RESEARCH ARTICLE

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

Interplay between native plant performance and environment shapes resistance to aquatic plant invasion

Shufeng Fan | **Tian Lv** | **Haihao Yu** | **Lei Yang** | **Ligong Wang** | **Yang Li** | **Chunhua Liu** | **Dan Yu**

The National Field Station of the Freshwater Ecosystem of Liangzi Lake, College of Life Science, Wuhan University, Wuhan, P.R. China

Correspondence
Chunhua Liu
Email: liuchh@163.com

Dan Yu
Email: lakeyd@163.com

Abstract

1. In the limited number of studies on biotic resistance in freshwater ecosystems, experimental studies have supported that native plants play a role in resisting exotic plant invasion, but field observations have often reported positive relationships between exotic and native plant richness.

2. To determine the reasons for the lack of evidence supporting biotic resistance in field observations, we surveyed the richness, biomass and coverage of exotic and native aquatic plants in 2801 quadrats at 287 sites in various freshwater ecosystems of China and examined the impacts of scale and environmental factors on the relationships between native and exotic plant richness and performance.

3. At both the site and quadrat scales, we observed a positive correlation between the richness of exotic and native plants. However, at the quadrat scale, high native plant richness was associated with a reduction in the biomass of exotic emergent and floating plants as well as the biomass of exotic submerged plants in low-nutrient water bodies. An increase in native plant performance, a metric that integrates the biomass and coverage of native plants, was associated with a decrease in both the richness and biomass of exotic plants at both scales. Furthermore, with increasing native plant performance at the quadrat scale, the richness of exotic plants declined more strongly in low-nutrient water bodies than in high-nutrient water bodies, and the decline in the biomass of exotic emergent and floating plants was more severe in shallow water than in deep water.

4. *Synthesis.* Our results indicate that native plant performance is more important than richness for resistance to invasion in freshwater ecosystems, and the strength of biotic resistance is related to environmental factors. This study highlights the importance of environmental variables and multiple native community features and invasibility metrics in field observational studies of invasion.

KEYWORDS
aquatic plants, biological invasions, biotic acceptance hypothesis, biotic resistance hypothesis, ecological restoration, eutrophication, exotic species, freshwater ecosystem, water depth

1 | INTRODUCTION

Freshwater ecosystems are particularly vulnerable to plant invasion, and their functions are deeply transformed by invasive species (Gallardo et al., 2016; Hussner, 2012; Strayer, 2010). Identifying the factors that determine the vulnerability of communities to invasion is essential for predicting the spatial distribution of invasive species and managing biodiversity (Cassey et al., 2018). In freshwater ecosystems, experimental studies have provided evidence that the presence of native plants, as well as high native plant diversity and abundance, can limit the invasion of exotic plants (Chadwell & Engelhardt, 2008; Evangelista et al., 2017; Gerhardt & Collinge, 2007; Michelan et al., 2013; Petruzzella et al., 2018, 2020; Teixeira et al., 2017). However, field observations have reported a positive or neutral relationship between exotic and native plant species richness (Capers et al., 2007; Chen et al., 2010; Fleming et al., 2021; Muthukrishnan et al., 2018; Tarasi & Peet, 2017; Thomaz et al., 2012).

The contradictory outcomes of experimental studies and field observations may result from differences in the processes driving species richness at different spatial scales (Fridley et al., 2007; Peng et al., 2019). At small scales, in which the environment is relatively homogeneous and resources are very limited, species interactions play a major role in community assembly. Species-rich communities can occupy more space, generate more biomass and utilize more resources because of complementary resource use among species and the increased probability of the presence of highly productive species (Fargione & Tilman, 2005). Consequently, communities with high species diversity are less likely to be invaded than those with low diversity (biotic resistance hypothesis, Levine & D'Antonio, 1999). At large scales, extrinsic factors, such as spatial environmental heterogeneity (Davies et al., 2005), dispersal processes (Von Holle & Simberloff, 2005), and anthropogenic disturbances (MacDougall et al., 2014), overwhelm biotic interactions in shaping regional biodiversity, resulting in high richness of both native and exotic species at sites with favourable growing conditions (biotic acceptance hypothesis, Stohlgren et al., 2006).

Different native community features and invasibility metrics used to study the relationship between native and exotic species could yield different results (Delavaux et al., 2023; Guo, 2015). During the early stages of succession or in a disturbed environment, species rarely have enough time to accomplish biomass production and niche occupancy (Clark & Johnston, 2011; Hagan et al., 2021), implying that in these circumstances, high native richness does not necessarily guarantee high resistance against invasion. Some studies have shown that the performance of native plant communities, as reflected in biomass, cover and density of native plants, rather than species richness, determines the capacity of a community to resist exotic plant invasion (Aguiar et al., 2006; Capers et al., 2007; Hill & Fischer, 2014; Iannone et al., 2016). Furthermore, such biotic resistance may be more effective at regulating the spread and impacts of invaders once they have become successfully established than at repelling them prior to establishment (Levine et al., 2004). Studies

have frequently reported a negative relationship between native diversity and invader performance and a positive relationship between native diversity and invasive species richness (Jeschke et al., 2018; Smith & Cote, 2019). Additionally, previous studies have shown that environmental factors, such as productivity (Davies et al., 2007), disturbance (Belote et al., 2008; Sandel & Corbin, 2010), climate (Stotz et al., 2016), and resource availability (Eskelinen & Harrison, 2014; Griffith et al., 2021; Hulvey & Teller, 2018; Maron & Marler, 2007), influence the relationships between native and exotic species in terrestrial and marine ecosystems. In freshwater ecosystems, the degree of eutrophication is intensifying, and the frequency and magnitude of water level fluctuations caused by extreme weather events are also increasing. These changes have the potential to alter the interaction between native and exotic plants (Byun et al., 2015; Meza-Lopez & Siemann, 2017).

Therefore, the failure to detect evidence of biotic resistance in field observations of freshwater ecosystems may be attributed to the limited focus on the richness of native and exotic plants or to the possibility that biotic resistance operates primarily at small scales or in specific environments. To verify this speculation, we surveyed the richness, biomass, and coverage of exotic and native aquatic plants in 2801 quadrats at 287 sites in various freshwater ecosystems in China. Some environmental factors that may be related to plant invasion were also investigated, including water nutrient status, climate, habitat, anthropogenic disturbance, and environmental heterogeneity. We used linear mixed-effects models to investigate the relationships between native and exotic plants under different environmental conditions at the site and quadrat scales. Although the negative correlation between exotic and native plants in field observations may arise from the competitive exclusion of native plants by established invaders, previous studies have confirmed the role of biotic resistance in shaping this correlation (Beaury et al., 2020; Ernst et al., 2022). We considered three hypotheses: (H1) higher native plant richness reduces the invasion of exotic plants only at small scales, (H2) plant biomass and coverage are more important than richness for resistance to invasion, and (H3) the strength of biotic resistance is related to the environmental factors investigated.

2 | METHODS

2.1 | Community surveys of aquatic plants

From 2015 to 2018, we surveyed aquatic plant communities in the eastern, central, southern, and southwestern regions of China (Figure 1), which are the main areas for exotic aquatic plants in China. To obtain the peak species richness and standing biomass, surveys were conducted from July to September in the north of the Tropic of Cancer (23°26′ N), while in the south of the Tropic of Cancer, surveys were conducted from May to November due to the longer growing season of plants in this region. Sites with extensive vegetation (at least 200 m^2) that were suitable for manual sampling (water depth generally less than 4 m) were selected. Before conducting sampling
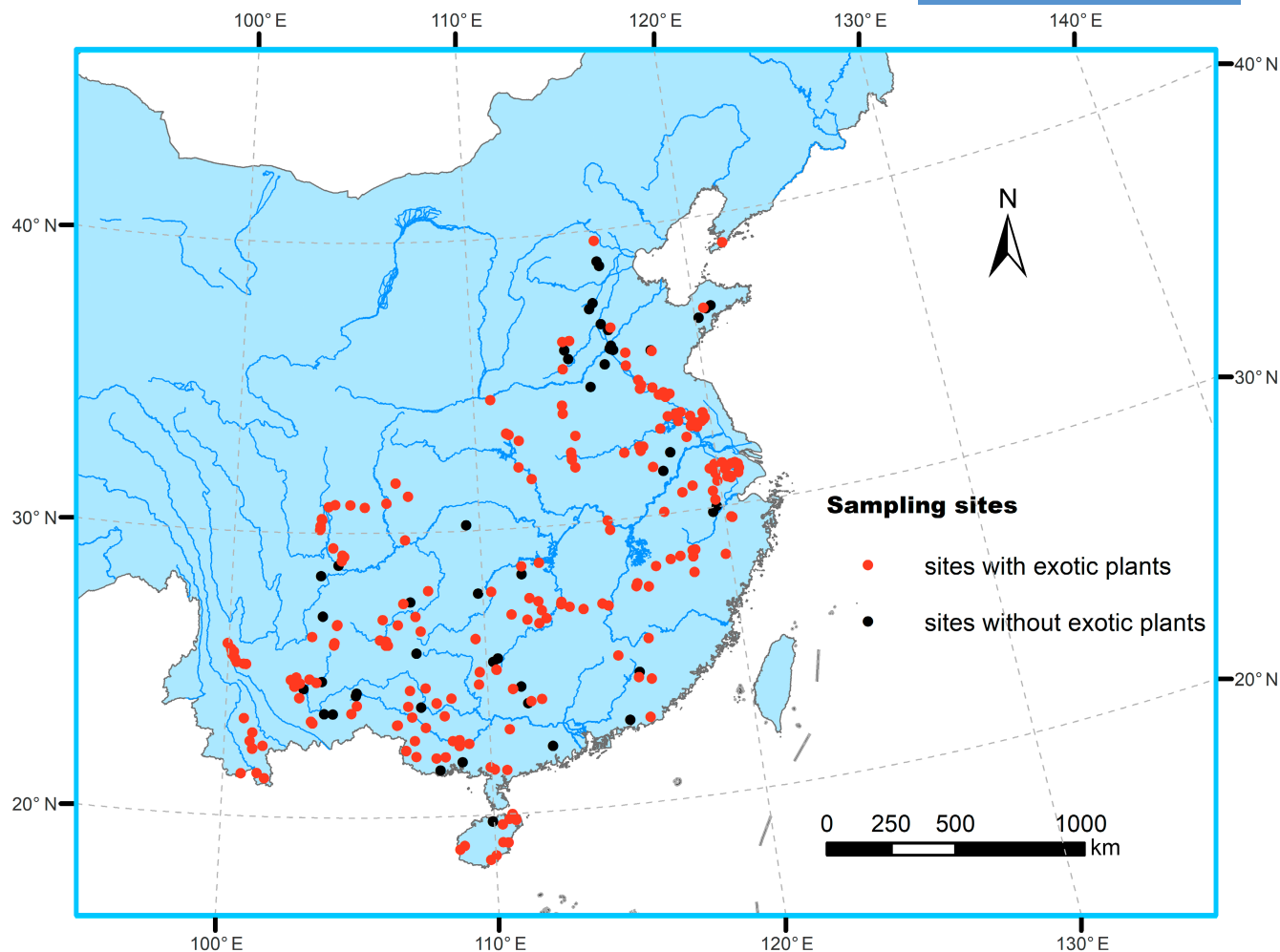
FIGURE 1 Geographical locations of the sampling sites. Field surveys were conducted in the southwestern, central, southern and eastern regions of China, which are the main areas with exotic aquatic plants in the country. A total of 235 sites with exotic plants and 52 sites without exotic plants were sampled in various freshwater ecosystems, including lakes, rivers, canals, wetlands, pools and reservoirs. A belt transect method with a nonuniform number of transects and quadrats as well as varying sampling ranges was employed to survey the plant communities at each site.

at each site, we undertook a shoreline walk (maximum distance of 3 km) for a preliminary assessment of the aquatic plant community structure and richness. Then, we recorded the position (latitude and longitude), habitat type and area ($T_{habitat}$ and $A_{habitat}$, Table S1), and species of plants. The origin of each species (native or exotic) was verified according to the Aquatic Plants of the World (Cook et al., 1974) and the List of Invasive Plants in China (https://www.iplant.cn/ias).

We employed a modified belt transect method to survey plant communities. Given the variations in habitat characteristics and community composition among the sampling sites, we used a non-uniform number of transects and quadrats (1 m × 1 m), as well as varying sampling ranges, to accurately reflect the community structure (Dalton et al., 2015). At sites with narrow vegetation (1 m < vegetation width < 5 m, mostly in small rivers and canals and a few in lakes and large rivers), one transect was established, and six quadrats were sampled at 10 m intervals along the transect (Figure S1A). When the vegetation width exceeded 5 m, 2–5 transects (depending

on the community size, with three transects accounting for 86% of the sites) were established equidistantly and perpendicular to the shoreline. The interval between two transects was 5, 10, 15, 20, 30, 40, 50, 70 or 100 m according to the community size. At sites where aquatic plants occurred in both the marginal and central parts of shallow pools, rivers and canals (water depth < 4 m generally), transects were established to traverse these water bodies, and 3–5 quadrats (5 ≤ water body width < 40 m, 3 quadrats; 40 ≤ water body width < 100 m, 4 quadrats; water body width ≥ 100 m, 5 quadrats) were sampled equidistantly along each transect (Figure S1B). At sites where aquatic plants were restricted to the margins of water bodies, where the water depth in the central area of water bodies was deep, or where the vegetation extended considerably far from the shoreline, transects (length: 10–350 m) were established starting from the shorelines and extending either to the edge of the vegetation or to the maximum depth (4 m) or the maximum distance from the shoreline (350 m) for manual sampling. 2–8 quadrats (depending on the transect length) were sampled at equidistant intervals along

each transect (Figure S1C). The interval between two quadrats on each transect was 5, 10, 15, 20, 30 or 50 m, depending on the length of the transect and species richness. A shorter interval was chosen when the transects were short and species richness was high, while a longer interval was chosen when the transects were long and species richness was low. Furthermore, quadrat placement was not deliberately avoided in bare areas.

For each quadrat, first, the species and life form (submerged, floating-leaved, free-floating and emergent) of the plants were recorded. Then, the coverage of each species (C) was determined via visual estimation at 22-degree scales: 0.5%, 1%, 5%, 10%, 15%, 20%, … 100%. Next, all the plant materials (above-and below-ground) in the quadrat were collected. The below-ground parts of emergent plants were harvested by excavating the soil with a shovel to a depth of approximately 30 cm, whereas the below-ground parts of submerged and floating-leaved plants were harvested by hand to a depth of approximately 10 cm (Figure S2). Finally, all plants were identified, washed and dried at 70°C for more than 48 h to determine the biomass of each species (B). We calculated the total coverage of native plants ($C_{native\_quadrat}$), total biomass of native plants ($B_{native\_quadrat}$) and total biomass of exotic plants ($B_{exotic\_quadrat}$) in each quadrat by summing the coverage or biomass of all native and exotic species. The mean coverage of native plants (C_{native_site}), mean biomass of native plants (B_{native_site}) and mean biomass of exotic plants (B_{exotic_site}) at each site were the sums of all $C_{native\_quadrat}$, $B_{native\_quadrat}$ and $B_{exotic\_quadrat}$ at the site divided by the number of quadrats, respectively. At sites where exotic species were present but their abundance was too low to appear in a quadrat, the values of B_{exotic_site} were zeros. The native plant communities in the quadrats were classified into five types ($T_{community}$: none, submerged, floating-leaved, free-floating and emergent communities) based on the life form of the aquatic plants with the largest total coverage and total biomass. When exotic plants were present in a site or quadrat, we determined the dominant exotic species based on their coverage and biomass.

2.2 | Environmental variables

At each site, the annual mean temperature (T) was used to characterize the climate, and the temperature dataset (unit:°C; year: 2015; resolution: 1 km) was obtained from the Resource and Environment Science and Data Center (http://www.resdc.cn/). We used the trophic level index method to evaluate the water nutrient status. A water sample was collected from each site, and total nitrogen (TN, mg/L), total phosphorus (TP, mg/L) and chemical oxygen demand (COD, mg/L) were determined using a Palintest 7500 Photometer (Palintest, UK). The trophic level index (TLI) was calculated by the following equation (Cao et al., 2021): $TLI = 1/3 (TLI(TP) + TLI(TN) + TLI(COD))$, $TLI(TP) = 10(9.436 + 1.624 \ lnTP)$, $TLI(TN) = 10(5.453 + 1.694 \ lnTN)$, and $TLI(COD) = 10(0.109 + 2.661 \ lnCOD)$. The water depth ($D_{quadrat}$, cm) in each quadrat was measured via a pole and ruler. Considering that environmental

heterogeneity is important for biological invasions (Melbourne et al., 2007), we used the degree of variation in water depth among quadrats (the standard deviation of all $D_{quadrat}$) to measure the heterogeneity of water depth (D_{heter}) at each site. Additionally, the linear distance between the site location and the nearest town ($L_{site-town}$, km) was determined to characterize the level of potential anthropogenic disturbance (Gosper et al., 2015).

2.3 | Data analyses

A total of 287 sites and 2801 quadrats were surveyed in various freshwater ecosystems. Among these, 235 sites and 1215 quadrats had at least one exotic species. Among the 1215 quadrats, most of the exotic plant biomass in 964 quadrats was contributed by emergent and floating species, whereas in the remaining 251 quadrats, most of the exotic plant biomass was contributed by submerged species.

We employed a linear mixed-effects modelling framework to address our questions. To test the hypotheses that higher native plant richness reduces the invasion of exotic plants only at a small scale (H1) and that plant biomass and coverage are more important than richness for resistance to invasion (H2), we separately fitted linear models for the site-level richness of exotic plants (M1), site-level biomass of exotic plants (M2), quadrat-level richness of exotic plants (M3), quadrat-level biomass of exotic submerged plants (M4) and quadrat-level biomass of exotic emergent and free-floating plants (M5) (Table S2). In each model, both native plant richness and native plant performance were set as predictors. Native plant performance (P_{native}) is a metric that integrates the biomass and coverage of native plants in each quadrat or site to simplify the models and make the results of the models easier to interpret. It was calculated via the following equation: $P_{native} = (ZB_{native} + ZC_{native})/2$, where ZB_{native} and ZC_{native} are the standardized values of biomass and coverage of native plants, respectively, using the zero-mean normalization method. To account for unequal environmental factors that may impact exotic plant invasion, the environmental factors $T_{habitat}$ (lake and reservoir, river and canal, pool and wetland, rapid), $A_{habitat}$, TLI, D_{heter}, T and $L_{site-town}$ were set as covariates in M1 and M2, whereas $T_{habitat}$, TLI, $D_{quadrat}$, T, $T_{community}$ and $L_{site-town}$ were set as covariates in M3, M4, and M5. Furthermore, to explore which environmental factors are related to the strength of biotic resistance to invasion (H3), interactions between these factors and both native plant richness and native plant performance were included in each initial model (Table S2). The sampling area and dominant exotic species were set as random effects in M2, whereas the dominant exotic species was set as a random effect in M4 and M5, to control their effects on the biomass of exotic plants. To further reduce the impact of sampling area variability on the biomass and richness of exotic plants, we selected 276 sites (230 sites with exotic plants) with a sampling area of 100–3000 m² to run M1 and M2.

The exotic plant biomass at both the site scale and the quadrat scale was modelled via fitting linear mixed-effects (LME) models. After trying Gaussian, Poisson, negative binomial and zero-inflated

Poisson error structures, we fitted a generalized linear mixed-effects model (GLMM) with Poisson error structure for the response variable site-level exotic plant richness and a GLMM with zero-inflated Poisson error structure for the response variable quadrat-level exotic plant richness, based on the assumption of homogeneity and the lowest AIC (Akaike information criterion) value. In LME and GLMM with Poisson error structure, we created a spatial matrix from the coordinates of the site or quadrat following an established approach (Kubelka et al., 2018) and incorporated it into each model to control for spatial autocorrelation after Moran's I test ($p \leq 0.05$). In zero-inflated GLMM, we set the sampling site as a random effect and included the longitude and latitude of the sites as covariates to reflect the spatial structure of the dataset (Sirami et al., 2019).

The LME and GLMM with Poisson error structure were implemented using the 'lme4qtl' package (Ziyatdinov et al., 2018), and zero-inflated models were implemented using the 'glmmTMB' package (Brooks et al., 2017). All the predictors were centred in the models to have a mean of zero and were scaled by their standard deviations to help with model convergence. To improve the normality of residuals, the site-level biomass of exotic plants, quadrat-level biomass of exotic submerged plants, and quadrat-level biomass of exotic emergent and free-floating plants were transformed using the $\log(x+1)$ function. Before modelling the data, we inspected the data for outliers and multicollinearity (the variable with the highest

variance inflation factor (VIF) was removed sequentially until all remaining VIFs were <5). The homogeneity of variances, normality of residuals, collinearity and overdispersion were tested via the 'check_model' and 'check_overdispersion' functions in the 'performance' package (Lüdecke et al., 2021). We employed a multimodel inference procedure to perform model selection by the 'MuMIn' package (Barton, 2009). This method creates a set of models with all possible combinations of the initial variables and ranks them based on the AICc fitted with maximum likelihood.

3 | RESULTS

Fifteen exotic aquatic plants were recorded in our field surveys. Among them, the emergent plant *Alternanthera philoxeroides*, free-floating plants *Eichhornia crassipes* and *Pistia stratiotes*, and submerged plant *Cabomba caroliniana* are invasive species that have reproduced and spread widely in China. The other plants are non-invasive species that have established localized reproducing populations (Table S3).

The best-fitting models (Table S4; Tables 1 and 2) revealed that both the site-level and quadrat-level richness of exotic plants increased with increasing native plant richness (Figure 2a, $Z=4.77$, $p<0.001$; Figure 3a, $Z=5.04$, $p<0.001$). As the native plant richness

TABLE 1 Results from the best-fitting GLMM and LME models examining the factors that affect the richness and biomass of exotic aquatic plants at the site scale.

Parameter	Richness of exotic plants			Biomass of exotic plants		
	Estimate ± SE	Z-value	p-value	Estimate ± SE	Z-value	p-value
Intercept	0.36 ± 0.96	0.37	0.71	1.46 ± 0.20	7.27	**<0.001**
R_{native_site}	0.27 ± 0.06	4.77	**<0.001**	-0.01 ± 0.03	0.29	0.77
P_{native_site}	-0.39 ± 0.07	5.54	**<0.001**	-0.71 ± 0.06	11.06	**<0.001**
TLI	0.07 ± 0.06	1.20	0.23	0.12 ± 0.05	2.39	**0.02**
D_{heter}	0.11 ± 0.06	1.84	0.06	0.03 ± 0.04	0.58	0.56
$L_{site-town}$	-0.002 ± 0.01	0.13	0.55	0.003 ± 0.02	0.18	0.86
$A_{habitat}$	-0.002 ± 0.02	0.10	0.92	-0.01 ± 0.03	0.35	0.73
T	0.13 ± 0.10	1.31	0.19	-0.20 ± 0.06	3.31	**<0.001**
$T_{habitat-lake\ and\ reservoir}$	—	—	—	0.23 ± 0.18	1.30	0.20
$T_{habitat-pool\ and\ wetland}$	—	—	—	0.53 ± 0.17	3.04	**0.002**
$T_{habitat\_river\ and\ canal}$	—	—	—	0.27 ± 0.14	1.97	**0.05**
$R_{native\_site}:N_{water}$	-0.004 ± 0.02	0.21	0.83	—	—	—
$P_{native\_site}:N_{water}$	—	—	—	0.03 ± 0.05	0.67	0.50
$R_{native\_sitet}:D_{heter}$	0.003 ± 0.02	0.20	0.83	—	—	—
$P_{native\_site}:D_{heter}$	0.06 ± 0.07	0.85	0.40	—	—	—
$P_{native\_site}:T$	0.001 ± 0.01	0.09	0.93	—	—	—

Note: Each predictor was standardized. Parameters and associated p values were estimated from the top models (ΔAICc <2, Table S4) predicting richness and biomass of exotic aquatic plants via the model averaging approach. Model parameter significance is denoted in boldface. Empty cells (—) denote the predictors were removed from the initial models to simplify models.

Abbreviations: $A_{habitat}$, habitat area; D_{heter}, heterogeneity of water depth at each site; GLMM, generalized linear mixed-effects model; LME, linear mixed-effects; $L_{site-town}$, linear distance between the site location and the nearest town; P_{native_site}, native plant performance at each site; R_{native_site}, native plant richness at each site; T, annual mean temperature; $T_{habitat}$, Habitat type; TLI, trophic level index.

TABLE 2 Results from the best-fitting GLMM and LME models examining the factors that affect the richness and biomass of exotic aquatic plants at the quadrat scale.

Parameter	Richness of exotic plants			Biomass of exotic emergent and floating plants			Biomass of exotic submerged plants		
	Estimate ± SE	Z-value	p-value	Estimate ± SE	Z-value	p-value	Estimate ± SE	Z-value	p-value
Intercept	−1.05±0.17	6.12	**<0.001**	2.06±6.29	0.33	0.74	1.90±1.11	1.70	0.09
$R_{native\_quadrat}$	0.24±0.05	5.04	**<0.001**	−0.15±0.02	6.27	**<0.001**	−0.09±0.05	1.89	0.06
$P_{native\_quadrat}$	−0.58±0.06	9.63	**<0.001**	−0.20±0.02	9.33	**<0.001**	−0.31±0.05	5.96	**<0.001**
TLI	0.29±0.06	5.07	**<0.001**	0.001±0.008	0.05	0.96	0.10±0.05	1.83	0.07
$D_{quadrat}$	0.02±0.04	0.44	0.66	−0.02±0.02	1.17	0.24	0.004±0.02	0.20	0.84
$L_{site\text{-}town}$	−0.002±0.01	0.10	0.92	—	—	—	0.19±0.05	3.92	**<0.001**
T	0.11±0.05	2.03	**0.04**	−0.005±0.05	0.10	0.92	—	—	—
$T_{community\_emergent}$	0.12±0.10	1.28	0.20	0.19±0.05	4.08	**<0.001**	−0.34±0.59	0.57	0.57
$T_{community\_free\text{-}floating}$	0.05±0.10	0.50	0.62	0.07±0.05	1.49	0.14	0.08±0.17	0.46	0.65
$T_{community\_floating\text{-}leaved}$	−0.82±0.22	3.73	**<0.001**	−0.59±0.12	5.03	**<0.001**	−0.33±0.32	1.01	0.31
$T_{community\_submerged}$	−0.92±0.12	7.87	**<0.001**	−0.38±0.07	5.41	**<0.001**	−0.31±0.15	2.06	**0.04**
$T_{habitat\text{-}lake\ and\ reservoir}$	0.30±0.19	1.58	0.11	0.09±0.12	0.75	0.46	—	—	—
$T_{habitat\text{-}pool\ and\ wetland}$	0.70±0.19	3.75	**<0.001**	0.16±0.16	0.99	0.32	—	—	—
$T_{habitat\_river\ and\ canal}$	0.62±0.16	3.92	**<0.001**	0.13±0.14	0.98	0.33	—	—	—
$R_{native\_quadrat}{:}N_{water}$	—	—	—	−0.003±0.01	0.25	0.80	0.20±0.05	4.37	**<0.001**
$P_{native\_quadrat}{:}N_{water}$	0.25±0.05	4.58	**<0.001**	—	—	—	0.01±0.03	0.32	0.75
$R_{native\_quadrat}{:}D_{quadrat}$	0.03±0.04	0.62	0.54	−0.02±0.03	0.87	0.38	—	—	—
$P_{native\_quadrat}{:}D_{quadrat}$	0.09±0.06	1.45	0.15	0.07±0.03	2.44	**0.01**	—	—	—
$R_{native\_quadrat}{:}T$	0.001±0.01	0.10	0.92	—	—	—	—	—	—
$P_{native\_quadrat}{:}T$	−0.003±0.02	0.12	0.90	—	—	—	—	—	—

Note: Each predictor was standardized. Parameters and associated *p*-values were estimated from the top models (ΔAICc < 2, Table S4) predicting richness and biomass of exotic aquatic plants via the model averaging approach. Model parameter significance is denoted in boldface. Empty cells (—) denote the predictors were removed from the initial models to simplify models.

Abbreviations: $D_{quadrat}$, water depth in each quadrat; GLMM, generalized linear mixed-effects model; LME, linear mixed-effects; $L_{site\text{-}town}$, linear distance between the site location and the nearest town; $P_{native\_quadrat}$, native plant performance in each quadrat; $R_{native\_quadrat}$, native plant richness in each quadrat; T, annual mean temperature; $T_{community}$, native plant community type; $T_{habitat}$, habitat type; TLI, trophic level index.

increased, the quadrat-level biomass of exotic emergent and floating plants decreased (Figure 3b, $Z=6.27$, $p<0.001$). However, no significant correlations were detected between the site-level biomass of exotic plants and native plant richness (Figure 2b, $Z=0.29$, $p>0.05$) or between the quadrat-level biomass of exotic submerged plants and native plant richness (Figure 3c, $Z=1.89$, $p>0.05$). In addition, as native plant performance increased, the richness and biomass of exotic plants decreased at both the site scale and the quadrat scale (Figures 2c,d and 3d–f).

Our models revealed that the relationships between exotic and native plants were related to environmental factors (Table 2). First, the quadrat-level richness of exotic plants decreased with increasing native plant performance more severely in low-nutrient water bodies than in high-nutrient water bodies (Figure 4a, $Z=4.58$, $p<0.001$). Second, the negative relationship between the biomass of submerged exotic plants and native plant richness shifted to a positive relationship as the trophic level index increased (Figure 4b, $Z=4.37$, $p<0.001$). Third, the biomass of exotic emergent and floating plants decreased with increasing native plant performance more severely

in shallow water than in deep water (Figure 4c, $Z=2.44$, $p=0.01$). In addition, the trophic level index, annual mean temperature, linear distance between the site location and the nearest town, habitat type and native community type were directly associated with exotic plant invasions (Tables 1 and 2).

4 | DISCUSSION

After taking into account various environmental variables, we found that the native-exotic richness relationship was positive at both the large (100–3000 m²) and small (1 m²) scales. In freshwater ecosystems, some favourable habitats, such as nonshaded, shallow, calm and low-current areas in lakes and rivers, and highly heterogeneous habitats, are prone to colonization by both native and exotic plants (Bornette & Puijalon, 2011; Fridley et al., 2007; Stohlgren et al., 2006). In addition, communities with high species richness have a high probability of containing species that facilitate the establishment of new immigrants by offering anchorage
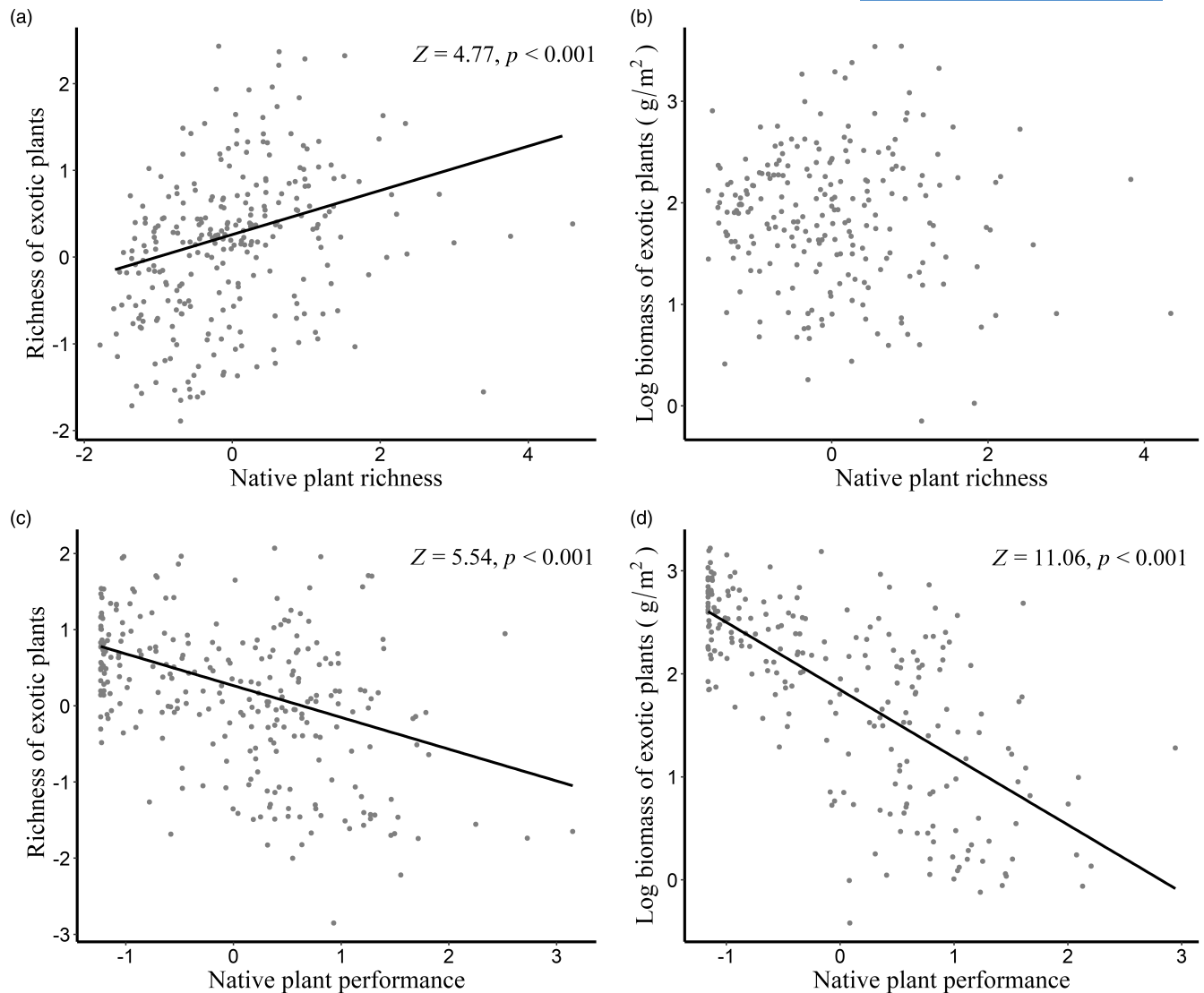
FIGURE 2 Relationships between the richness of exotic plants and native plant richness (a), the biomass of exotic plants and native plant richness (b), the richness of exotic plants and native plant performance (c), and the biomass of exotic plants and native plant performance (d) at the site scale. The native plant richness was standardized, and native plant performance was the average of the standardized values of the biomass and coverage of native plants. The plots are constructed under the condition that the other predictors are the intercept values, the parameter estimates are listed in Table 1.

(Santos et al., 2011; Thiébaut & Martinez, 2015). In contrast, the biomass of exotic emergent and floating plants, as well as the biomass of exotic submerged plants in low-nutrient water bodies, was lower in quadrats with high native plant richness. The different invasibility metrics convey different types of information; richness of exotic plants indicates the number of species that have successfully invaded, while biomass of exotic plants quantifies the dominance and impact of exotic plants (Carniatto et al., 2013; Jeschke et al., 2018). This finding suggests that native plant richness does not play a role in preventing the successful establishment of exotic aquatic plants. However, high native plant richness may mitigate the subsequent severity of plant invasions at small scales, and this buffering effect is environment-dependent (Delavaux et al., 2023; Jeschke et al., 2018).

Our study indicated that strong native plant performance is associated with a reduction in population growth and the impact of exotic aquatic plants at both the large and small scales. Furthermore, it is related to a community's ability to repel some exotic plants before they become established. Native plants with high density, biomass and coverage can reduce the successful establishment of exotic plants by occupying available niche space and nutrients (Chadwell & Engelhardt, 2008), enhancing shading (Evangelista et al., 2017) and preventing fragments of exotic plants from rooting into sediment (Thiébaut & Martinez, 2015). With sufficient density, native plants can also act as a barrier to prevent exotic plants from migrating into the community from neighbouring areas. These findings indicate that the invasion resistance in freshwater ecosystems is more closely related to the native plant
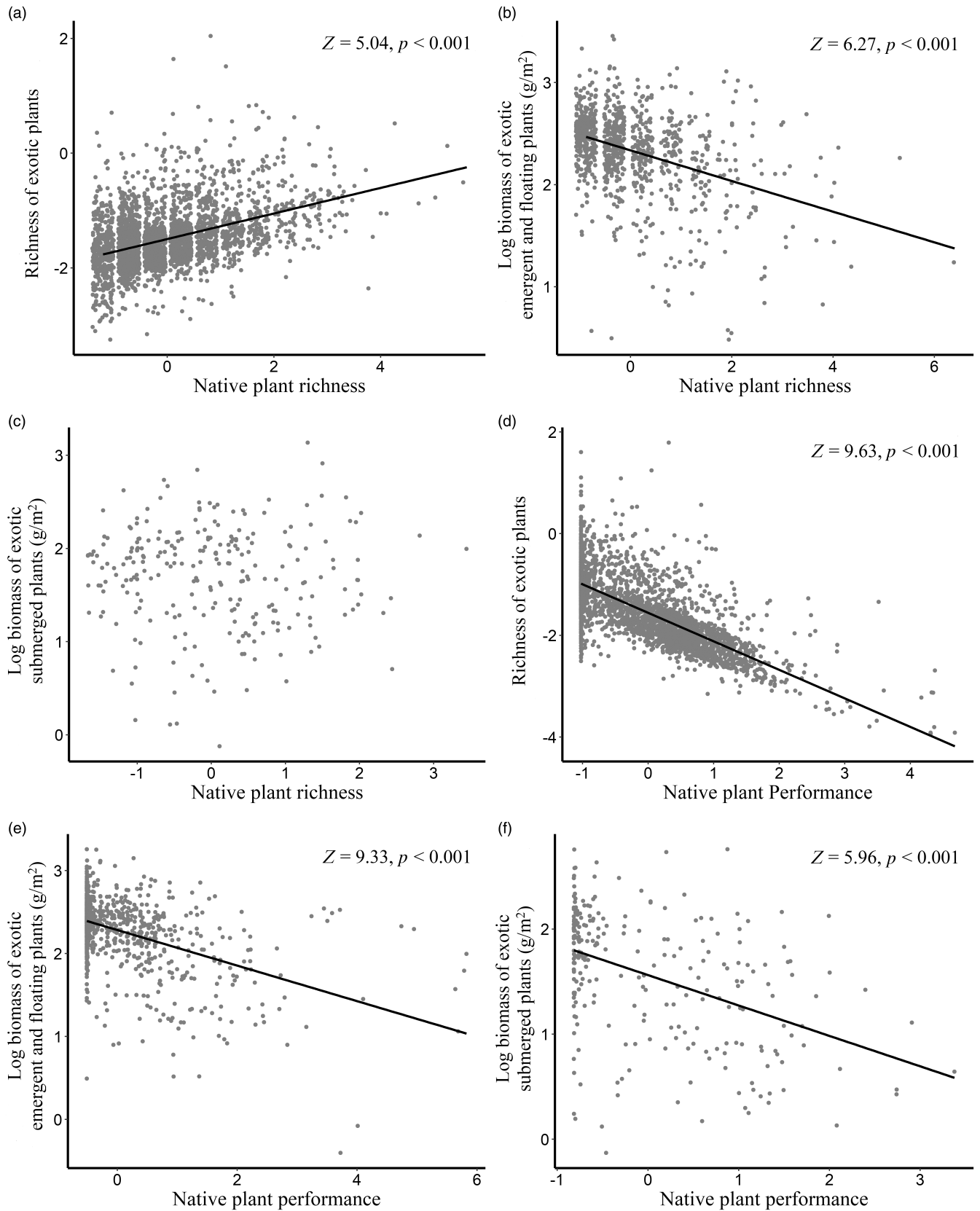
FIGURE 3 Relationships between the richness of exotic plants and native plant richness (a), the biomass of exotic emergent and floating plants and native plant richness (b), the biomass of exotic submerged plants and native plant richness (c), the richness of exotic plants and native plant performance (d), the biomass of exotic emergent and floating plants and native plant performance (e), and the biomass of exotic submerged plants and native plant performance (f) at the quadrat scale. The native plant richness was standardized, and the native plant performance was the average of the standardized values of the biomass and coverage of native plants. The plots are constructed under the condition that the other predictors are the intercept values, the parameter estimates are listed in Table 2.
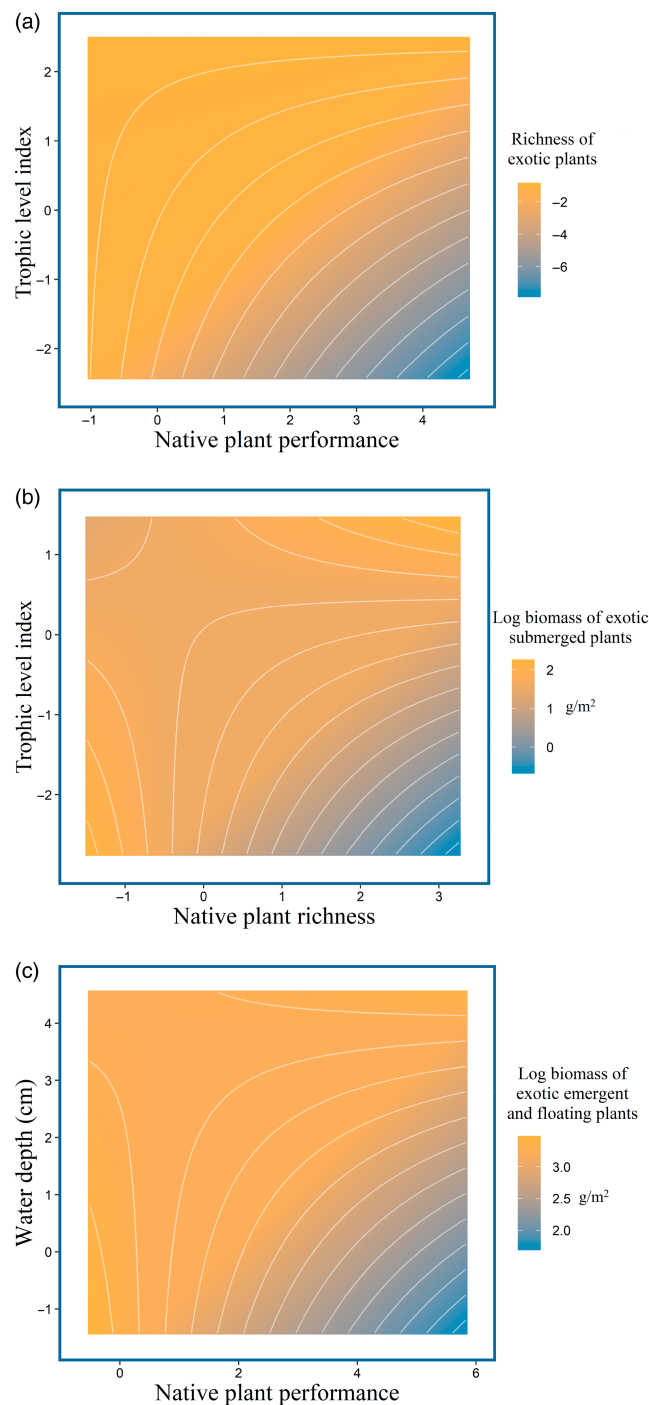
FIGURE 4 Effects of the interaction between native plant performance and the trophic level index on the richness of exotic plants (a), the interaction between native plant richness and the trophic level index on the biomass of exotic submerged plants (b), and the interaction between native plant performance and water depth on the biomass of exotic emergent and floating plants (c) at the quadrat scale. The native plant richness was standardized, and the native plant performance was the average of the standardized values of the biomass and coverage of native plants. The trophic level index was calculated based on the concentrations of total nitrogen (mg/L), total phosphorus (mg/L), and chemical oxygen demand (mg/L) in the water. The interactions shown represent the given predicted value of the richness or biomass of exotic aquatic plants under each group mean-centred biotic and environmental factors.

The observed negative relationships between native and exotic plants may be caused by the effects of biotic resistance and/or the impact of exotic plants on native communities. Our models included many environmental factors, which are often strongly correlated with the abundance of exotic plants. For example, high nitrogen and phosphorus contents in water increase the abundance and competitiveness of almost all exotic emergent and floating plants and enhance the harmful impacts of these exotic plants (Henry-Silva et al., 2008; Hussner et al., 2009; Wilson et al., 2005; Zhang et al., 2017). If biotic resistance was not in effect, exotic emergent and floating plants would be expected to dominate all eutrophic water bodies regardless of the richness and performance of the native plants. Rather, the biomass of exotic emergent and floating plants decreased with increasing native plant richness and native plant performance in high-nutrient water bodies, as it did in low-nutrient water bodies (there were nonsignificant interactions between native plant richness/performance and the trophic level index in the model for the biomass of exotic emergent and floating plants, as shown in Table 2). An experimental study also shown that biotic resistance effectively suppressed the growth of the emergent invasive plant *Urochloa arrecta* under both nutrient-enriched and non-enriched conditions (Teixeira et al., 2017). This suggests that biotic resistance contributes to the observed negative relationships between native and exotic plants, which is similar to the findings of a previous report (Beaury et al., 2020). Another factor that should not be overlooked is that exotic plants competitively exclude native species, leading to the negative relationships. While exotic plants have a negligible effect on native communities during their early establishment phase in a new ecosystem (Sapsford et al., 2020), they inevitably have adverse effects on native plants once they have developed considerable populations. Our field survey did not completely clarify the causal relationship between native plants and exotic plant invasion. It is necessary to continue exploring resistance of aquatic plant communities to exotic plant invasions under various environmental conditions and at different phases of invasive plant establishment through controlled and in situ experiments.

performance (in terms of biomass and coverage) than to native plant richness. The efficacy of biotic resistance to aggressive invasive species was considered to be lower than to exotic noninvasive species (Bufford et al., 2016; Nunez-Mir et al., 2017). In our study, although only four plants were identified as aggressive invasive species, they were the dominant exotic species in 86% of the exotic emergent and floating plant communities and in 65% of the exotic submerged plant communities. This implies that in freshwater ecosystems, native plants could mitigate the impact of exotic plants regardless of the characteristics and life forms of the exotic plants.

In our study, water eutrophication was associated with a decrease in the biotic resistance of native plant performance to the

richness of exotic plants. High nutrient availability can improve the growth, size, reproduction capacity, overwinter rates, and competitiveness of exotic aquatic plants (Xie et al., 2010; Yu et al., 2019), thus promoting the successful establishment of exotic plants that are in competition with native plants. An increase in water nutrients even turned the negative relationship between the biomass of exotic submerged plants and native plant richness into a positive relationship (Figure 4b). This finding was consistent with the stress-gradient hypothesis: net competitive effects are intense in relatively benign, low-stress environments, whereas facilitative effects are common under high abiotic stress conditions (Maestre et al., 2009). Eutrophication, which leads to high phytoplankton concentration and low light availability in water bodies, creates a harsh, high-stress environment for both exotic and native submerged plants (Phillips et al., 2016; Wersal & Madsen, 2011). Under eutrophic conditions, a high abundance of exotic submerged plants improves the biodiversity of native submerged plants by reducing phytoplankton populations, suspended solids concentrations and light attenuation (Rybicki & Landwehr, 2007; Scheffer & Carpenter, 2003). Similarly, a high diversity of native submerged plants increases the likelihood of the presence of shade-tolerant species, which can increase the growth and biomass of exotic submerged plants by buffering the effects of eutrophication (Le Bagousse-Pinguet et al., 2012).

In addition, the biotic resistance strength of the native community to exotic emergent and floating plants was related to water depth. Water depth is a crucial factor determining the distribution, reproduction, and growth of aquatic plants (Bornette & Puijalon, 2011). In shallow water, diverse native plant communities with complex community structures can compete with exotic emergent and floating plants for most of the resources required for the growth of the exotic plants. However, in deep water, the dominant native species are usually submerged plants (Fu et al., 2014; Ma et al., 2021), and they can only compete with exotic floating plants for the nutrients in water but not for space or light. Therefore, the biotic resistance strength of native plant performance to exotic emergent and floating plants is lower in deep waters than in shallow waters.

In conclusion, we conducted an extensive, multiscale field survey and studied the impacts of environmental factors on the relationship between native and exotic plants. The results show that the native plant performance is more important than richness for resistance to invasion in freshwater ecosystems. Furthermore, the strength of biotic resistance is influenced by environmental factors. These findings reveal why biotic resistance in freshwater ecosystems was not detected in previous field observations. In addition, our study suggests that, rather than focusing on biodiversity conservation alone, we should incorporate additional strategies such as enhancing the coverage and productivity of native vegetation as well as improving habitat conditions by reducing nutrient levels in water bodies to more effectively control aquatic invasive plants.

AUTHOR CONTRIBUTIONS

Shufeng Fan, Tian Lv and Haihao Yu contributed equally to the study; Dan Yu, Chunhua Liu and Shufeng Fan designed the research and executed the research project; Shufeng Fan, Tian Lv, Haihao Yu, Lei Yang, Ligong Wang and Yang Li collected most of the field data; Shufeng Fan, Tian Lv, Chunhua Liu and Lei Yang analysed data; Shufeng Fan, Haihao Yu and Chunhua Liu led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14439.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.3j9kd51tz (Fan et al., 2024).

ORCID

Shufeng Fan https://orcid.org/0000-0002-5930-2631

Tian Lv https://orcid.org/0000-0003-2613-6734

Yang Li https://orcid.org/0000-0001-8555-0201

Chunhua Liu https://orcid.org/0000-0002-3932-477X

REFERENCES

Aguiar, F. C., Ferreira, M. T., & Albuquerque, A. (2006). Patterns of exotic and native plant species richness and cover along a semi-arid Iberian river and across its floodplain. *Plant Ecology*, *184*(2), 189–202. https://doi.org/10.1007/s11258-005-9064-5

Barton, K. (2009). *MuMIn: Multi-model inference, R package version 0.12.0*. Httpr-Forg-Proj. https://ci.nii.ac.jp/naid/10030574914/

Beaury, E. M., Finn, J. T., Corbin, J. D., Barr, V., & Bradley, B. A. (2020). Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecology Letters*, *23*(3), 476–482. https://doi.org/10.1111/ele.13446

Belote, R. T., Jones, R. H., Hood, S. M., & Wender, B. W. (2008). Diversity-invasibility across an experimental disturbance gradient in Appalachian forests. *Ecology*, 89(1), 183–192. https://doi.org/10.1890/07-0270.1

Bornette, G., & Puijalon, S. (2011). Response of aquatic plants to abiotic factors: A review. *Aquatic Sciences*, 73(1), 1–14. https://doi.org/10.1007/s00027-010-0162-7

Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400. https://doi.org/10.3929/ethz-b-000240890

Bufford, J. L., Lurie, M. H., & Daehler, C. C. (2016). Biotic resistance to tropical ornamental invasion. *Journal of Ecology*, 104(2), 518–530. https://doi.org/10.1111/1365-2745.12534

Byun, C., de Blois, S., & Brisson, J. (2015). Interactions between abiotic constraint, propagule pressure, and biotic resistance regulate plant invasion. *Oecologia*, 178(1), 285–296. https://doi.org/10.1007/s00442-014-3188-z

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 Science*, 33(2), 405–413. https://doi.org/10.18307/2021.0203

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. https://doi.org/10.1890/06-1911.1

Carniatto, N., Thomaz, S. M., Cunha, E. R., Fugi, R., & Ota, R. R. (2013). Effects of an invasive alien Poaceae on aquatic macrophytes and fish communities in a Neotropical reservoir. *Biotropica*, 45(6), 747–754. https://doi.org/10.1111/btp.12062

Cassey, P., García-Díaz, P., Lockwood, J. L., Blackburn, T. M., Jeschke, J., & Heger, T. (2018). Invasion biology: Searching for predictions and prevention, and avoiding lost causes. In J. M. Jeschke & T. Heger (Eds.), *Invasion biology: Hypotheses and evidence* (pp. 3–13). CAB International.

Chadwell, T. B., & Engelhardt, K. A. M. (2008). Effects of pre-existing submersed vegetation and propagule pressure on the invasion success of *Hydrilla verticillata*. *Journal of Applied Ecology*, 45(2), 515–523. https://doi.org/10.1111/j.1365-2664.2007.01384.x

Chen, H., Qian, H., Spyreas, G., & Crossland, M. (2010). Native-exotic species richness relationships across spatial scales and biotic homogenization in wetland plant communities of Illinois, USA. *Diversity and Distributions*, 16(5), 737–743. https://doi.org/10.1111/j.1472-4642.2010.00679.x

Clark, G. F., & Johnston, E. L. (2011). Temporal change in the diversity-invasibility relationship in the presence of a disturbance regime. *Ecology Letters*, 14(1), 52–57. https://doi.org/10.1111/j.1461-0248.2010.01550.x

Cook, C. D. K., Gut, G. J., Rix, E. M., Schneller, J., & Seitz, M. (1974). *Water plants of the world: A manual for the identification of the genera of freshwater macrophytes: Springer Dordrecht* (1st ed.). Pro-ed.

Dalton, R. L., Boutin, C., & Pick, F. R. (2015). Nutrients override atrazine effects on riparian and aquatic plant community structure in a north American agricultural catchment. *Freshwater Biology*, 60(7), 1292–1307. https://doi.org/10.1111/fwb.12563

Davies, K. F., Chesson, P., Harrison, S., Inouye, B. D., Melbourne, B. A., & Rice, K. J. (2005). Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology*, 86(6), 1602–1610. https://doi.org/10.1890/04-1196

Davies, K. F., Harrison, S., Safford, H. D., & Viers, J. H. (2007). Productivity alters the scale dependence of the diversity-invasibility relationship. *Ecology*, 88(8), 1940–1947. https://doi.org/10.1890/06-1907.1

Delavaux, C. S., Crowther, T. W., Zohner, C. M., Robmann, Z. M., Lauber, T., van den Hoogen, J., Kuebbing, S., Liang, J., de-Miguel, S., Nabuurs, G., Reich, P. B., Abegg, M., Yao, Y. C. A., Alberti, G., Zambrano, A. M. A., Alvarado, B. V., Alvarez-Dávila, E., Alvarez-Loayza, P., Alves, L. F., ... Maynard, D. S. (2023). Native diversity buffers against severity of non-native tree invasions. *Nature*, 621, 773–781. https://doi.org/10.1038/s41586-023-06440-7

Ernst, A. R., Barak, R. S., Hipp, A. L., Kramer, A. T., Marx, H. E., & Larkin, D. J. (2022). The invasion paradox dissolves when using phylogenetic and temporal perspectives. *Journal of Ecology*, 110, 443–456. https://doi.org/10.1111/1365-2745.13812

Eskelinen, A., & Harrison, S. (2014). Exotic plant invasions under enhanced rainfall are constrained by soil nutrients and competition. *Ecology*, 95(3), 682–692. https://doi.org/10.1890/13-0288.1

Evangelista, H. B., Michelan, T. S., Gomes, L. C., & Thomaz, S. M. (2017). Shade provided by riparian plants and biotic resistance by macrophytes reduce the establishment of an invasive Poaceae. *Journal of Applied Ecology*, 54(2), 648–656. https://doi.org/10.1111/1365-2664.12791

Fan, S., Lv, T., Yu, H., Yang, L., Wang, L., Li, Y., Liu, C., & Yu, D. (2024). Data from: Interplay between native plant performance and environment shapes resistance to aquatic plant invasion. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.3j9kd51tz

Fargione, J. E., & Tilman, D. (2005). Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, 8(6), 604–611. https://doi.org/10.1111/j.1461-0248.2005.00753.x

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), 349–364. https://doi.org/10.3391/ai.2021.16.2.09

Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D. F., Seabloom, E. W., Smith, M. D., Stohlgren, T. J., Tilman, D., & Holle, B. V. (2007). The invasion paradox: Reconciling pattern and process in species invasions. *Ecology*, 88(1), 3–17. https://doi.org/10.1890/0012-9658(2007)88[3:TIPRPA]2.0.CO;2

Fu, H., Zhong, J., Yuan, G., Ni, L., Xie, P., & Cao, T. (2014). Functional traits composition predict macrophytes community productivity along a water depth gradient in a freshwater lake. *Ecology and Evolution*, 4(9), 1516–1523. https://doi.org/10.1002/ece3.1022

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. https://doi.org/10.1111/gcb.13004

Gerhardt, F., & Collinge, S. K. (2007). Abiotic constraints eclipse biotic resistance in determining invasibility along experimental vernal pool gradients. *Ecological Applications*, 17(3), 922–933. https://doi.org/10.1890/05-1146

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. https://doi.org/10.1007/s10531-015-0973

Griffith, A. B., Rodgers, V. L., & Dukes, J. S. (2021). Demographic analysis of invasible habitat fraction identifies context-dependent roles of resource availability and biotic resistance in determining invasion success. *Journal of Ecology*, 109(2), 714–726. https://doi.org/10.1111/1365-2745.13498

Guo, Q. (2015). No consistent small-scale native-exotic relationships. *Plant Ecology*, 216(9), 1225–1230. https://doi.org/10.1007/s11258-015-0503-7

Hagan, J. G., Vanschoenwinkel, B., & Gamfeldt, L. (2021). We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. *Ecology Letters*, 24(12), 2537–2548. https://doi.org/10.1111/ele.13874

Henry-Silva, G. G., Camargo, A. F. M., & Pezzato, M. M. (2008). Growth of free-floating aquatic macrophytes in different concentrations of

nutrients. *Hydrobiologia*, *610*(1), 153–160. https://doi.org/10.1007/s10750-008-9430-0

Hill, K. C., & Fischer, D. G. (2014). Native-exotic species richness relationships across spatial scales in a prairie restoration matrix. *Restoration Ecology*, *22*(2), 204–213. https://doi.org/10.1111/rec.12067

Hulvey, K. B., & Teller, B. J. (2018). Site conditions determine a key native plant's contribution to invasion resistance in grasslands. *Ecology*, *99*(6), 1257–1264. https://doi.org/10.1002/ecy.2227

Hussner, A. (2012). Alien aquatic plant species in European countries. *Weed Research*, *52*(4), 297–306. https://doi.org/10.1111/j.1365-3180.2012.00926.x

Hussner, A., Meyer, C., & Busch, J. (2009). The influence of water level and nutrient availability on growth and root system development of *Myriophyllum aquaticum*. *Weed Research*, *49*(1), 73–80. https://doi.org/10.1111/j.1365-3180.2008.00667.x

Iannone, B. V., Potter, K. M., Hamil, K. A. D., Huang, W., Zhang, H., Guo, Q., Oswalt, C. M., Woodall, C. W., & Fei, S. (2016). Evidence of biotic resistance to invasions in forests of the eastern USA. *Landscape Ecology*, *31*(1), 85–99. https://doi.org/10.1007/s10980-015-0280-7

Jeschke, J. M., Debille, S., Lortie, C. J., & Heger, T. (2018). Biotic resistance and Island susceptibility hypotheses. In J. M. Jeschke & T. Heger (Eds.), *Invasion biology: Hypotheses and evidence* (pp. 60–70). CAB International.

Kubelka, V., Šálek, M., Tomkovich, P., Végvári, Z., Freckleton, R. P., & Székely, T. (2018). Global pattern of nest predation is disrupted by climate change in shorebirds. *Science*, *362*(6415), 680–683. https://doi.org/10.1126/science.aat8695

Le Bagousse-Pinguet, Y., Liancourt, P., Gross, N., & Straile, D. (2012). Indirect facilitation promotes macrophyte survival and growth in freshwater ecosystems threatened by eutrophication. *Journal of Ecology*, *100*(2), 530–538. https://doi.org/10.1111/j.1365-2745.2011.01931.x

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. https://doi.org/10.1111/j.1461-0248.2004.00657.x

Levine, J. M., & D'Antonio, C. M. (1999). Elton revisited: A review of evidence linking diversity and invasibility. *Oikos*, *87*, 15–26. https://doi.org/10.2307/3546992

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139

Ma, F., Yang, L., Lv, T., Zuo, Z., Zhao, H., Fan, S., Liu, C., & Yu, D. (2021). The biodiversity-biomass relationship of aquatic macrophytes is regulated by water depth: A case study of a shallow mesotrophic lake in China. *Frontiers in Ecology and Evolution*, *9*, 338. https://doi.org/10.3389/fevo.2021.650001

MacDougall, A. S., Bennett, J. R., Firn, J., Seabloom, E. W., Borer, E. T., Lind, E. M., Orrock, J. L., Harpole, W. S., Hautier, Y., Adler, P. B., Cleland, E., Davies, K., Melbourne, B., Prober, S. M., Bakker, J. D., Fay, P. A., Jin, V. L., Kendig, A., La Pierre, K. J., ... Stevens, C. J. (2014). Anthropogenic-based regional-scale factors most consistently explain plot-level exotic diversity in grasslands. *Global Ecology and Biogeography*, *23*(7), 802–810. https://doi.org/10.1111/geb.12157

Maestre, F. T., Callaway, R. M., Valladares, F., & Lortie, C. J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *Journal of Ecology*, *97*(2), 199–205. https://doi.org/10.1111/j.1365-2745.2008.01476.x

Maron, J., & Marler, M. (2007). Native plant diversity resists invasion at both low and high resource levels. *Ecology*, *88*(10), 2651–2661. https://doi.org/10.1890/06-1993.1

Melbourne, B. A., Cornell, H. V., Davies, K. F., Dugaw, C. J., Elmendorf, S., Freestone, A. L., Hall, R. J., Harrison, S., Hastings, A., Holland, M., Holyoak, M., Lambrinos, J., Moore, K., & Yokomizo, H. (2007). Invasion in a heterogeneous world: Resistance, coexistence or hostile takeover? *Ecology Letters*, *10*, 77–94. https://doi.org/10.1111/j.1461-0248.2006.00987.x

Meza-Lopez, M. M., & Siemann, E. (2017). Nutrient enrichment increases plant biomass and exotic plant proportional cover independent of warming in freshwater wetland communities. *Plant Ecology*, *218*(7), 835–842. https://doi.org/10.1007/s11258-017-0733-y

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. https://doi.org/10.1371/journal.pone.0060004

Muthukrishnan, R., Hansel-Welch, N., & Larkin, D. J. (2018). Environmental filtering and competitive exclusion drive biodiversity-invasibility relationships in shallow lake plant communities. *Journal of Ecology*, *106*(5), 2058–2070. https://doi.org/10.1111/1365-2745.12963

Nunez-Mir, G. C., Liebhold, A. M., Guo, Q., Brockerhoff, E. G., Jo, I., Ordonez, K., & Fei, S. (2017). Biotic resistance to exotic invasions: Its role in forest ecosystems, confounding artifacts, and future directions. *Biological Invasions*, *19*(11), 3287–3299. https://doi.org/10.1007/s10530-017-1413-5

Peng, S., Kinlock, N. L., Gurevitch, J., & Peng, S. (2019). Correlation of native and exotic species richness: A global meta-analysis finds no invasion paradox across scales. *Ecology*, *100*(1), e02552. https://doi.org/10.1002/ecy.2552

Petruzzella, A., da SSR Rodrigues, T. A., van Leeuwen, C. H. A., de Assis Esteves, F., Figueiredo-Barros, M. P., & Bakker, E. S. (2020). Species identity and diversity effects on invasion resistance of tropical freshwater plant communities. *Scientific Reports*, *10*(1), 1–10. https://doi.org/10.1038/s41598-020-62660-1

Petruzzella, A., Manschot, J., van Leeuwen, C. H. A., Grutters, B. M. C., & Bakker, E. S. (2018). Mechanisms of invasion resistance of aquatic plant communities. *Frontiers in Plant Science*, *9*, 134. https://doi.org/10.3389/fpls.2018.00134

Phillips, G., Willby, N., & Moss, B. (2016). Submerged macrophyte decline in shallow lakes: What have we learnt in the last forty years? *Aquatic Botany*, *135*, 37–45. https://doi.org/10.1016/j.aquabot.2016.04.004

Rybicki, N. B., & Landwehr, J. M. (2007). Long-term changes in abundance and diversity of macrophyte and waterfowl populations in an estuary with exotic macrophytes and improving water quality. *Limnology and Oceanography*, *52*(3), 1195–1207. https://doi.org/10.4319/lo.2007.52.3.1195

Sandel, B., & Corbin, J. D. (2010). Scale, disturbance and productivity control the native-exotic richness relationship. *Oikos*, *119*(8), 1281–1290. https://doi.org/10.1111/j.1600-0706.2010.18230.x

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*(2), 443–457. https://doi.org/10.1007/s10530-010-9840-6

Sapsford, S. J., Brandt, A. J., Davis, K. T., Peralta, G., Dickie, I. A., Gibson, R. D., Green, J. L., Hulme, P. E., Nuñez, M. A., Orwin, K. H., Pauchard, A., & Peltzer, D. A. (2020). Towards a framework for understanding the context dependence of impacts of non-native tree species. *Functional Ecology*, *34*(5), 944–955. https://doi.org/10.1111/1365-2435.13544

Scheffer, M., & Carpenter, S. R. (2003). Catastrophic regime shift in ecosystems: Linking theory to observation. *Trends in Ecology & Evolution*, *18*, 648–656. https://doi.org/10.1016/j.tree.2003.09.002

Sirami, C., Gross, N., Baillod, A. B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., ... Fahrig, L. (2019). Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(33), 16442–16447. https://doi.org/10.1073/pnas.1906419116

Smith, N. S., & Cote, I. M. (2019). Multiple drivers of contrasting diversity-invasibility relationships at fine spatial grains. *Ecology, 100*(2), e02573. https://doi.org/10.1002/ecy.2573

Stohlgren, T. J., Jarnevich, C., Chong, G. W., & Evangelista, P. H. (2006). Scale and plant invasions: A theory of biotic acceptance. *Preslia, 78*(4), 405–426.

Stotz, G. C., Pec, G. J., & Cahill, J. F. (2016). Is biotic resistance to invaders dependent upon local environmental conditions or primary productivity? A meta-analysis. *Basic and Applied Ecology, 17*(5), 377–387. https://doi.org/10.1016/j.baae.2016.04.001

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. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Tarasi, D. D., & Peet, R. K. (2017). The native-exotic species richness relationship varies with spatial grain of measurement and environmental conditions. *Ecology, 98*(12), 3086–3095. https://doi.org/10.1002/ecy.2028

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. https://doi.org/10.1111/fwb.12849

Thiébaut, G., & Martinez, L. (2015). An exotic macrophyte bed may facilitate the anchorage of exotic propagules during the first stage of invasion. *Hydrobiologia, 746*(1), 183–196. https://doi.org/10.1007/s10750-014-1982-6

Thomaz, S. M., Silveira, M. J., & Michelan, T. S. (2012). The colonization success of an exotic Poaceae is related to native macrophyte richness, wind disturbance and riparian vegetation. *Aquatic Sciences, 74*, 809–815. https://doi.org/10.1007/s00027-012-0264-5

Von Holle, B. V., & Simberloff, D. (2005). Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology, 86*(12), 3212–3218. https://doi.org/10.1890/05-0427

Wersal, R. M., & Madsen, J. D. (2011). Influences of water column nutrient loading on growth characteristics of the invasive aquatic macrophyte *Myriophyllum aquaticum* (Vell.) Verdc. *Hydrobiologia, 665*, 93–105. https://doi.org/10.1007/s10750-011-0607-6

Wilson, J. R., Holst, N., & Rees, M. (2005). Determinants and patterns of population growth in water hyacinth. *Aquatic Botany, 81*(1), 51–67. https://doi.org/10.1016/j.aquabot.2004.11.002

Xie, D., Yu, D., Yu, L. F., & Liu, C. H. (2010). 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. https://doi.org/10.1007/s10750-010-0402-9

Yu, H., Dong, X., Yu, D., Liu, C., & Fan, S. (2019). Effects of eutrophication and different water levels on overwintering of *Eichhornia crassipes* at the northern margin of its distribution in China. *Frontiers in Plant Science, 10*, 1261. https://doi.org/10.3389/fpls.2019.01261

Zhang, H., Chang, R., Guo, X., Liang, X., Wang, R., & Liu, J. (2017). Shifts in growth and competitive dominance of the invasive plant *Alternanthera philoxeroides* under different nitrogen and phosphorus supply. *Environmental and Experimental Botany, 135*, 118–125. https://doi.org/10.1016/j.envexpbot.2016.12.014

Ziyatdinov, A., Vázquez-Santiago, M., Brunel, H., Martinez-Perez, A., Aschard, H., & Soria, J. M. (2018). lme4qtl: Linear mixed models with flexible covariance structure for genetic studies of related individuals. *BMC Bioinformatics, 19*(1), 1–5. https://doi.org/10.1186/s12859-018-2057-x

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: Habitat types in the field surveys.

Table S2: The initial GLMM and LME models for richness and biomass of exotic plants at the site and quadrat scales.

Table S3: List of surveyed exotic aquatic plants.

Table S4: The top models (ΔAICc <2) for predicting richness and biomass of exotic plants at the site and quadrat scales.

Figure S1: Diagrammatic investigation methods of the plant communities in small rivers and canals (1m $<$width $<$5m) or waterbodies with narrow vegetation (A), in shallow pools, rivers, and canals where aquatic plants occurred in both the marginal and central parts (B), in waterbodies where aquatic plants were restricted to the margins of waterbodies, the water depth in the central area of waterbodies was deep, or the vegetation extended considerably far from the shoreline (C).

Figure S2: Photos of field works. (A) community survey in lake, (B) community survey in wetland, (C) community survey in river, (D) community survey in reservoir, (E) community survey in pond, (F) counting plants in shallow water, (G) artificial collection of plants in deep water, (H) artificial collection of plants by boat in deep water, (I) Diving to collect plants in deep water, (J) Collecting aquatic plants in rapids.