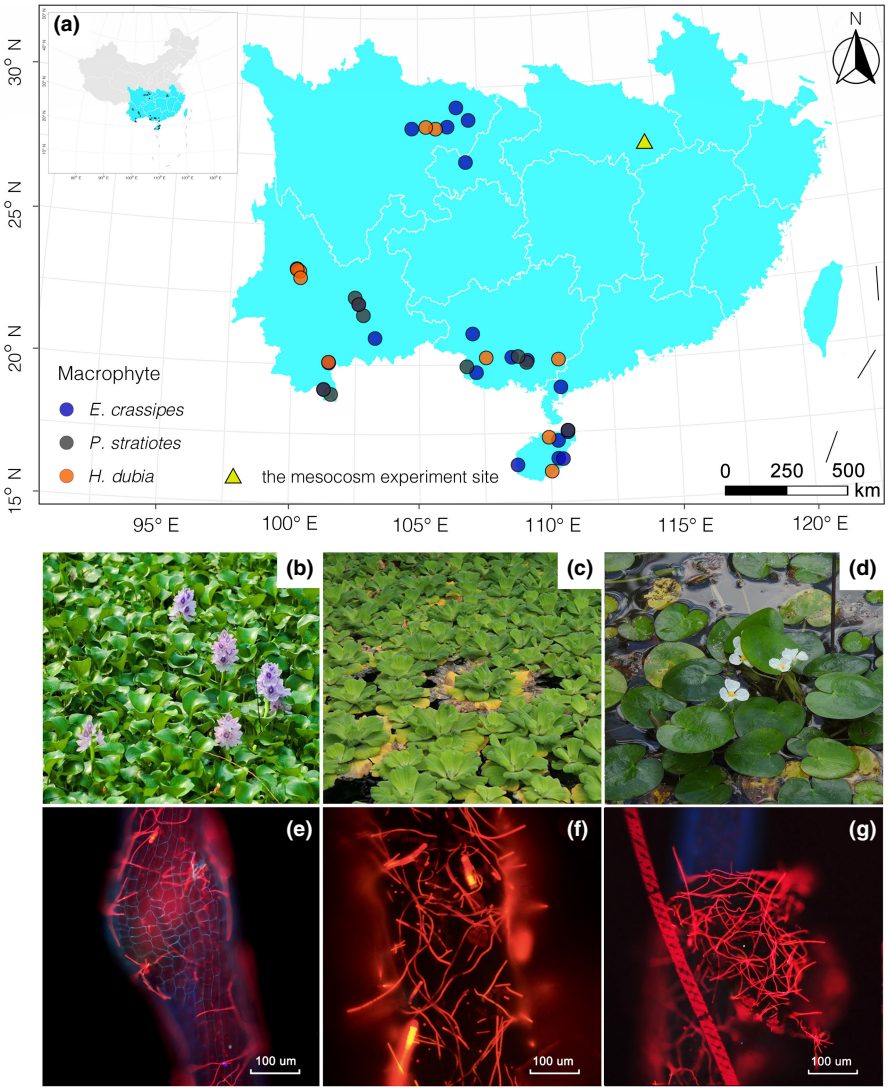


FIGURE 1 Geographical locations of the sampling sites in southern China (a) (n = 40). Photographs of the three free-floating macrophyte communities (b) is *Eichhornia crassipes*, (c) is *Pistia stratiotes* and (d) is *Hydrocharis dubia* included in the field investigation. Microscope observations of epiphytic algae on the roots of the three free-floating macrophytes (e) is *E. crassipes*, (f) is *P. stratiotes* and (g) is *H. dubia* in the mesocosm experiment. Samples were observed under a fluorescence microscope. Algae cells show red or yellow fluorescence; the scale bars indicate 100 μm

was calculated as the mean across the investigated quadrats. The numbers of plants in each quadrat were counted. Twenty plants were randomly selected within each quadrat for the determination of dry weight (plants were dried at 70°C for >48 h; the leaves and roots were dried separately). The biomass of each quadrat was calculated as the dry weight multiplied by the number of plants divided by 20. The biomass of each macrophyte community (MB) was calculated as the mean biomass across the investigated quadrats in each sampling site. The water physical and chemical characteristics, epiphytic algae and macrophyte allelochemicals in each sampling site were sampled and measured; the specific methods for acquiring these measurements are detailed in the *Sample measurement and analysis* section.

2.2 | Mesocosm experiment

An outdoor mesocosm experiment was conducted at the National Field Station of Freshwater Ecosystems of Liangzi Lake (hereafter referred to as the Liangzi Lake Station), Hubei Province, China (Figure 1). Sixty glass fibre-reinforced polymer cuboid aquariums (length = 1 m, width = 0.5 m, height = 0.6 m) were placed on a cement platform (50 m long, 20 m wide). We added 250 L lake water (TN, 0.52 mg L^{-1}; TP, 0.025 mg L^{-1}) to each aquarium. Subsequently, a solution of NH_4NO_3 (ACS reagent, ≥98%, Sigma–Aldrich) and $NH_4H_2PO_4$ (ACS reagent, ≥98%, Sigma–Aldrich) was added to ensure that the initial concentrations of total nitrogen (TN) and total phosphorus (TP) in each aquarium reached 4.0 and 0.25 mg L^{-1} (mean value of 40 field investigation sites), respectively. No more nutrients were added during the experiment, and only pure water was added to maintain a volume of 250 L in each aquarium.

On June 1, 2020, 150 individual plants of *E. crassipes*, *P. stratiotes* and *H. dubia* were collected from homogeneous populations in the nursery ponds of the Liangzi Lake Station. Each species had a similar fresh biomass and height (*E. crassipes*: 51.8 ± 2.56 g and 15.0 ± 0.46 cm (mean ± SD); *P. stratiotes*: 50.9 ± 9.45 g and 13.7 ± 0.33 cm; *H. dubia*: 36.8 ± 4.50 g and 10.8 ± 0.42 cm). All the plants were carefully washed to remove periphyton, and 2, 4, 8 and 16 specimens of each macrophyte species were planted in each aquarium.

A two-way factorial experiment was carried out for the three free-floating macrophyte species (*E. crassipes*, *P. stratiotes* or *H. dubia*) and four density treatments (2, 4, 8 or 16 specimens), with 5 replicates of each treatment, resulting in a total of 60 free-floating macrophyte communities in 60 aquariums. The experiment was conducted on June 1, 2020, and ended on September 1, 2020. Three months was the exact vegetative growth period need for these three species, and we harvested them before they flowered. On September 1, 2020, we harvested the experiment, the water physical and chemical characteristics, epiphytic algal abundances and macrophyte allelochemical concentrations were measured. The specific methods for acquiring these measurements are detailed in the *Sample measurement and analysis* section. To measure the macrophytes community traits in each aquarium (i.e. coverage and biomass), we used the same methods as in the field investigation. In addition, we observed the epiphytic algae on the roots of the three free-floating macrophyte species in situ under a fluorescence microscope (BX53, OLYMPUS).

2.3 | Sample measurement and analysis

We used the same methods of sample measurement and analysis in the field investigation and mesocosm experiment. Ten pieces of roots of each free-floating macrophyte species (i.e. *E. crassipes*, *P. stratiotes* or *H. dubia*) were carefully selected to ensure uniformity in size before placing each into plastic containers with 100 ml of tap water in its respective community. Epiphytic algae were removed in water with a banister brush and preserved in a well-labelled plastic container, and 1 ml Lugol's solution was added to fix the epiphytic algal samples. The epiphytic algal samples were centrifuged at 1789 *g* for 10 min, and the supernatant was discarded. Then, the volume was adjusted to 30 ml and the solution was mixed. The number and species of epiphytic algae were counted using a counting plate at 400× magnification under a microscope (BX53, OLYMPUS). For each sample, 50 microscopic fields of view were examined and counted (Effiong & Inyang, 2015; Hu & Wei, 2006; Qian et al., 2015). Then, the brushed roots were dried at 70°C for >48 h to determine the dry weight. The quantity of epiphytic algae was the individual amount of each species divided by the dry weight of roots at each site. The abundance of each community (*N*) was the sum of all the epiphytic algal species quantities in each sample.

Each root sample was dried, milled and finally sieved with a number 60 mesh to obtain a homogenous particle size. The organic compounds of each sample were obtained by successive extraction from a 0.5 g sample using methanol and a Soxhlet extractor (Fileto-Perez et al., 2015). The methanol extract of each sample was analysed by GC–MS (GCMS-QP 2020NX, SHIMADZU). The GC injector temperature was 220°C. The oven temperature was maintained at 40°C for 3 min, then increased from 40°C to 250°C at 5°C/min, and maintained at 250°C for 2 min. The transfer line temperature was 250°C. Helium was the carrier gas. The carrier gas flow rate was 1 ml/min. The MS source was operated in electron impact mode at 70 eV. The MS was scanned from 40 to 500 m/z. The concentrations of five class allelochemicals (i.e. alkaloids, amines, esters, organic acids and phenols) were the sum of relative peak area (RPA) of each class compounds (Table S3).

Water samples were collected at a depth of 10 cm to measure the physical and chemical parameters in each community. The temperature (*T*), dissolved oxygen (DO), conductivity (Cond) and pH of the water samples were measured with a portable water quality monitor (PROPLUS, YSI). Turbidity (Turb) was measured with a turbidity metre (2100Q, HACH). Ammonia nitrogen (NH_3-N), nitrate nitrogen (NO_3-N), TN, TP and chemical oxygen demand (COD) were analysed with a digestion solution for each corresponding parameter (DR900, HACH) and at each site.

2.4 | Data analysis

The epiphytic algal abundance on the roots of the three free-floating macrophytes (i.e. *E. crassipes*, *P. stratiotes* and *H. dubia*), the macrophyte biomass and coverage of the three free-floating macrophytes, and the RPAs of the total or individual allelochemicals (i.e. alkaloids, amines, esters, organic acids and phenols) from the three free-floating macrophytes in the field investigation and mesocosm experiment were compared using the Kruskal–Wallis test (major parameters did not conform to the normal distribution, or the variances between groups were heterogeneous), followed by the post hoc Fisher's least significant difference test (Périllon et al., 2017).

Partial least squares path models (PLS-PMs) were constructed to test the direct and indirect effects of water properties (T, DO, Cond, pH and Turb), water nutrients (TN, TP, COD, NO_3-N and NH_3-N) macrophyte traits (MB and MC) and allelochemicals (alkaloids, amines, esters, organic acids and phenols) on epiphytic algal abundance (Table S5) (Hu et al., 2021). Linear regressions were used to test the patterns of epiphytic algal abundance along the biomass and coverage gradients of the three macrophytes in the field investigation and mesocosm experiment. Analyses were performed with the "diffslope" function in R using randomization tests of the differences between slopes of regression models (Nekola et al., 1999). The difference between the slopes was calculated and compared with the distribution of the differences between the slopes of the 999 randomized data sets to determine the significance level (Steinitz et al., 2006). Linear regressions with *X* axis and *Y* axis density distributions were used to test the patterns of epiphytic algal abundance along the gradients of the total allelochemical RPAs in the field investigation and mesocosm experiment, and the squared regression coefficients were corrected for multiple tests (Lv et al., 2019).

To make the data conform to a normal distribution, some of the parameters were $\log_{10}(x)$ transformed before performing PLS-PMs and linear regressions. Statistics were performed using R version 3.6.3 (R Development Core Team, 2020) and the packages "agricolae" (Mendiburu, 2020) and "plspm" (Sanchez et al., 2015).

3 | RESULT

3.1 | Comparison of epiphytic algal communities

Macrophyte species markedly affected the abundance of epiphytic algae in both the field investigation ($\chi^2 = 18.9$, $p < .001$; Figure 2) and mesocosm experiment ($\chi^2 = 23.7$, $p < .001$; Figure 2). The epiphytic algal abundance in the presence of the native macrophyte species (*H. dubia*) was significantly greater than that in the presence of the two invasive macrophytes (*E. crassipes* and *P. stratiotes*) in both the field investigation and mesocosm experiments (Figure 2). In the field investigation, the epiphytic algae on *H. dubia* had a mean abundance of 1.02×10^8 cells g^{-1} Dw, which was 4.31 and 1.18 times higher than those on *E. crassipes* and *P. stratiotes*, respectively (Figure 2). In terms of the mesocosm experiment, the epiphytic algae on *H. dubia* had a mean abundance of 1.58×10^8 cells g^{-1} Dw, which was 3.00 and 1.28 times higher than those on *E. crassipes* and *P. stratiotes*, respectively (Figure 2).

A total of 55 epiphytic algal species belonging to 5 phyla (i.e. Bacillariophyta, Chlorophyta, Cryptophyta, Cyanobacteria and Euglenozoa) were identified on the roots of the three free-floating macrophytes (Table S1). Diatoms, green algae and blue–green algae accounted for the largest proportion of species in both the field investigation and mesocosm experiment (Figure 3). The compositions of the epiphytic algal communities were significantly different between the native and invasive macrophytes in both the field investigations and mesocosm experiments (Figure S1). The relative abundance of diatoms on *H. dubia* (81.47% in the field investigation, 49.28% in the mesocosm experiment) was higher than that on *E. crassipes* (64.16% in the field investigation, 32.95% in the mesocosm experiment) and *P. stratiotes* (69.97% in the field investigation, 38.89% in the mesocosm experiment) in both the field investigation and mesocosm experiment (Figure 3). The relative abundance of blue–green algae on *E. crassipes* (30.57% in the field investigation, 54.45% in the mesocosm experiment) and *P. stratiotes* (19.67% in the field investigation, 20.50% in the mesocosm experiment) was higher than that on *H. dubia* (16.45% in the field investigation, 16.36% in the mesocosm experiment) in both the field investigation and mesocosm experiment (Figure 3).

3.2 | Comparison of macrophyte traits and allelochemicals from macrophytes

The coverage of the two invasive macrophytes was greater than that of the native macrophytes in both the field investigation and mesocosm experiment (Figure 4a). In the field investigation, *H. dubia* had a mean coverage of 53.3%, which was 0.68 and 0.81 times that of *E. crassipes* and *P. stratiotes*, respectively (Figure 4a). In the mesocosm experiment, *H. dubia* had a mean coverage of 31.6%, which was 0.63 and 0.77 times greater than that of *E. crassipes* and *P. stratiotes*, respectively (Figure 4a). The biomass of the two invasive macrophytes were greater than that of the native macrophytes in the field investigation, and the mean biomass of *H. dubia* was 51 g, which was 0.35 and 0.53 times greater than that of *E. crassipes* and *P. stratiotes*, respectively (Figure 4b). The biomass of *E. crassipes* and *H. dubia* was significantly greater than that of *P. stratiotes* in the mesocosm experiment (Figure 4b). *Hydrocharis dubia* had a mean biomass of 59.1 g, which was 0.84 and 1.84 times higher than that of *E. crassipes* and *P. stratiotes*, respectively (Figure 4b).

Organic acids, alkaloids, amines, esters and phenols were the main allelochemicals secreted by the three free-floating macrophytes (Table S3). The concentration of total allelochemicals was the sum of five class compounds (i.e. alkaloids, amines, esters, organic acids and phenols). The total allelochemical concentration of the native macrophytes was significantly lower than that of the two invasive macrophytes in both the field investigation and mesocosm experiment (Figure 4c). In the field investigation, *H. dubia* had a mean total allelochemical concentration of 33.78%, which was 0.51 and 0.57 times that of *E. crassipes* and *P. stratiotes*, respectively

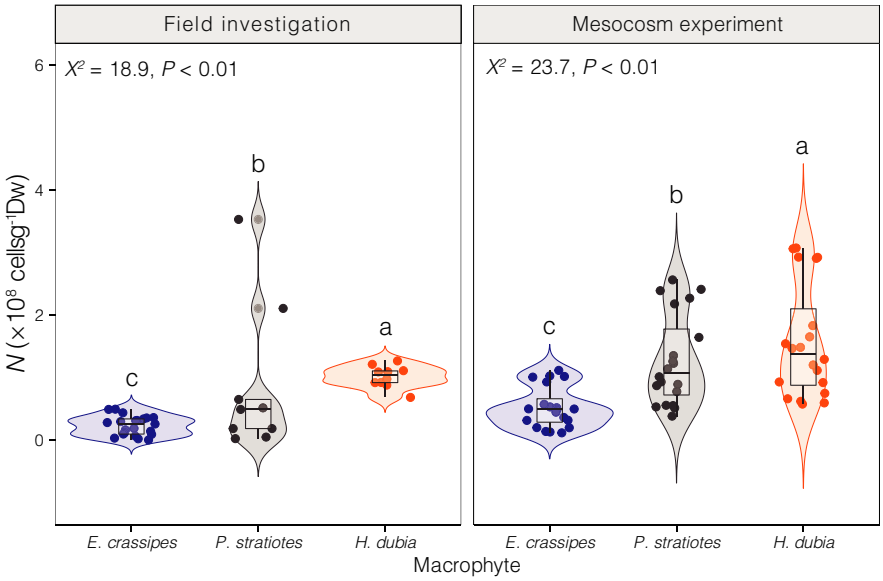


FIGURE 2 Comparison of epiphytic algal abundances on the roots of three free-floating macrophytes (*Eichhornia crassipes*, *Pistia stratiotes* and *Hydrocharis dubia*) in the field investigation ($n = 40$) and mesocosm experiments ($n = 60$). The different letters indicate significant differences at a significance level of $p < .05$

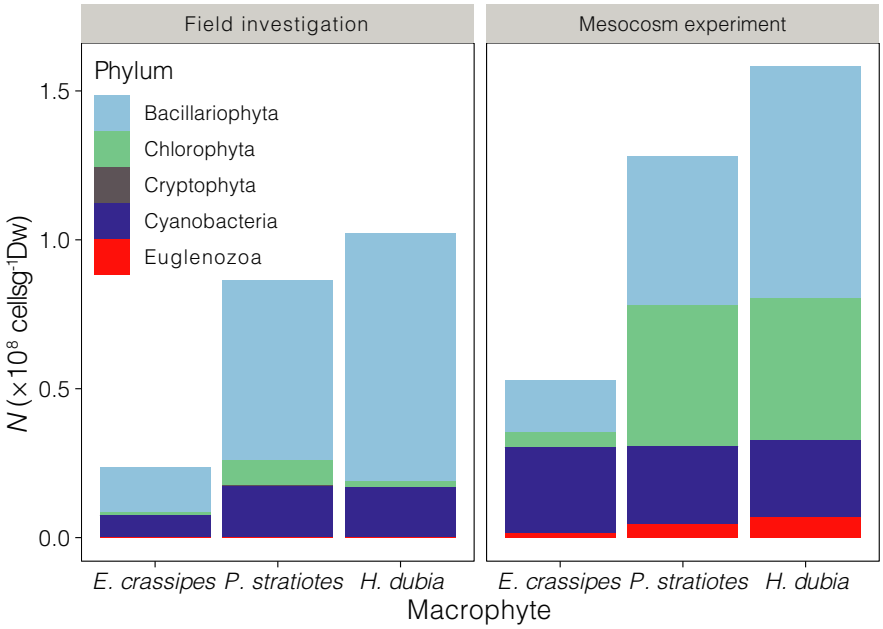


FIGURE 3 Comparison of the division of epiphytic algae on the roots of three free-floating macrophytes (*Eichhornia crassipes*, *Pistia stratiotes* and *Hydrocharis dubia*) in the field investigation and mesocosm experiment. The abundance of each phylum is calculated as the mean of the values obtained in the field investigation ($n = 40$) or mesocosm experiment ($n = 60$)

(Figure 4c). In the mesocosm experiment, *H. dubia* had a mean total allelochemical concentration of 39.85%, which was 0.65 and 0.75 times that of *E. crassipes* and *P. stratiotes*, respectively (Figure 4c). The concentrations of alkaloids, amines, organic acids and phenols from the two invasive macrophytes were significantly greater than those from the native macrophyte in both the field investigation and mesocosm experiment (Figure 4d,e,g,h). Except for *P. stratiotes* in the mesocosm experiment, there were no significant differences in the concentration of esters between the native and invasive macrophytes (Figure 4f).

3.3 | The effects of biotic and abiotic factors on epiphytic algal abundance

Macrophyte traits had a negative effect on epiphytic algal abundance in both the field investigation (path coefficient, $C = -0.75$, $p < .001$; Figure 5a) and mesocosm experiment ($C = -0.60$, $p < .001$; Figure 5b). Macrophyte coverage and biomass had positive effects on macrophyte traits in both the field investigation (Figure 5a) and mesocosm experiment (Figure 5b). Epiphytic algal abundance was negatively affected by allelochemicals in both the field investigation ($C = -0.70$, $p < .001$; Figure 5a) and mesocosm experiment ($C = -0.45$, $p < .001$; Figure 5b). Alkaloids (weights of the outer model, $W = 0.31$), organic acids ($W = 0.31$) and phenols ($W = 0.29$) contributed the most to the allelochemicals observed in the field investigation (Figure 5a). In the mesocosm experiment, the alkaloids ($W = 0.52$) and organic acids ($W = 0.54$) contributed the most to the observed allelochemicals (Figure 5b). Water properties and water nutrients had positive but not significant effects on epiphytic algal abundance (Figure 5a,b).

The abundance of epiphytic algae on the three free-floating macrophytes showed decreasing trends across gradients of macrophyte biomass and coverage in both the field investigation and mesocosm experiment (Figure 6). The linear model slopes of epiphytic algal abundance across the gradient of native macrophyte (i.e. *H. dubia*) coverage were significantly smaller than those across the gradients of coverage for the two invasive macrophytes in both the field investigation and mesocosm experiment (Figure 6c,d). The linear model slopes of epiphytic algal abundance across the gradients of *H. dubia* biomass were significantly smaller than those across the gradients of *E. crassipes* and *P. stratiotes* biomass in the mesocosm experiment (Figure 6a). In the field investigation, the slope of *H. dubia* was similar to those of *E. crassipes* and *P. stratiotes* (Figure 6b). Thus, the results showed that the two invasive macrophytes had more substantial inhibitory effects on epiphytic algal abundance than the native macrophyte, *H. dubia*.

The epiphytic algal abundance showed decreasing trends across gradients of allelochemicals in both the field investigation ($K = -0.016$, $R^2_{adj} = 0.17$, $p = .005$; Figure 7a) and mesocosm experiment ($K = -0.02$, $R^2_{adj} = 0.38$, $p < .001$; Figure 7b). *Hydrocharis dubia* had lower allelochemical concentrations and greater epiphytic algal abundance than the other macrophyte species in both the field investigation and mesocosm experiment (Figure 7).

4 | DISCUSSION

4.1 | Invasive free-floating macrophytes had a stronger inhibitory effect than native macrophytes on epiphytic algae

Previous studies found that the invasion of *E. crassipes* and *P. stratiotes* caused great harm to the local biodiversity of aquatic plants, phytoplankton and aquatic animals (Coetzee et al., 2014; Mengistu et al., 2017; Thamaga & Dube, 2018; Wang et al., 2016). In this study, we found that the abundance of epiphytic algae on the native

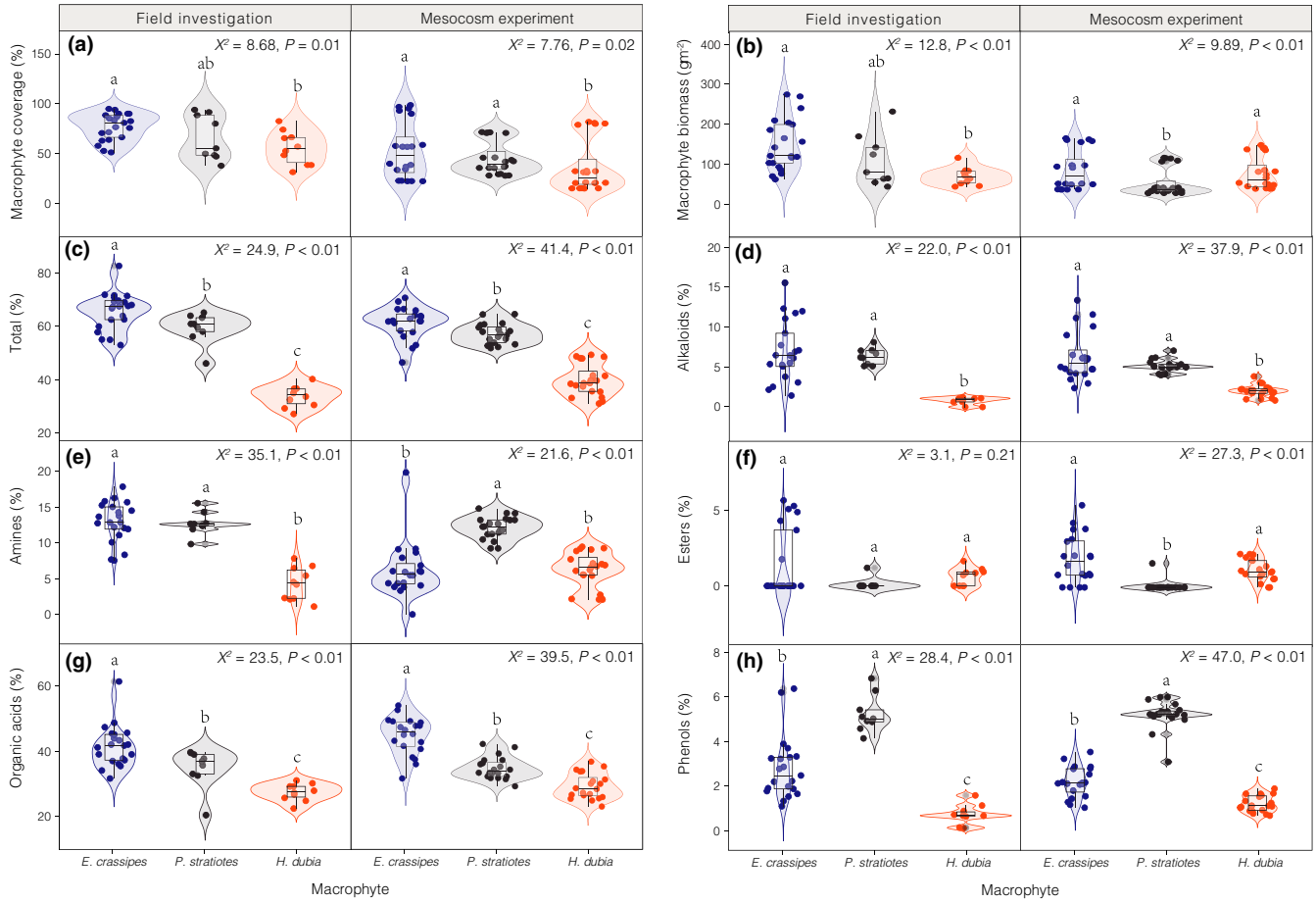


FIGURE 4 Composition of macrophyte traits and allelochemicals extracted from three free-floating macrophytes (*Eichhornia crassipes*, *Pistia stratiotes* and *Hydrocharis dubia*) in the field investigation ($n = 40$) and mesocosm experiment ($n = 60$). (a) Macrophyte coverage, (b) Macrophyte biomass, (c) Total allelochemicals, (d) Alkaloids, (e) Amines, (f) Esters, (g) Organic acids, and (h) Phenols. The different letters indicate significant differences at $p < .05$

macrophyte species (*H. dubia*) was greater than that on the invasive species (*E. crassipes* and *P. stratiotes*) in both the field investigation and mesocosm experiment (Figure 2), which suggested that invasive free-floating macrophytes might have a stronger inhibitory effect than native free-floating macrophytes on epiphytic algae. We also observed this phenomenon under a fluorescence microscope (Figure 1e–g).

The composition of the epiphytic algal communities was significantly different between the native and invasive macrophytes, which was demonstrated by the effects of dominant groups (i.e. diatoms, green algae and blue–green algae; Figure 3). The observation that diatoms dominate the periphyton community on free-floating macrophytes confirms earlier reports (Effiong & Inyang, 2015; Rodriguez et al., 2011). The abundance of diatoms on *H. dubia* was greater than that on the invasive macrophytes (i.e. *E. crassipes* and *P. stratiotes*) in both the field investigation and mesocosm experiment, while blue–green algae were more abundant on the invasive macrophytes than on *H. dubia* (Figure 3). This result suggested that the invasive macrophytes mainly reduced the epiphytic algal abundance by inhibiting diatom growth.

4.2 | Community traits and macrophyte allelochemicals are the main contributors to the inhibitory effect on epiphytic algae

The physical, chemical and biological conditions that can influence the epiphytic algal community have been widely demonstrated (Lv et al., 2019; Vadeboncoeur et al., 2006). In this study, epiphytic algal abundance on free-floating macrophytes was mainly influenced by community traits (biomass and coverage) and allelochemicals, and invasive macrophytes had a more significant inhibitory effect than native macrophytes on epiphytic algae (Figures 5 and 6).

Free-floating macrophytes usually develop dense mats on the surface of the water (Greenfield et al., 2007; Meerhoff et al., 2007). In this study, we observed this phenomenon in both field investigations and a mesocosm experiment, especially in the invasive species communities (Figure 1b–d). These dense mats monopolize light, minimizing the rate of photosynthesis by algae (Coetzee et al., 2011). The macrophyte traits (composed of macrophyte coverage and macrophyte biomass) had a significantly negative effect on epiphytic algal abundance (Figure 5), which suggested

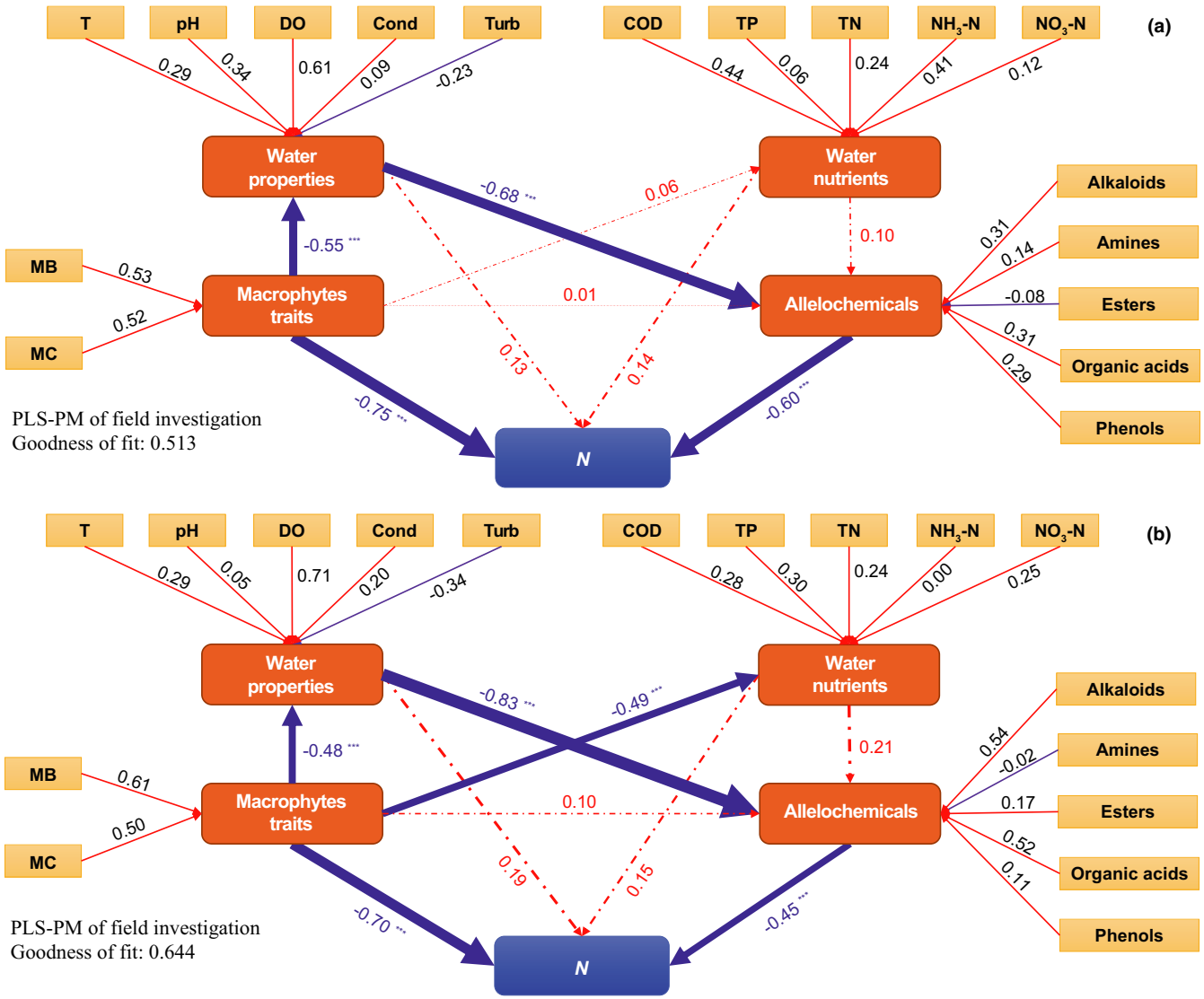


FIGURE 5 Partial least squares path models of water properties, water nutrients, macrophyte traits, allelochemicals and epiphytic algal abundance in the field investigation (a) and mesocosm experiment (b). The graduated arrow widths are proportional to the strength of the path coefficient. The red and blue lines represent positive and negative pathways, and the solid and dotted lines represent significant and nonsignificant correlations, respectively. Significance levels are indicated by asterisks: ***$p < .001$. Reflective latent variables (orange blocks) are indicated by the measured variables (green blocks), with their respective weights shown

that free-floating mats increase shading in the water column, preventing epiphytic algal photosynthesis and thereby reducing epiphytic algal abundance. Moreover, we found that the invasive macrophytes had higher coverage and biomass than the native macrophyte in both the field investigation and mesocosm experiment (Figure 4). Previous studies have found that invasive macrophytes have advantages over native species for occupying empty niches (Khanna et al., 2012), such as space above the water surface. As a result, invasive macrophytes use more light resources, thus inhibiting photosynthesis by epiphytic algae more than native macrophytes.

Free-floating mats also result in reduced DO concentrations by increasing shading in the water column, preventing photosynthesis and oxygen release from primary producers under water (Kara et al., 2010). The path from the macrophyte traits to epiphytic algal abundance via water properties (Figure 5) showed that macrophytes decreased the abundance of epiphytic algae by reducing the levels of water properties (mainly through a decrease in DO). Although the path from water properties to epiphytic algal abundance was not significant in the PLS-PMs, the results of the correlation showed that DO have a significant positive effect on the abundance of epiphytic algae ($r = 0.57$, $p < .001$ in the field investigation; $r = 0.80$, $p < .001$ in the mesocosm experiment; Figure S2). High plant densities can prevent water column mixing, which reduces the extent to which atmospheric oxygen diffused into surface waters can reach the water column (Fleming & Dibble, 2015). High plant densities also lead to increased levels of organic material (COD increased with macrophyte biomass, Table S4, Figure S2) and decomposition, which consumes oxygen that may otherwise be available (John et al., 1991). The fitness of aerobic organisms,

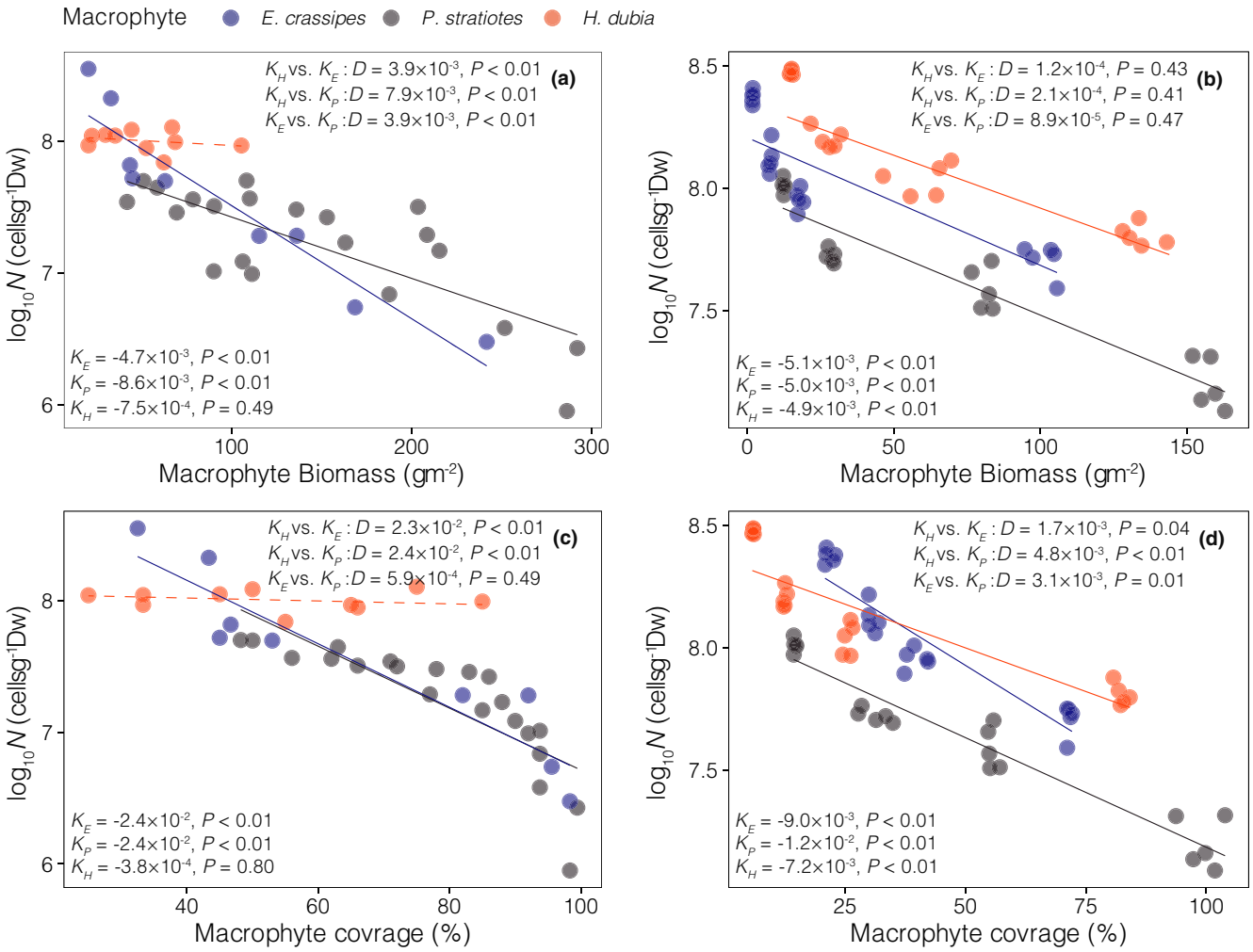


FIGURE 6 Linear models of the effects of macrophyte biomass and coverage on epiphytic algal abundance in field investigations and mesocosm experiments. (a and c) show data from the field investigation (n = 40), and (b and d) show data from the mesocosm experiment (n = 60). The differences between the slopes (D) and their significance level (P) based on randomization tests are shown. The solid and dotted lines represent significant and non-significant regressions, respectively. K_E, K_P and K_H represent the slopes of *Eichhornia crassipes*, *Pistia stratiotes* and *Hydrocharis dubia*, respectively

including algae, declines under low DO conditions (Kalff, 2002). Thus, the free-floating macrophytes inhibited epiphytic algae by blocking the production of oxygen and promoting the consumption of oxygen. By comparing the DO and COD in the native and invasive macrophyte communities, we found that the DO in the invasive macrophyte communities was significantly lower than that in native macrophyte community, while the COD was significantly higher in the invasive community than in the native community (Table S2). This result suggested that the presence of invasive macrophytes resulted in more limited oxygenation, thus inhibiting epiphytic algae.

On the other hand, free-floating macrophytes with high effective absorption capacity have been observed in several laboratory-based experiments and field studies (Brendonck et al., 2003; Jayaweera & Kasturiarachchi, 2004). The absorption of nutrients by free-floating macrophytes was significant (path from the macrophyte traits to the water nutrient concentration: C = −0.49, p < .001; Figure 5) in the mesocosm experiment. It has been widely demonstrated that a decrease in nutrients leads to a reduction in the biomass and density of epiphytic algae (Hao et al., 2020; Song et al., 2017; Trochine et al., 2014). Water nutrients (TN, TP, NH_3-N and NO_3-N) positively affected epiphytic algal abundance (Figure 5 and Figure S2) in the mesocosm experiment, which suggested that the free-floating macrophytes inhibited epiphytic algal growth by absorbing nutrients from the water column. In addition, the performance of the invasive macrophytes may indicate a superior resource acquisition ability (Fleming & Dibble, 2015), leading to the invasive macrophytes having a stronger inhibitory effect on epiphytic algae than native macrophytes. In the mesocosm experiment, we found that the slopes of the MB and water nutrient concentrations (i.e. TN, TP, NH_3-N and NO_3-N) of the invasive macrophytes were higher than those of the native macrophytes (Table S4), which indicated that invasive macrophytes have

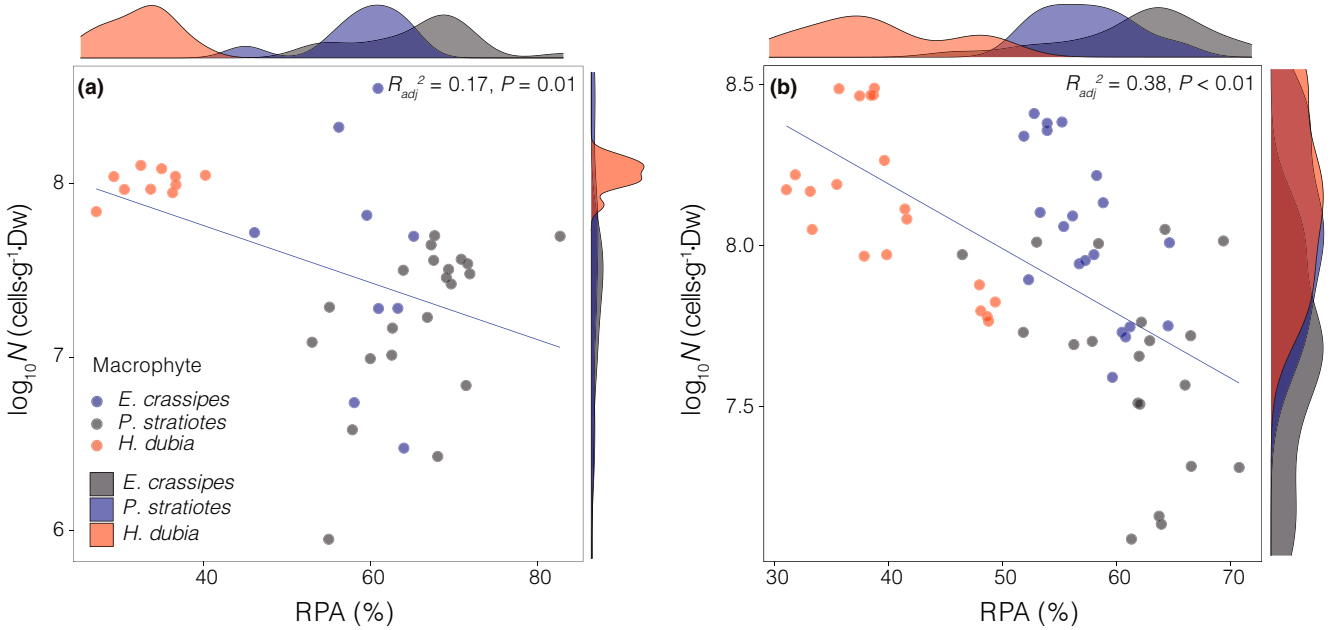


FIGURE 7 Linear models of allelochemical (sum of the relative peak areas of five compound classes) effects on epiphytic algal abundance in the field investigation (a, $n = 40$) and mesocosm experiment (b, $n = 60$). The squared regression coefficients and p values of the regressions with correction for multiple tests are shown

stronger nutrient acquisition ability than native species; therefore, invasive species have a stronger inhibitory effect on the plant algae.

In addition, previous studies have found that macrophytes both release and accumulate bioactive secondary metabolites with allelochemical properties in quantities sufficient to inhibit algal growth (Ping, 2001; Shanab et al., 2010; Zhu et al., 2021). The allelochemicals released by *E. crassipes* and *P. stratiotes* are mainly fatty acids, steroids, polyphenols and tannins (Fileto-Perez et al., 2015; Shanab et al., 2010; Wu et al., 2015), which is consistent with the results of this study (Table S3). This study found that the allelochemicals released by the macrophytes had significant adverse effects on epiphytic algal abundance (Figure 5), which suggested that the free-floating macrophytes could inhibit epiphytic algae, especially epiphytic diatoms, by releasing allelochemicals (Figure S3). Among the allelochemicals observed in this study, organic acids and alkaloids are thought to have the greatest effect on epiphytic algal abundance (Figure 5 and Figure S2). Organic acids are widely confirmed to be toxic to algae, and alkaloids, which play key defensive roles in interactions between plants and algae, are the most frequently reported compounds; alkaloids exhibit the most significant inhibitory effects on algal growth (Zhu et al., 2021). In addition, allelopathy results in increased competitive ability, promoting invasion and changing succession trajectories in aquatic communities (Fleming & Dibble, 2015; Ni et al., 2012). The contents of total allelochemicals, organic acids and alkaloids released by invasive macrophytes (*E. crassipes* and *P. stratiotes*) were significantly higher and had greater inhibitory effects than those released by the native species (*H. dubia*) in this study (Figures 4 and 7). In summary, invasive macrophytes have a more substantial inhibitory effect than native species on epiphytic algae because they release more allelochemicals.

5 | CONCLUSION

We conclude that the inhibitory effect of invasive free-floating macrophytes on epiphytic algae is stronger than that of the native macrophyte *H. dubia*. The main reason for this difference is that invasive macrophytes have greater biomass; occupy more space; and limit solar radiation, oxygenation and nutrients in the water to a greater extent. Moreover, invasive macrophytes secrete more allelochemicals than native species, thus causing a stronger inhibitory effect on epiphytic algae.

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CONFLICT OF INTEREST

We have no conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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BIOSKETCH

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Author contributions: Chunhua Liu, Dan Yu and Tian Lv designed and executed the research project. Dan Yu provided funding support. Tian Lv and SF collected the data of field investigation. Tian Lv, Huiyuan Wang, Dexiang Li, Qiuyue Wang and Xinyi Lei conducted the mesocosm experiment. Tian Lv led the data analysis and drafted the manuscript with the assistance of Chunhua Liu. All the co-authors commented on and approved the final manuscript.

SUPPORTING INFORMATION

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