

Competitive exclusion from native plants and co-occurring exotic plants was the most important factor influencing plant invasion in freshwater ecosystems

shufeng fan¹, Haihao Yu¹, Tian Lv¹, Lei Yang¹, Yang Li¹, Ligong Wang¹, Chunhua Liu¹, and Dan Yu¹

¹Wuhan University

July 13, 2023

Abstract

Few studies have evaluated the relative importance of various factors in the invasion process of exotic plants in freshwater ecosystems due to the difficulty of observing numerous factors simultaneously. In this study, to explore how various biotic and abiotic factors determine the overall invasion extent of all exotic plants and the invasion extent of different life-form exotic plants as well as assess their relative importance, we surveyed 236 exotic aquatic plant communities using 2267 fine quadrats in China's freshwater ecosystems. We found that competition from native plants was the most vital factor determining the mean biomass of all exotic plants and biomass of submerged plant *Cabomba caroliniana*, while competition from co-occurring exotics was the most important for biomass of emergent plant *Alternanthera philoxeroides* and free-floating plant *Eichhornia crassipes*. The population biomass of different exotic species responded differently to climate change. Water eutrophication could accelerate the invasion of exotic plants by directly favoring them and indirectly weakening the resistance of native plants. Water depth, habitat size, herbivory, and anthropogenic disturbance had relatively weak impacts on the biomass of exotic plants. Moreover, some factors have different modes of influence on different exotic plants. Our study suggested interspecific competition plays a more important role in the population spread of exotic plants than climate and abiotic environment once the plants have successfully established, implying that biodiversity conservation and vegetation restoration were the fundamental methods to control invasion. In addition, our study highlights the importance of studying the overall invasion extent of all exotic plants and interactions among invaders in multi-invader communities.

Title: Competitive exclusion from native plants and co-occurring exotic plants was the most important factor influencing plant invasion in freshwater ecosystems

Abstract

Few studies have evaluated the relative importance of various factors in the invasion process of exotic plants in freshwater ecosystems due to the difficulty of observing numerous factors simultaneously. In this study, to explore how various biotic and abiotic factors determine the overall invasion extent of all exotic plants and the invasion extent of different life-form exotic plants as well as assess their relative importance, we surveyed 236 exotic aquatic plant communities using 2267 fine quadrats in China's freshwater ecosystems. We found that competition from native plants was the most vital factor determining the mean biomass of all exotic plants and biomass of submerged plant *Cabomba caroliniana*, while competition from co-occurring exotics was the most important for biomass of emergent plant *Alternanthera philoxeroides* and free-floating plant *Eichhornia crassipes*. The population biomass of different exotic species responded differently to climate change. Water eutrophication could accelerate the invasion of exotic plants by directly favoring them and indirectly weakening the resistance of native plants. Water depth, habitat size, herbivory, and anthropogenic disturbance had relatively weak impacts on the biomass of exotic plants. Moreover, some factors have

different modes of influence on different exotic plants. Our study suggested interspecific competition plays a more important role in the population spread of exotic plants than climate and abiotic environment once the plants have successfully established, implying that biodiversity conservation and vegetation restoration were the fundamental methods to control invasion. In addition, our study highlights the importance of studying the overall invasion extent of all exotic plants and interactions among invaders in multi-invader communities.

Key words:

aquatic plants, biotic resistance, climate warming, enemy, plant invasion, relative importance, water eutrophication

Introduction

Freshwater ecosystems play vital roles in nutrient and water cycling, biodiversity maintenance, and providing various ecological services to human society (Dudgeon et al. 2006, Carpenter et al. 2011, Rinke et al. 2019). Hundreds of exotic plants have invaded freshwater ecosystems around the world over the past centuries (Strayer 2010, Hussner 2012, Wang et al. 2016). These invaders reduce biodiversity, change community composition, habitat, and ecosystem function, interrupt ecosystem services, and degrade human health (Gallardo et al. 2016). Furthermore, the invasion of exotic aquatic plants is expected to become increasingly serious due to the rise in international commerce and global change (Seebens et al. 2017). Therefore, there is an urgent need to determine the factors that influence the invasion of exotic aquatic plants and their relative importance since it is necessary for the management of invaders and biodiversity conservation.

Numerous studies have examined the roles of various biotic and abiotic factors in the plant invasion process. Some studies have found that plant communities with higher species richness and abundance exhibit greater competitive resistance to the invasion of exotic aquatic plants (Levine et al. 2004, Capers et al. 2007, Michelan et al. 2013, Petruzzella et al. 2018, Zhang et al. 2021a). The consumptive resistance of native generalist herbivores and introduced specialist enemies also reduces the establishment and performance of exotic aquatic plants (Parker and Hay 2005, Coetzee et al. 2011, Ribas et al. 2017). However, climate warming (Rahel and Olden 2008, Gillard et al. 2017), water eutrophication (Henry-Silva et al. 2008; Salgado et al. 2019), and disturbances (Trebitz and Taylor 2007; Quinn et al. 2011) are considered to facilitate aquatic plant invasions. Water depth is a crucial factor that determines the distribution, reproduction, and growth of exotic aquatic plants because it is closely related to light, temperature, dissolved oxygen, nutrient availability, and water movement (Gerhardt and Collinge 2003; Santos et al. 2011; Bornette and Puijalon 2011; Fleming et al. 2021). Additionally, in communities with multiple invasive plants, an invader is influenced by co-occurring invaders (Kuebbing and Nuñez 2015). The invasive plants may facilitate each other by suppressing shared resident competitors, increasing resource availability, providing protection from herbivores, enhancing pollinator visitation rates as magnet species, and promoting their dispersal and establishment as nurse species (Simberloff 2006, Tecco et al. 2007, Molina-Montenegro et al. 2008, Cushman et al. 2011, Flory and Bauer, 2014), or interfere with each other by competing for resources and pollinators (Belote and Weltzin 2006, Yang et al. 2011, Zhang et al. 2021b).

Evaluating the relative importance of various factors in contributing to exotic plant invasion is important (Eschtruth and Battles 2009, Bansal and Sheley 2016, Szymura et al. 2018). In freshwater ecosystems, native plant coverage has been found to account for most of the variation in exotic plant richness (Yu et al. 2018). Whereas few studies have quantitatively assessed the relative importance of various factors influencing the biomass of exotic aquatic plants. Different measures of exotic plants convey different information; richness indicates the number of species that have successfully invaded, while biomass quantifies the dominance and impact of exotic plants (Catford et al. 2012). Furthermore, because the living environment of four life-forms of aquatic plants (emergent, submerged, floating-leaved, and free-floating) varies greatly (Gallego et al. 2015, Hussner et al. 2021, Hu et al. 2021), the effect and relative importance of the same factors on different life-form exotic plants may differ. Additionally, freshwater ecosystems often experienced multiple invasions (Zhang et al. 2021b), a general understanding of the relative importance of various factors in the invasion process necessitates taking into account the overall performance of all invasive plants, as well as the

performance of single invaders.

In this study, we surveyed the communities invaded by exotic plants in freshwater ecosystems in China. Various biotic and abiotic factors that may affect invasions were determined, including the richness, biomass, and coverage of native communities, water nutrient status, climate, habitat features, herbivory level, and anthropogenic disturbance. We used biomass to measure the overall invasion extent of all exotic plants in communities and the invasion extent of different life-form exotic plants, and employed regression analysis, structural equation modeling, and hierarchical partitioning to (1) examine which factors determine the invasion of exotic plants in freshwater ecosystems and how they work; (2) quantify the relative importance of these factors; and (3) determine the differences in the effects of the same factors on the overall invasion extent of all exotic plants and the invasion extent of different life-form exotic plants.

Methods

Community surveys of aquatic plants

The field surveys were conducted in eastern, central, southern, and southwestern China. 236 sites where exotic aquatic plants had invaded were sampled from 2015 to 2018 (Fig. 1). To obtain peak species richness and standing biomass, surveys in the northern and southern areas of the Tropic of Cancer were conducted from July to September and from May to November, respectively. At each site, we first recorded the position (latitude and longitude), habitat type (lake, river, rapid, canal, wetland, pool, and reservoir), habitat size ($A_{habitat}$, the continuous water area supporting the community), and species of plants. The origin of each species (native or exotic) was verified according to the Aquatic Plant of the World (Cook et al., 1974) and the List of Invasive Plants in China (<http://www.iplant.cn/ias/protlist>). Then, we used a systematic sampling technique to survey plant communities. Transects were laid out in species-rich and dense vegetation. The selection of the number of transects and quadrats, as well as the surveyed area, was based on the principle of sampling to accurately reflect the community structure. At sites with narrow vegetation ($1\text{ m} < \text{width} < 5\text{ m}$, mostly in small rivers and canals, a few in lakes and large rivers), one transect was placed, and 6 quadrats ($1\text{ m} \times 1\text{ m}$, Fang et al. 2009) were sampled at 10 m intervals along the transect (Appendix S1: Fig. S1A). When the width of vegetation was more than 5 m, 2~4 transects (depending on the size of the community) were placed equidistantly perpendicular to the bank. These transects started from the banks and traversed the shallow rivers and pools (generally water depth $< 4\text{ m}$) if vegetation covered the whole habitat (Appendix S1: Fig. S1B); otherwise, they ended at the edge of vegetation or the limit water depth and distance (generally $< 500\text{ m}$) of manual sampling (Appendix S1: Fig. S1C). The interval between two transects was chosen at 5 m, 10 m, 15 m, 20 m, 30 m, 40 m, 50 m, 70 m, or 100 m according to the size of the community. 2~8 quadrats ($1\text{ m} \times 1\text{ m}$, depending on the size of the community) were sampled equidistantly along each transect, and the interval between two quadrats was chosen at 5 m, 10 m, 15 m, 20 m, 30 m, or 50 m according to the size, species richness and structure of community (Appendix S1: Table. S1).

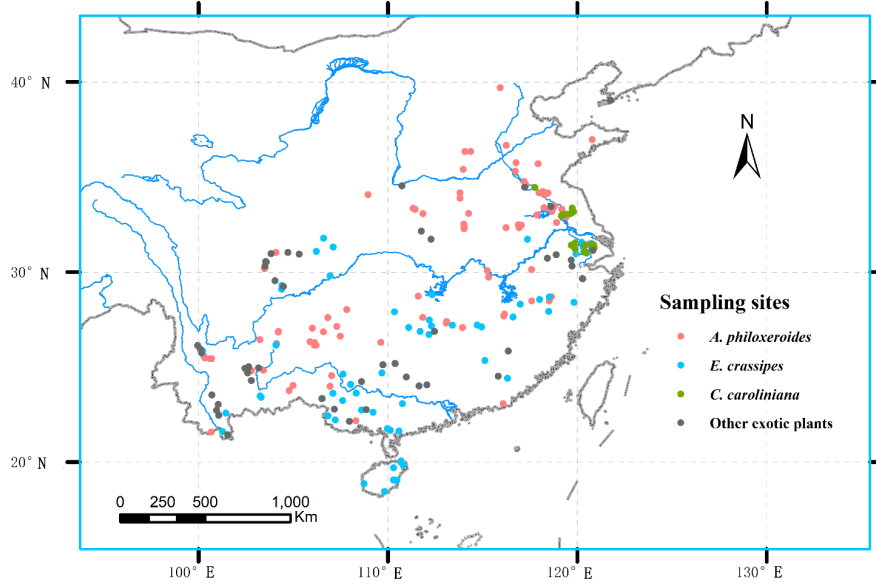


Fig. 1 Geographical locations of the sampling sites. The color of the circle indicates the dominant species of exotic plants

We sampled a total of 2267 quadrats in the 236 sites. For each quadrat, first, plant species were recorded. Then, the coverage of each species (C) was determined by visual estimation on 22-degree scales: 0.5%, 1%, 5%, 10%, 15%, 20% ... 100%. Next, all plant materials, including shoots, leaves, and roots, in the quadrat were collected by careful manual digging. Finally, all plants were classified, washed, and dried at 70 °C for more than 48 h to determine the biomass of each species (B). The total biomass of native/exotic plants in each quadrat (TBQ_N / TBQ_E) = $[?]B_n$, total coverage of native/exotic plants in each quadrat (TCQ_N / TCQ_E) = $[?]C_n$, n was the species number of natives or exotics in a quadrat. The mean biomass of native/exotic plants at each site (MBS_N / MBS_E) = $\frac{\sum TBQ_i}{i}$, the mean overage of native/exotic plants at each site (MCS_N / MCS_E) = $\frac{\sum TCQ_i}{i}$, and i is the number of quadrats at a site. When the abundance of exotic plants in a site was too low to appear in any quadrat, we determined the values of MBS_E and MCS_E of the site were zeros. In addition, the defoliation (D_{leaf} , % of leaf area removed) of exotic plants by herbivores was assessed. 10~20 fresh shoots (all shoots when the total shoots < 10) of each exotic plant were randomly selected for defoliation assessments in each quadrat, and D_{leaf} was measured using our previously described method (Fan et al. 2016).

Environmental variables

At each site, the annual mean temperature (T) was used to characterize the climate, and the dataset (unit: 0.1 degC, year: 2015, resolution: 1 km) was obtained from the Resource and Environment Science and Data Center (<http://www.resdc.cn/>). A water sample was collected, and the total nitrogen (TN), total phosphorus (TP), and chemical oxygen demand (COD) were determined using a Palintest 7500 Photometer (Palintest, UK). Trophic state indices were calculated by the following equations: $TLI(TP) = 10(9.436 + 1.624 \ln TP)$, $TLI(TN) = 10(5.453 + 1.694 \ln TN)$, $TLI(COD) = 10(0.109 + 2.661 \ln COD)$. Water nutrient status (N_{water}) was the mean value of $TLI(TP)$, $TLI(TN)$, and $TLI(COD)$ (Cao et al. 2021). The water depth ($H_{quadrat}$) in each quadrat was measured by a pole and ruler, average water depth at each site (H_{site}) was the mean value of $H_{quadrat}$ s of all quadrats. In addition, the linear distance between the site location and the nearest town ($L_{site-town}$) was determined to measure the anthropogenic disturbance level (Gosper et al. 2015).

Data analyses

To study which factors affected the overall invasion extent of exotic aquatic plants in the sites, we used regression analysis to examine the relationships between the site-level mean biomass of exotic aquatic plants (MBS_E) and the site-level richness of native plants (R_{native_site}), site-level performance of native plants [P_{native_site} , a metric integrating MBS_N and MCS_N by principal component analysis (PCA), data values were scores of PC1 (proportion variances = 0.86)], T , N_{water} , H_{site} , $L_{site-town}$, and $A_{habitat}$. For each regression analysis, we trialed linear regression and nonlinear regression (quadratic and cubic) models and selected the best-fitting models with the highest fitting coefficient (R^2) and a significant P-value ($P < 0.05$).

To study the differences in the effects of the same factors on different life-form exotic plants, we selected three exotic plants belonging to different life-forms with the highest frequency in our field surveys: emergent plant *Alternanthera philoxeroides* (in 483 quadrats and 145 sites), free-floating plant *Eichhornia crassipes* (in 515 quadrats and 87 sites), submerged plant *Cabomba caroliniana* (in 170 quadrats and 25 sites). We used linear regression analysis to examine the relationships between the quadrat-level population biomass of the three exotic plants and the quadrat-level richness of native plants ($R_{native_quadrat}$), quadrat-level performance of native plants ($P_{native_quadrat}$, a metric integrating TBQ_N and TCQ_N by PCA, data values were scores of PC1 and proportion variances ranged from 0.74~0.87), quadrat-level performance of co-occurring exotic plants ($P_{exotic_quadrat}$, a metric integrating TBQ_E and TCQ_E of all exotic plants except the target exotic plant by PCA, data values were scores of PC1 and proportion variances ranged from 0.82~0.98), T , N_{water} , $H_{quadrat}$, and D_{leaf} .

To investigate how native plants, water nutrient status, climate, habitat features, herbivory level, and anthropogenic disturbance influence the overall invasion extent of exotic aquatic plants and the invasion extent of different life-form plants, we employed structural equation modeling (SEM) to explore the relationships between the factors and MBS_E and quadrat-level population biomass of *A. philoxeroides*, *E. crassipes*, and *C. caroliniana* individually. For MBS_E , we constructed *a priori* models and hypothesized that (1) all abiotic factors (T , N_{water} , H_{site} , $L_{site-town}$, $A_{habitat}$) would influence the MBS_E , R_{native_site} , and P_{native_site} , (2) R_{native_site} and P_{native_site} would further influence the MBS_E , and R_{native_site} would predict P_{native_site} , (3) N_{water} would be predicted by $A_{habitat}$, H_{site} , and $L_{site-town}$ (Appendix S1: Fig. S2A). For biomass of *A. philoxeroides*, *E. crassipes*, and *C. caroliniana*, we constructed *a priori* models and hypothesized that (1) T , N_{water} , $H_{quadrat}$, $R_{native_quadrat}$, $P_{native_quadrat}$, and $P_{exotic_quadrat}$ would influence biomass of the three exotics, (2) T , N_{water} , $H_{quadrat}$, $R_{native_quadrat}$, and $P_{native_quadrat}$ also would influence $P_{exotic_quadrat}$, (3) both $R_{native_quadrat}$ and $P_{native_quadrat}$ would be predicted by T , N_{water} , and $H_{quadrat}$, and $R_{native_quadrat}$ would predict the $P_{native_quadrat}$ (Appendix S1: Fig. S2B). The D_{leaf} was not included in the models because it neither reduced the biomass of exotic plants nor affected other factors.

The SEM models were fitted by the PiecewiseSEM R-package (Lefcheck 2016). Before modeling of the data, we inspected the data for outliers and multi-collinearity. To facilitate interpretation and ensure model convergence, we standardized all variables (except the richness of native plants) to have a mean of zero and a standard deviation. In the sub-models of P_{native_site} and MBS_E , we included the random effect of the sampling area to control the effect of the sampling area on the biomass of exotic and native plants. In all sub-models of quadrat-level response variables, we included random effects of the site to account for the non-independence of quadrats within the same site. Both site-level and quadrat-level richness of native plants were modeled with generalized linear models (GLMs) or generalized mixed-effects models (GLMMs) using a Poisson distribution and log-link function. The other response variables were modeled using linear models (LMs) or linear mixed-effects models (LMEs). All LMs, LMEs, GLMs, and GLMMs were performed by the "lme4" package (Bates et al. 2014). To obtain the best model, we removed the nonsignificant paths with the highest p-value in a stepwise manner. We added any link that was initially ignored when the D-separation test revealed significant missing relationships between variables, and including the significant missing path would improve the model fit. We assessed the goodness-of-fit of the model (Fisher's C statistic) using Shipley's test of directional separation. Models with an adequate fit ($p > 0.05$) were considered as candidate models, and their AICs were computed and compared. The model with the lowest AIC value was considered as the best-fit model. Standardized coefficients for the GLM and GLMM components of the piecewise SEM (not provided by PiecewiseSEM) were calculated by the latent theoretic approach (Lefcheck

2019).

To determine the relative importance of various factors that influence the overall invasion extent of exotic aquatic plants and the invasion extent of different life-form plants, we employed hierarchical partitioning (hier.part R package, Walsh and MacNally 2015) to analyze the independent explanatory power (I) of R_{native_site} , P_{native_site} , T , N_{water} , H_{site} , $L_{site-town}$, and $A_{habitat}$ for the MBS_E , and the independent explanatory power ($\bar{I}$) of T , N_{water} , $H_{quadrat}$, $R_{native_quadrat}$, $P_{native_quadrat}$, and $P_{exotic_quadrat}$ for the biomass of *A. philoxeroides*, *E. crassipes*, and *C. caroliniana*. The statistical significance of each I was determined by randomizing the data matrix 200 times to produce the distribution of I values, with observed I value that exceeded the 95th percentile considered significant. The results of the significance tests were expressed as Z-scores. All analyses were conducted by R v4.2.0 (R Development Team 2022). The biomass of *A. philoxeroides*, *E. crassipes*, and *C. caroliniana* was transformed using $\ln(x)$ function.

Results

Effects of the biotic and abiotic factors on the overall invasion extent of exotic aquatic plants

Regression models showed that the site-level mean biomass of exotic plants (MBS_E) decreased with increased native plant richness (R_{native_site} , $P < 0.001$), native plant performance (P_{native_site} , $P < 0.001$), and habitat size ($A_{habitat}$, $P < 0.05$), but increased as water nutrient status (N_{water} , $P < 0.001$) and mean water depth (H_{site} , $P < 0.05$) increased (Fig. 2A-E). The best-fit SEM showed that P_{native_site} had a direct effect on MBS_E , but H_{site} and $A_{habitat}$ had indirect effects by influencing R_{native_site} positively or negatively; R_{native_site} and N_{water} not only had direct effects on MBS_E , but also had indirect effects by positively influencing the P_{native_site} or negatively influencing the R_{native_site} and P_{native_site} (Fig. 4A). In addition, although there were no significant relationships between the MBS_E and annual mean temperature (T , $P > 0.05$) and distance to town ($L_{site-town}$, $P > 0.05$), T and $L_{site-town}$ could affect MBS_E by negatively influencing the R_{native_site} and N_{water} (Fig. 2F and G, Fig. 4A). Hierarchical partitioning results indicated that P_{native_site} was the most important determinant factor for MBS_E (independent effect = 54.55%), followed by R_{native_site} , N_{water} , H_{site} , T , $A_{habitat}$, and $L_{site-town}$ (independent effects were 25.84%, 13.47%, 3.67%, 1.26%, 1.09%, and 0.12%) (Fig. 5A).

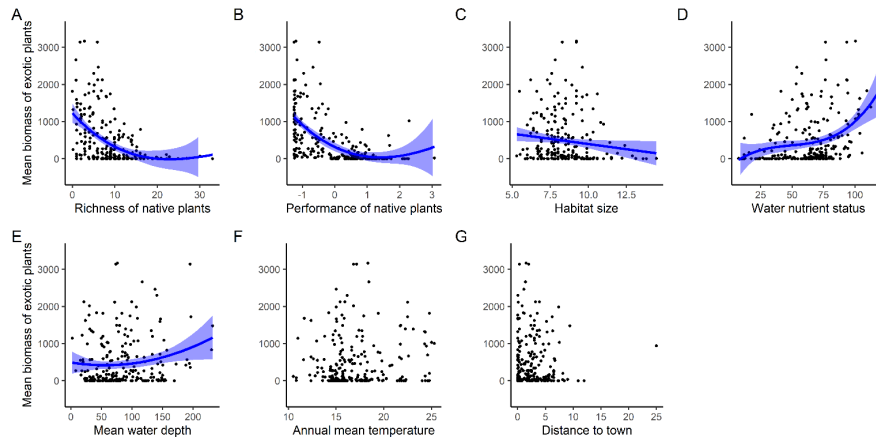


Fig. 2 Relationships of site-level mean biomass of exotic plants and site-level richness (A) and performance (B) of native plants, habitat size (C), water nutrient status (D), mean water depth (E), annual mean temperature (F), and distance between site to the nearest town (G).

Effects of the biotic and abiotic factors on invasions of different plants

The biomass of *A. philoxeroides* and *E. crassipes* decreased as the performance of co-occurring exotic plants ($P_{exotic_quadrat}$) increased, but the biomass of *C. caroliniana* was not affected by $P_{exotic_quadrat}$ (Fig. 3A).

As the richness ($R_{native_quadrat}$) and performance ($P_{native_quadrat}$) of native plants increased, the biomass of *A. philoxeroides*, *E. crassipes*, and *C. caroliniana* all increased (Fig. 3B, C). The best-fit SEMs revealed that the $R_{native_quadrat}$ and $P_{native_quadrat}$ affected the biomass of three plants in different ways. $P_{native_quadrat}$ affected the biomass of *A. philoxeroides* and *E. crassipes* directly and indirectly by negatively influencing the $P_{exotic_quadrat}$, whereas, it only had a direct effect on the biomass of *C. caroliniana*; $R_{native_quadrat}$ had direct and indirect effects on the biomass of *A. philoxeroides* and *E. crassipes*, but only an indirect effect on the biomass of *C. caroliniana*. (Fig. 4B-D). None of the three plants showed a decrease in biomass as defoliation increased (Fig. 3D), which suggests that herbivory does not control the invasion of aquatic plants.

As T increased, the biomass of *A. philoxeroides* increased, but the biomass of *E. crassipes* decreased (Fig. 3E). T not only had a direct positive effect on the biomass of *A. philoxeroides*, but also had indirect effects on the latter by negatively influencing the $R_{native_quadrat}$ and positively influencing the $P_{exotic_quadrat}$ (Fig. 4B). Whereas, high T increased the biomass of *E. crassipes* only by indirectly reducing the $R_{native_quadrat}$ and $P_{exotic_quadrat}$ (Fig. 4C). The biomass of *A. philoxeroides* and *C. caroliniana* increased with the increased N_{water} (Fig. 3F). High N_{water} could directly increase the biomass of *C. caroliniana* and indirectly by reducing the $R_{native_quadrat}$, while it only increased the biomass of *A. philoxeroides* indirectly by reducing the $R_{native_quadrat}$ (Fig. 4B, D). N_{water} also affected the biomass of *E. crassipes* by negatively influencing the $R_{native_quadrat}$ (Fig. 4C), even though regression analysis showed no significant correlation between N_{water} and the biomass of *E. crassipes* ($P > 0.05$). Similarly, although the relationships between the $H_{quadrat}$ and the biomass of *E. crassipes*, *A. philoxeroides* and *C. caroliniana* were not significant (Fig. 3G), SEMs showed that $H_{quadrat}$ could affect the biomass of *A. philoxeroides* and *C. caroliniana* by influencing the $P_{exotic_quadrat}$ and $R_{native_quadrat}$ positively or negatively (Fig. 4B, D).

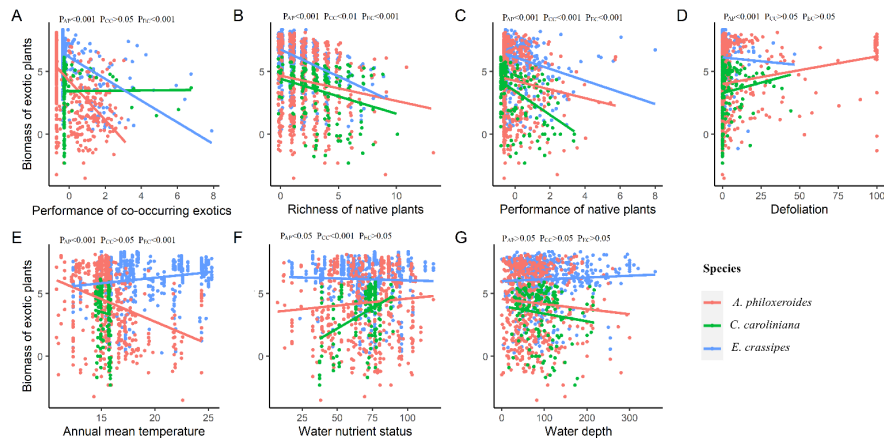


Fig. 3 Relationships of quadrat-level biomass of *E. crassipes*, *A. philoxeroides*, and *C. caroliniana* and quadrat-level performance of co-occurring exotic plants (A), quadrat-level richness (B) and performance (C) of native plants, defoliation (C), annual mean temperature (E), water nutrient status (F), and water depth (G).

Hierarchical partitioning results indicated that $P_{exotic_quadrat}$ was the most important determinant factor for biomass of *A. philoxeroides* (independent effect = 68.11%), followed by T , $R_{native_quadrat}$, $P_{native_quadrat}$, N_{water} , and $H_{quadrat}$ (independent effects were 17.08%, 8.31%, 4.91%, 1.09%, and 0.50%); $P_{exotic_quadrat}$ was the most important determinant factor for biomass of *E. crassipes* (independent effect = 54.55%) too, followed by $R_{native_quadrat}$, $P_{native_quadrat}$, T , $H_{quadrat}$, and N_{water} (independent effects were 32.37%, 8.91%, 2.96%, 0.93%, and 0.28%); $P_{native_quadrat}$ was the most important determinant factor for biomass of *C. caroliniana* (independent effect = 45.19%), followed by N_{water} , $R_{native_quadrat}$, $H_{quadrat}$, T , and $P_{exotic_quadrat}$ (independent effects were 38.44%, 11.72%, 2.68%, 1.50%, and 0.47%) (Fig. 5B).

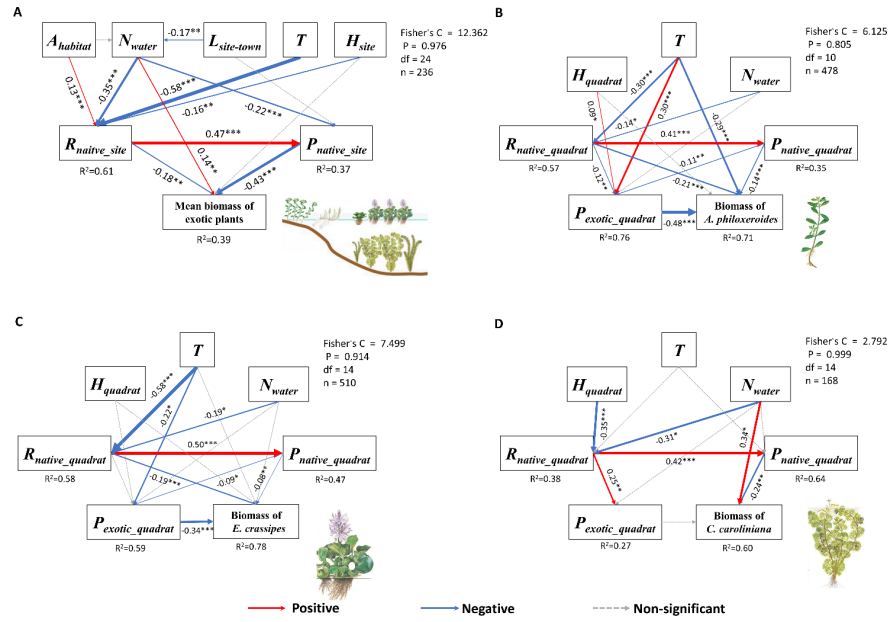


Fig. 4 The best-fit SEMs showing the influences of site-level native plant performance (P_{native_site}), site-level native plant richness (R_{native_site}), annual mean temperature (T), water nutrient status (N_{water}), average water depth (H_{site}), habitat size ($A_{habitat}$) and distance to the nearest town ($L_{site-town}$) on site-level mean biomass of exotic plants (A), and the influences of quadrat-level native plant performance ($P_{native_quadrat}$), quadrat-level native plant richness ($R_{native_quadrat}$), quadrat-level co-occurring exotic plant performance ($P_{exotic_quadrat}$), T , N_{water} , and water depth ($H_{quadrat}$) on quadrat-level population biomass of *A. philoxeroides* (B), *E. crassipes* (C), and *C. caroliniana* (D). Arrow widths are proportional to standardized path coefficients (values are also given, *P < 0.05, **P < 0.01, *** P < 0.001), and R^2 values are given for each endogenous variable.

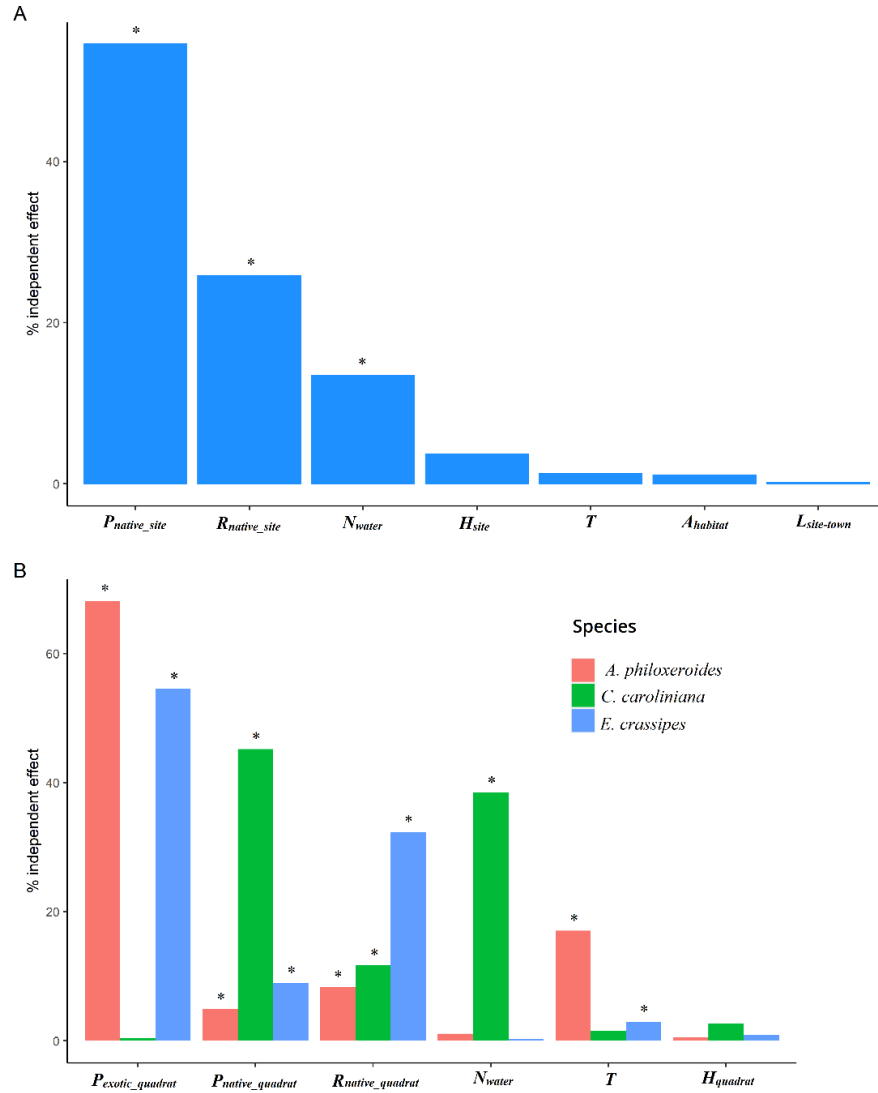


Fig. 5 Percent independent explanatory power of each factor of the site-level mean biomass of exotic plants (A) and the quadrat-level biomass of *A. philoxeroides*, *E. crassipes*, and *C. caroliniana* (B).

P_{native_site} = site-level native plant performance; R_{native_site} = site-level native plant richness; $P_{native_quadrat}$ = quadrat-level native plant performance; $R_{native_quadrat}$ = quadrat-level native plant richness; $P_{exotic_quadrat}$ = quadrat-level co-occurring exotic plant performance; N_{water} = water nutrient status; T = annual mean temperature; H_{site} = average water depth in sites; $H_{quadrat}$ = water depth in quadrats; $A_{habitat}$ = habitat size; $L_{site-town}$ = distance to the nearest town. * denotes significance ($p < 0.05$).

Discussion

In our study, competitive exclusion was the most important factor affecting plant invasion in freshwater ecosystems. Previous studies considered climate and habitat-related factors were the most important factors driving plant invasion at broad scales, the biotic interactions became more important at fine scales (Pearson and Dawson 2003, Milbau et al. 2009, Hortal et al. 2010, Bellard et al. 2016, Catford et al. 2017). However, our study showed that habitat characteristics, such as water depth, habitat size, and anthropogenic disturbance, had relatively weak impacts on the biomass of exotic aquatic plants, and just affected the

latter indirectly by influencing native plants. Our surveys covered a vast geographical area and targeted communities that had been invaded by exotic species, which suggested that even at a large scale, once the exotic plants adapt to the local climate and environment and successfully establish their population, interspecific competition plays a more important role in their population expansion than climate and physical environment. The competition came from both native plants and co-occurring exotic plants. In fact, *A. philoxeroides* and *E. crassipes* experienced stronger competitive exclusion from co-occurring exotic plants than from native plants. Invasive plants are characterized by fast growth and strong competitiveness, therefore, the competition among invasive plants, especially plants with the same niche, is more intense (Van Kleunen et al. 2010, Zhang and van Kleunen 2019). The submerged plant *C. caroliniana* was not affected by the co-occurring exotic plants, because there is only one exotic submerged plant, *Elodea nuttallii*, in its distribution area, and their growth periods are different: *E. nuttallii* in winter and early spring, while *C. caroliniana* in summer and autumn (Yu 2017).

Unlike interspecific competition, we found that natural enemies did not inhibit the population expansion of exotic aquatic plants in the field. This may be because native generalist herbivores can only effectively control invasive plants when plant density is below some threshold, but they can't bring sufficient herbivore pressure to limit exotic plants after plant density crosses the threshold (Maron and Vila 2001). Although some specialist herbivores are introduced as biological control agents for invasive aquatic plants (such as *Neochetina eichhorniae* and *Agasicles hygrophila*) and reach a high population density (Jayanth 1988, Julien et al. 1995), these specialist herbivores only establish populations and persist in sites where the abundance of the host plant is enormous. And they do not reduce plant performance once the plant develops a large population (Yu and Fan 2018). In addition, invasive aquatic plants often have strong compensatory abilities (Soti and Volin 2010, Lu and Ding 2012). Therefore, specialist herbivores may lower the population expansion speed of invaders but cannot eliminate or reduce the developed population. What's more, in multi-invader communities, it is rare that specialist herbivores of each invasive plant appear and all plants are effectively controlled (Zhang et al. 2021b). Even if enemies can successfully control one invasive plant, the co-occurring invasive plants can still dominate the communities (Center et al. 2005, Hill et al. 2020). Taken together, top-down controls are not the primary drivers affecting the population dynamics of invasive plants in the field natural community (Davis 2009, Bohl Stricker and Stiling 2014, Silveira et al. 2018). Conversely, fragmentation by herbivory can facilitate the spread of some aquatic exotic plants (Ribas et al. 2017).

Our results showed that water eutrophication accelerated the invasion of exotic aquatic plants by directly favoring them and indirectly weakening the resistance of native plants. The growth and reproduction of exotic aquatic plants are enhanced in high nutrient availability environments (Hussner et al. 2009, Henry-Silva et al. 2008, Xie et al. 2010, Wersal and Madsen 2011). Excessive nutrients in water are harmful to submerged plants because a high density of periphyton and phytoplankton and low light availability caused by eutrophication can inhibit the growth of submerged plants, subsequently reducing the biodiversity, coverage area, and biomass of aquatic plants (Hautier et al. 2009, Arthaud et al. 2017, O'Hare et al. 2018). However, when compared to the site-level mean biomass of exotic plants and the quadrat-level biomass of *C. caroliniana*, the relative effects of water nutrient status on the quadrat-level biomass of *E. crassipes* and *A. philoxeroides* were weak. This may be due to these two plants' inherent high growth rate, which enables them to colonize a large area and reach peak biomass at a fine scale in a short time, regardless of the nutrient concentrations (Edwards and Musil 1975, Pan et al. 2007). In addition, our results showed that the effect of water nutrient status on invasion was lower than that of community properties. Previous research has also found that the characteristics of the resident plant community are more critical than resource fluctuations in determining the invasion of exotic plants, which may be because the biotic resistance of native plants buffers the effects of nutrient enrichment on invasions (Walker et al. 2005, Teixeira et al. 2017). This finding indicates that as long as resident plants occupy enough space and resources, they can prevent plant invasions even when resources are in excess in the community.

We found that climate had completely different impacts on the overall performance of all exotic plants and the population performance of individual species. The optimal climates for various species are different, as a result, different exotic plants respond differently to climate change (Hoveka et al. 2016, Merow et al.

2017). In multi-invader communities, there must be one or some invaders that perform best under a given climate, and maximize the ecosystem's productivity, so the overall performance of invaders does not vary in different climate regions. Whereas climate warming can facilitate the establishment and dispersal of exotic aquatic plants by altering streamflow and thermal regimes, reducing ice cover in waterbodies, and increasing water development activities (Rahel and Olden 2008). In addition, climate change has the potential to influence plant invasions by influencing native communities and co-occurring exotic plants (Li et al. 2017, Zhang et al. 2021b). Given the complexity of the effects of climate change on biological invasion, the study on predicting biological invasion under climate change should involve numerous invasive species, multiple measures of invaders, and the interactions between native and invasive plants, as well as among invaders.

Conclusion

Our study demonstrated that the resistance from both native plants and co-occurring exotic plants was the most important factor determining plant invasion in freshwater ecosystems. It implied that biodiversity conservation and native vegetation restoration are essential to control plant invasion. If no native vegetation fills the blank niches left by the removal of invasive plants through enemies or mechanical control, invasive plants will return or be replaced by other invasive plants. And it also suggested that managing and modeling the invasive species must take into account the interactions between invaders which have always been ignored (Kuebbing et al. 2013). In addition, we found that the effects of some factors on different exotic aquatic plants were varied as well as the relative importance and modes of their effects, more studies involving multiple approaches and multiple invasive species are required to address the invasion patterns in freshwater ecosystems (Thomaz et al. 2015).

References

- Arthaud, F., Vallod, D., Robin, J., & Bornette, G. (2012). Eutrophication and drought disturbance shape functional diversity and life-history traits of aquatic plants in shallow lakes. *Aquatic Sciences*, 74, 471-481.
- Bansal, S., & Sheley, R. L. (2016). Annual grass invasion in sagebrush steppe: the relative importance of climate, soil properties and biotic interactions. *Oecologia*, 181, 543-557.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.
- Bellard, C., Leroy, B., Thuiller, W., Rysman, J. F., & Courchamp, F. (2016). Major drivers of invasion risks throughout the world. *Ecosphere*, 7(3), e01241.
- Belote, R. T., & Weltzin, J. F. (2006). Interactions between two codominant, invasive plants in the understory of a temperate deciduous forest. *Biological Invasions*, 8(8), 1629-1641.
- Bohl Stricker, K., & Stiling, P. (2014). Release from herbivory does not confer invasion success for *Eugenia uniflora* in Florida. *Oecologia*, 174, 817-826.
- Bornette, G., & Puijalon, S. (2011). Response of aquatic plants to abiotic factors: a review. *Aquatic sciences*, 73, 1-14.
- Cao C., Wang S., Li J., Zhao H., Shen W., & Xie Y. (2021) MODIS-based monitoring of spatial distribution of trophic status in 144 key lakes and reservoirs of China in summer of 2018. *Journal of Lake Sciences*, 33(2), 405-413.
- Capers, R. S., Selsky, R., Bugbee, G. J., & White, J. C. (2007). Aquatic plant community invasibility and scale-dependent patterns in native and invasive species richness. *Ecology*, 88(12), 3135-3143.
- Carpenter, S. R., Stanley, E. H., & Vander Zanden, M. J. (2011). State of the world's freshwater ecosystems: physical, chemical, and biological changes. *Annual review of Environment and Resources*, 36, 75-99.
- Catford, J. A., Kalisz, S., Simberloff, D., & Wardle, D. A. (2017). A framework for understanding human-driven vegetation change. *Oikos* 126, 1687-1698.

- Catford, J. A., Vesk, P. A., Richardson, D. M., & Pyšek, P. (2012). Quantifying levels of biological invasion: towards the objective classification of invaded and invisable ecosystems. *Global Change Biology*, 18(1), 44-62.
- Center, T. D., Van, T. K., Dray Jr, F. A., Franks, S. J., Rebelo, M. T., Pratt, P. D., & Rayamajhi, M. B. (2005). Herbivory alters competitive interactions between two invasive aquatic plants. *Biological Control*, 33(2), 173-185.
- Coetzee, J. A., Hill, M. P., Byrne, M. J., & Bownes, A. (2011). A review of the biological control programmes on *Eichhornia crassipes* (C. mart.) solms (Pontederiaceae), *Salvinia molesta* DS Mitch. (Salviniaceae), *Pistia stratiotes* L.(Araceae), *Myriophyllum aquaticum* (vell.) verdc.(Haloragaceae) and *Azolla filiculoides* Lam.(Azollaceae) in South Africa. *African Entomology*, 19(1), 451-468.
- Cook, C. D. K., G. J. Gut, E. M. Rix, J. Schneller, and M. Seitz. (1974) Water Plants of the World. *Bulletin of the Torrey botanical club* 102:282.
- Cushman, J. H., Lortie, C. J., & Christian, C. E. (2011). Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. *Journal of Ecology*, 99(2), 524-531.
- Davis, M. A. (2009). *Invasion biology*. Oxford University Press on Demand.
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., ... & Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological reviews*, 81(2), 163-182.
- Edwards, D., & Musil, C. J. (1975). *Eichhornia crassipes* in South Africa-a general review. *Journal of the Limnological Society of southern Africa*, 1(1), 23-27.
- Eschtruth, A. K., & Battles, J. J. (2009). Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecological Monographs*, 79(2), 265-280.
- Fan, S., Yu, H., Dong, X., Wang, L., Chen, X., Yu, D., & Liu, C. (2016). Invasive plant *Alternanthera philoxeroides* suffers more severe herbivory pressure than native competitors in recipient communities. *Scientific reports*, 6(1), 1-10.
- Fang, J., Wang, X., Shen, Z., Tang, Z., He, J., Yu, D., ... & Guo, Z. (2009). Methods and protocols for plant community inventory. *Biodiversity Science*, 17(6), 533-548.
- Fleming, J. P., Wersal, R. M., Madsen, J. D., & Dibble, E. D. (2021). Weak non-linear influences of biotic and abiotic factors on invasive macrophyte occurrence. *Aquatic Invasions*, 16(2).
- Flory, S. L., & Bauer, J. T. (2014). Experimental evidence for indirect facilitation among invasive plants. *Journal of Ecology*, 102(1), 12-18.
- Gallardo, B., Clavero, M., Sánchez, M. I., & Vilà, M. (2016). Global ecological impacts of invasive species in aquatic ecosystems. *Global change biology*, 22(1), 151-163.
- Gallego, I., Pérez-Martínez, C., Sánchez-Castillo, P. M., Fuentes-Rodríguez, F., Juan, M., & Casas, J. J. (2015). Physical, chemical, and management-related drivers of submerged macrophyte occurrence in Mediterranean farm ponds. *Hydrobiologia*, 762(1), 209-222.
- Gerhardt, F., & Collinge, S. K. (2003). Exotic plant invasions of vernal pools in the Central Valley of California, USA. *Journal of Biogeography*, 30(7), 1043-1052.
- Gillard, M., G. Thiebaut, C. Deleu & B. Leroy, 2017. Present and future distribution of three aquatic plants taxa across the world: decrease in native and increase in invasive ranges. *Biological Invasions* 19: 2159-2170.
- Gosper, C. R., Prober, S. M., Yates, C. J., & Scott, J. K. (2015). Combining asset-and species-led alien plant management priorities in the world's most intact Mediterranean-climate landscape. *Biodiversity and Conservation*, 24(11), 2789-2807.

- Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, 324(5927), 636-638.
- Henry-Silva, G. G., Camargo, A. F., & Pezzato, M. M. (2008). Growth of free-floating aquatic macrophytes in different concentrations of nutrients. *Hydrobiologia*, 610, 153-160.
- Hoveka, L. N., Bezeng, B. S., Yessoufou, K., Boatwright, J. S., & Van der Bank, M. (2016). Effects of climate change on the future distributions of the top five freshwater invasive plants in South Africa. *South African Journal of Botany*, 102, 33-38.
- Hill, M. P., Coetzee, J. A., Martin, G. D., Smith, R., & Strange, E. F. (2020) Invasive alien aquatic plants in South African freshwater ecosystems. In *Biological Invasions in South Africa* (pp. 97-114). Springer, Cham.
- Hortal, J., Roura-Pascual, N., Sanders, N. J., & Rahbek, C. Understanding (insect) species distributions across spatial scales. *Ecography* 33, 51-53 (2010).
- Hu, J., Yu, H., Li, Y., Wang, J., Lv, T., Liu, C., & Yu, D. (2021). Variation in resource allocation strategies and environmental driving factors for different life-forms of aquatic plants in cold temperate zones. *Journal of Ecology*, 109(8), 3046-3059.
- Hussner, A. (2009). Growth and photosynthesis of four invasive aquatic plant species in Europe. *Weed Research*, 49(5), 506-515.
- Hussner, A. (2012). Alien aquatic plant species in European countries. *Weed research*, 52(4), 297-306.
- Hussner, A., Heidebuchel, P., Coetzee, J., & Gross, E. M. (2021). From introduction to nuisance growth: a review of traits of alien aquatic plants which contribute to their invasiveness. *Hydrobiologia*, 848(9), 2119-2151.
- Jayanth, K. P. (1988). Successful biological control of water hyacinth (*Eichhornia crassipes*) by *Neochetina eichhorniae* (Coleoptera: Curculionidae) in Bangalore, India. *International Journal of Pest Management*, 34(3), 263-266.
- Julien, M. H., Skarratt, B., & Maywald, G. F. (1995). Potential geographical distribution of alligator weed and its biological control by *Agasicles hygrophila*. *Journal of Aquatic Plant Management*, 33(1), 55-60.
- Kuebbing, S. E., Nunez, M. A., & Simberloff, D. (2013). Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. *Biological Conservation*, 160, 121-129.
- Kuebbing, S. E., & Nunez, M. A. (2015). Negative, neutral, and positive interactions among nonnative plants: patterns, processes, and management implications. *Global Change Biology*, 21(2), 926-934.
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573-579.
- Lefcheck, J. S. (2019). Structural equation modeling in R for ecology and evolution.
- Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology letters*, 7(10), 975-989.
- Li, Z., He, L., Zhang, H., Urrutia-Cordero, P., Ekvall, M. K., Hollander, J., & Hansson, L. A. (2017). Climate warming and heat waves affect reproductive strategies and interactions between submerged macrophytes. *Global change biology*, 23(1), 108-116.
- Lu, X., & Ding, J. (2012). History of exposure to herbivores increases the compensatory ability of an invasive plant. *Biological Invasions*, 14(3), 649-658.
- Maron, J. L., & Vila, M. (2001). When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos*, 95(3), 361-373.

- Merow, C., Bois, S. T., Allen, J. M., Xie, Y., & Silander Jr, J. A. (2017). Climate change both facilitates and inhibits invasive plant ranges in New England. *Proceedings of the National Academy of Sciences*, 114(16), E3276-E3284.
- Michelan, T. S., Thomaz, S. M., & Bini, L. M. (2013). Native macrophyte density and richness affect the invasiveness of a tropical Poaceae species. *PLoS One*, 8(3), e60004.
- Milbau, A., Stout, J. C., Graae, B. J., & Nijs, I. (2009). A hierarchical framework for integrating invasibility experiments incorporating different factors and spatial scales. *Biological Invasions*, 11(4), 941-950.
- Molina-Montenegro, M. A., Badano, E. I., & Cavieres, L. A. (2008). Positive interactions among plant species for pollinator service: Assessing the ‘magnet species’ concept with invasive species. *Oikos*, 117(12), 1833–1839.
- O’Hare, M. T., Baattrup-Pedersen, A., Baumgarte, I., Freeman, A., Gunn, I. D., Lazar, A. N., . . . & Bowes, M. J. (2018). Responses of aquatic plants to eutrophication in rivers: a revised conceptual model. *Frontiers in plant science*, 9, 451.
- Pan, X., Geng, Y., Sosa A. J., Zhang, W., Li, B., & Chen J. (2007). Invasive *Alternanthera philoxeroides* : biology, ecology and management. *Journal of Systematics and Evolution*, 45(6), 884.
- Parker, J. D., & Hay, M. E. (2005). Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecology Letters*, 8(9), 959-967.
- Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global ecology and biogeography*, 12(5), 361-371.
- Petruzzella, A., Manschot, J., van Leeuwen, C. H., Grutters, B., & Bakker, E. S. (2018). Mechanisms of invasion resistance of aquatic plant communities. *Frontiers in plant science*, 9, 134.
- Quinn, L. D., C. Jarnevich, G. W. Chong & P. H. Evangelista, 2011. Effects of land use and environment on alien and native macrophytes: lessons from a large-scale survey of Australian rivers. *Diversity and Distribution* 17: 132–143.
- R Development Core Team. (2022). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation biology*, 22(3), 521-533.
- Ribas, L. G. D. S., Cunha, E. R., Vitule, J. R. S., Mormul, R. P., Thomaz, S. M., & Padial, A. A. (2017). Biotic resistance by snails and fish to an exotic invasive aquatic plant. *Freshwater Biology*, 62(7), 1266-1275.
- Rinke, K., Keller, P. S., Kong, X., Borchardt, D., & Weitere, M. (2019). Ecosystem services from inland waters and their aquatic ecosystems. *Atlas of ecosystem services: Drivers, risks, and societal responses*, 191-195.
- Salgado, J., M. I. Velez, L. C. Caceres-Torres, J. A. Villegas-Ibagon, L. C. Bernal-Gonzalez, L. Lopera-Congote, N. M. Martinez-Medina & C. Gonzalez-Arango, 2019. Long term habitat degradation drives neotropical macrophyte species loss while assisting the spread of invasive plant species. *Frontiers in Ecology and Evolution* 7: 140.
- Santos, M. J., Anderson, L. W., & Ustin, S. L. (2011). Effects of invasive species on plant communities: an example using submersed aquatic plants at the regional scale. *Biological Invasions*, 13, 443-457.
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., . . . & Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature communications*, 8(1), 1-9.
- Simberloff, D. (2006). Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, 9(8), 912-919.

- Silveira, M. J., Chollet, S., Thiebaut, G., & Thomaz, S. M. (2018). Abiotic factors, not herbivorous pressure, are primarily responsible for the performance of an invasive aquatic plant. In *Annales de Limnologie-International Journal of Limnology* (Vol. 54, p. 12). EDP Sciences.
- Soti, P. G., & Volin, J. C. (2010). Does water hyacinth (*Eichhornia crassipes*) compensate for simulated defoliation? Implications for effective biocontrol. *Biological control*, 54(1), 35-40.
- Strayer, D. L. (2010). Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater biology*, 55, 152-174.
- Szymura, T. H., Szymura, M., Zajac, M., & Zajac, A. (2018). Effect of anthropogenic factors, landscape structure, land relief, soil and climate on risk of alien plant invasion at regional scale. *Science of the Total Environment*, 626, 1373-1381.
- Tecco, P. A., Diaz, S., Gurvich, D. E., Perez-Harguindeguy, N., Cabido, M., & Bertone, G. A. (2007). Facilitation and interference underlying the association between the woody invaders *Pyracantha angustifolia* and *Ligustrum lucidum*. *Applied Vegetation Science*, 10(2), 211-218.
- Teixeira, M. C., Bini, L. M., & Thomaz, S. M. (2017). Biotic resistance buffers the effects of nutrient enrichment on the success of a highly invasive aquatic plant. *Freshwater Biology*, 62(1), 65-71.
- Thomaz, S. M., Mormul, R. P., & Michelan, T. S. (2015). Propagule pressure, invasibility of freshwater ecosystems by macrophytes and their ecological impacts: a review of tropical freshwater ecosystems. *Hydrobiologia*, 746, 39-59.
- Trebitz, A. S. & D. L. Taylor, 2007. Exotic and invasive aquatic plants in great lakes coastal wetlands: distribution and relation to watershed land use and plant richness and cover. *Journal of Great Lakes Research* 33: 705-721.
- Van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology letters*, 13(2), 235-245.
- Walker, S., Bastow Wilson, J., & Lee, W. G. (2005). Does fluctuating resource availability increase invasibility? Evidence from field experiments in New Zealand short tussock grassland. *Biological Invasions*, 7, 195-211.
- Walsh C, & MacNally R. Hierarchical partitioning. An Online Reference Version, 2015: 1.0-4.
- Wang, H., Wang, Q., Bowler, P. A., & Xiong, W. (2016). Invasive aquatic plants in China. *Aquatic Invasions*, 11(1).
- Wersal, R. M., & Madsen, J. D. (2011). Comparative effects of water level variations on growth characteristics of *Myriophyllum aquaticum*. *Weed Research*, 51(4), 386-393.
- Xie, D., Yu, D., Yu, L. F., & Liu, C. H. Asexual propagations of introduced exotic macrophytes *Elodea nuttallii*, *Myriophyllum aquaticum*, and *M. propinquum* are improved by nutrient-rich sediments in China. *Hydrobiologia* 655, 37-47 (2010).
- Yang, S., Ferrari, M. J., & Shea, K. (2011). Pollinator behavior mediates negative interactions between two congeneric invasive plant species. *The American Naturalist*, 177(1), 110-118.
- Yu, H., Wang, L., Liu, C., & Fan, S. (2018). Coverage of native plants is key factor influencing the invasibility of freshwater ecosystems by exotic plants in China. *Frontiers in Plant Science*, 9, 250.
- Yu H. (2017) The Flora, Distribution pattern, Diffusion pathway of Alien Species of Aquatic Plants in China. Ph.D. thesis, Wuhan University.
- Yu, H., & Fan, S. (2018). Differences in physiological traits and resistances of *Alternanthera philoxeroides* after herbivory by generalists and specialists. *Aquatic Ecology*, 52(4), 323-332.

Zhang, X., Yu, H., Yu, H., Liu, C., Fan, S., & Yu, D. (2021a). Highly competitive native aquatic species could suppress the growth of invasive aquatic species with similar traits. *Biological Invasions*, 23, 267-280.

Zhang, X., Yu, H., Lv, T., Yang, L., Liu, C., Fan, S., & Yu, D. (2021b). Effects of different scenarios of temperature rise and biological control agents on interactions between two noxious invasive plants. *Diversity and Distributions*, 27(12), 2300-2314.

Zhang, Z., & van Kleunen, M. (2019). Common alien plants are more competitive than rare natives but not than common natives. *Ecology Letters*, 22(9), 1378-1386.