Effects of different scenarios of temperature rise and biological control agents on interactions between two noxious invasive plants

Xiaoliang Zhang | Haihao Yu | Tian Lv | Lei Yang | Chunhua Liu | Shufeng Fan | Dan Yu

The National Field Station of Freshwater Ecosystem of Liangzi Lake, College of Ecology, Wuhan University, Wuhan, China

Correspondence
Chunhua Liu and Shufeng Fan, The National Field Station of Freshwater Ecosystem of Liangzi Lake, College of Ecology, Wuhan University, Wuhan 430072, China. Emails: liuchh@163.com; fanran911@163.com

Funding information
This research was supported by the National Natural Science Foundation of China (31500295) and Major Science and Technology Program for Water Pollution Control and Treatment (2015ZX07503-005)

Editor: Marta Carboni

Abstract
Aim: An increasing number of exotic plants and their biological control agents are being introduced into new regions. Therefore, it is necessary to study their interactions and to manage the future directions of plant invasions under different scenarios of temperature rise.

Location: China.

Method: We investigated the distribution patterns of the two most prevalent invasive aquatic plants in the world, Alternanthera philoxeroides and Eichhornia crassipes, at a large scale and studied the interactions of both invasive plants with their respective biological control agents, Agasicles hygrophila and Neochetina eichhorniae, in response to different scenarios of temperature rise.

Results: Both plants performed better in warmer climates in common garden experiments. However, large populations of A. philoxeroides occurred only in the temperate zone because this species experienced competitive exclusion from E. crassipes and suppression due to A. hygrophila herbivory in tropical and subtropical areas. Moreover, in both subtropical zones, where the two plants and A. hygrophila co-occur, and the temperate zone, where only A. philoxeroides occurs at present, A. hygrophila herbivory and the competition from E. crassipes hindered the performance of A. philoxeroides. Moreover, in the extreme high-temperature environment, A. philoxeroides performance improved, while E. crassipes performance worsened. In addition, the combination of N. eichhorniae herbivory and competition from A. philoxeroides also reduced the performance of E. crassipes, but E. crassipes still dominated when in competition with A. philoxeroides.

Main conclusions: Our results indicate that climate warming and the introduction of herbivores do not alter the interspecific relationship between E. crassipes and A. philoxeroides. Moreover, our study suggests that under climate warming, E. crassipes will replace A. philoxeroides as the dominant species in some communities in...
1 | INTRODUCTION

When exotic plants are introduced into new ranges, they develop novel interactions with native plants. Therefore, many researchers have proposed hypotheses to explain the invasion mechanisms of exotic plants and to predict and manage exotic plants according to the interactions between exotic plants and natives (Jeschke, 2014; Mitchell et al., 2006). After an increasing number of exotic species have invaded the same region (Seebens et al., 2018), one exotic species encountering another exotic species within a habitat becomes unavoidable. Most habitats have been invaded multiple times, and studies of the interactions between multiple invasive species may be as important as studies of native–invasive interactions for understanding the invasion process and for future management of invasive species. However, few studies have analysed invader interactions (Kuebbing & Nuñez, 2015; Kuebbing et al., 2013).

The invasion meltdown hypothesis suggests that some exotic species can facilitate one another’s invasions even if they did not undergo co-evolution (Simberloff, 2006; Simberloff & Von Holle, 1999). One exotic plant can facilitate the invasion of other exotic plants by suppressing shared resident competitors, increasing resource availability (Flory & Bauer, 2014), providing protection from herbivores (Cushman et al., 2011), increasing soil nitrogen availability (Kuebbing & Nuñez, 2015; Von Holle et al., 2006), enhancing pollinator visitation rates as magnet species (Molina-Montenegro et al., 2008) and promoting their dispersal and establishment as nurse species (Tecco et al., 2007). In areas where negative and neutral interactions among exotic plants prevail (Kuebbing & Nuñez, 2015), they exclude and interfere with each other by competing for resources and pollinators (Belote & Weltzin, 2006; Jäger et al., 2009; Metlen et al., 2013; Pfeifer-Meister et al., 2008; Yang et al., 2011).

Herbivory is an important factor affecting interactions among exotic plants (Clay et al., 1993; Hartley & Amos, 1999; Mulder & Russ, 1998; Van et al., 1998). In their introduced ranges, native herbivores tend to accumulate on invasive plants over time due to exotic plants lacking effective defences against them (Parker et al., 2006) or due to the rapid adaptation of predators to invasive species (Siemann et al., 2006). Moreover, the co-evolved specialist enemies of some invasive plants may be introduced into the same area as biological control agents for these invasive plants (Bellows, 2001). Herbivores cause different levels of damage to exotic plants (Carpenter & Cappuccino, 2005; Jogesh et al., 2008), which may alter the interactions among exotic plants. The invasive plant *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae) is highly competitive and can replace other invasive plants, but it was found that *Pistia stratiotes* L. could replace *E. crassipes* after specialist insects were introduced to control the latter species (Center et al., 2005).

Climate warming is the major component of global change (Walther et al., 2009) and can affect the distribution, performance and competitive displacement of invasive plants (Cornellissen et al., 2019; Lehmann et al., 2020; Lu et al., 2013). Many studies have confirmed that climate warming can enhance the competitiveness of exotic invasive plants towards native plants (He et al., 2012; Liu et al., 2017; Wu et al., 2017). Occasionally, it has also reduced an invader’s dominance in areas where invasive plants and native plants grow together (Verlinden et al., 2014). Climate warming can also indirectly alter interactions among plants by affecting the interactions between plants and herbivores. Specialist enemies of invaders can expand their distribution ranges under climate warming, and native plants can be released from competition via disproportionate increases in herbivory on the invader. Therefore, the plant community shifts from being dominated by the invading plant to being dominated by native plants (Lu et al., 2016). In ecosystems that have undergone multiple invasions, climate warming may affect exotic–exotic interactions in the same way that it affects exotic–native interactions. However, there have not been reports on the effects of herbivores and climate warming on the interactions among invasive plants. In addition to the increase in climate warming, extreme high-temperature events are predicted to become more frequent, more intense and longer in duration (Easterling et al., 2000; Meehl & Tebaldi, 2004). Previous studies have also paid little attention to the effects of extreme high-temperature events on the interactions among invasive plants and between plants and their herbivores. Therefore, the relationships among invasive plants and the interactions between invasive plants and their specialist enemies must be considered in the context of climate warming and extremely high temperatures.

Here, we report on a study of the interactions between invasive plants under herbivory and different scenarios of temperature rise. Two invasive aquatic plants, *Alternanthera philoxeroides* (Martius) Grisebach (Amaranthaceae) and *E. crassipes*, and their specialist enemies, *Agasicles hygrophila* Selman and Vogt (Coleoptera: Chrysomelidae) and *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae), were employed as a model system. *A. philoxeroides* and *E. crassipes* are two of the world’s most prevalent invasive aquatic plants. Both species originated from South America and have invaded many countries in the tropical, subtropical and temperate zones of Africa, Asia, North America, Europe and Oceania (Francis, 2012). *A. philoxeroides* and *E. crassipes* were introduced to China in the 1930s and 1950s, respectively. Currently, *A. philoxeroides* has invaded large
areas south of the Yellow River Basin, and _E. crassipes_ is prevalent in south of the Yangtze River (Li & Xie, 2002). Both species have invaded various freshwater bodies in China, where they have changed hydrological environments by destroying native animals and plant communities, reducing species diversity, altering ecosystem structure and function and disrupting food chains and nutrient cycling (Lolis et al., 2020; Portela et al., 2020; Tanveer et al., 2018). To control these two noxious weeds, the specialist beetles _A. hygrophila_ (for _A. philoxeroides_) and _N. eichhorniae_ (for _E. crassipes_) were introduced to China from the original ranges of the two plants in 1986 and 1995, respectively (Ding et al., 2001; Ma, 2001). Currently, _A. hygrophila_ occurs in areas ranging from 20°N to 32°N, whereas the distribution area of _N. eichhorniae_ in China is not yet clear.

In this study, to investigate the distribution patterns of _A. philoxeroides_ and _E. crassipes_ at a large scale, we surveyed the population performance and defoliation of _A. philoxeroides_ and _E. crassipes_ throughout China. To predict the responses of _A. philoxeroides_, _E. crassipes_, _A. hygrophila_ and _N. eichhorniae_ and their interactions to different scenarios of temperature rise, we conducted common garden experiments in environments experiencing two different temperature scenarios. We attempted to address the following questions: (a) What are the distribution patterns and interspecific relationships between these two plant species? (b) How do specialist enemies affect the population performances of these two plant species and their interactions? (c) How do different scenarios of temperature rise affect the plant species, their specialist enemies and their interactions?

### 2 | METHODS

#### 2.1 | Studied species

_Eichhornia crassipes_ is a free-floating aquatic plant. It reproduces both sexually and asexually. In invaded regions, it increases in population size mainly through vegetative reproduction, forming new ramets from axillary buds on stolons that are produced through the elongation of internodes. Under suitable conditions, the population of _E. crassipes_ can double between 1 and 3 weeks through the spread of these daughter plants and will form thick, extensive mats that affect their ecosystems (Gopal, 1987). Sexual reproduction rarely occurs, owing to the lack of suitable pollinators and of appropriate sites for germination and seedling establishment in invaded regions (Barrett, 1980). In tropical China, _E. crassipes_ can grow throughout the year. In subtropical regions, the plant dies in the winter and sprouts new plants from axillary buds on the stem base in the following year.

_Alternanthera philoxeroides_ is a perennial herbaceous plant that is both stoloniferous and amphibious. It can grow prostrate along the ground or across the water surface, rooting at the nodes, anchoring to the shore and forming tangled mats that affect ecosystems. _A. philoxeroides_ expands its population by producing new shoots from each stem node; these shoots can become new plants if they are disconnected. Sexual reproduction in _A. philoxeroides_ is absent in China.

_Neochetina eichhorniae_ originated from South America and is one of the most widely distributed biological control agents of _E. crassipes_. The adult weevils are nocturnal, and they feed externally (foliage and petiole) within _E. crassipes_, causing a decline in photosynthesis in _E. crassipes_. Their eggs are often laid in holes that are chewed into the petiole of _E. crassipes_ by females. _N. eichhorniae_ experiences three larval instar stages. Newly hatched larvae tunnel towards the bases of petioles and into the crowns of the plants, where they excavate small burrows. Water flows into these tunnels and burrows, causing tissue decay and host death. Fully grown larvae exit the crown and move down to the roots to pupate underwater. The minimum generation time is 10 weeks, and the average lifespan of adults is over 90 days (Julien, 2001).

_Agasicles hygrophila_ is a monophagous flea beetle used as a biological control agent for _A. philoxeroides_. It is native to the Paraná River basin, Rio de la Plata and the maritime borders of Uruguay and southern Brazil. Females deposit an average of 32 eggs in a mass of two parallel rows on the undersides of the leaves of _A. philoxeroides_ (Telesnicki et al., 2011). The three larval instars and the adults feed on the leaves and stems of _A. philoxeroides_, producing feeding holes and trenches on the leaves. Prepucae chew a circular hole into the internode of the plant and then pupate in the hollow stems. Generally, the period from egg laying to adults hatching is three weeks, and the average lifespan of adults in South China is approximately 6 weeks (Fu, 2007).

#### 2.2 | Field surveys

To examine the effects of temperature rise on the distributions and defoliation of _A. philoxeroides_ and _E. crassipes_, we surveyed communities of _A. philoxeroides_ and _E. crassipes_ in various freshwater ecosystems throughout mainland China and Hainan Island from June to October in 2015, 2016 and 2017. In each location, a systematic sampling technique was employed to survey the plant communities. Generally, 9–20 quadrats (1 m × 1 m) were placed along three to six transects, and more quadrats and transects were placed in communities with high species richness and complex community structures. In some communities with low species richness, the distances between the two quadrats and transects were long (30 m, 50 m, 100 m, 200 m); in some communities with high species richness and complex community structures, the distances were shorter (5 m, 10 m, 20 m). Briefly, the quadrats in each community were selected to fully reflect the local community structure as much as possible. For each quadrat, the coverages of _A. philoxeroides_ and _E. crassipes_ were determined by visual estimation on a 22-degree scale: 0.5%, 1%, 5%, 10%, 15%, 20% …100%. Then, all the plants of _A. philoxeroides_ and _E. crassipes_ were collected and dried at 70°C for more than 48 hr to determine the total biomass of each species. Next, the mean coverage and biomass of _A. philoxeroides_ and _E. crassipes_ in each location were calculated.
The defoliation (% of leaf area removed) of A. philoxeroides and E. crassipes by herbivores was also assessed. First, the existence of specialist enemies (N. eichhorniae and A. hygrophila) was determined directly by, searching for the specialist enemies in the communities, or indirectly, by looking for traces of foliage feeding. Then, 10–20 plants of A. philoxeroides or E. crassipes in each quadrat were randomly selected. The damaged leaves on each of the selected plants were checked, and the damage was scored on a seven-degree scale: 1 (the whole leaf was damaged), 3/4 (most parts of the leaf were damaged), 1/2 (half of the leaf was damaged), 1/4, 1/8, 1/16 and 1/32.

The defoliation of each plant (D) was calculated as follows:

\[ D = \frac{N_r}{N_t} \times 100\% \]

where \( N_r \) is the total number of individual plants and \( N_t \) is calculated as the sum of the leaf damage scores.

### 2.3 Common garden experiment

In order to examine the effects of different scenarios of temperature rise on the interactions between A. philoxeroides and E. crassipes under the pressure of herbivory, we adopted the temperature difference caused by the difference in latitudes to examine these effects. Therefore, common garden experiments were established at two sites (Ezhou City, 30.271713°N, 114.568791°E; Xinmi City, 34.463588°N, 113.355276°E) in China. Meanwhile, the same experimental set-up that was established in the natural environments at Ezhou and Xinmi was established in a greenhouse in Ezhou city. The air temperature during our experiment in the Ezhou greenhouse could reach 50°C at midday on certain days; hence, the Ezhou greenhouse was considered to represent extreme high-temperature events. Ezhou and Xinmi experience a monsoon climate, with hot, wet summers and cold winters. Ezhou is located in a subtropical zone. Over the past 30 years, the mean annual precipitation was 1402 mm, the minimum mean air temperature was 1.9°C (in January), and the maximum mean temperature was 33.3°C (in July). In contrast, Xinmi is located in a temperate zone. Over the past 30 years, the mean annual precipitation was 640.9 mm, the minimum mean temperature was −3.7°C (in January), and the maximum mean temperature was 31.7°C (in July) (http://data.cma.cn/). During our experiment, the daily average temperature and accumulated light intensity in Ezhou were both higher than those in Xinmi (Figure 1a,c). The average temperature in the greenhouse was 1.86°C higher than that in the natural environment (Figure 1b). During the experiment, the average temperature in the greenhouse was 33.13°C, and the instantaneous maximum temperature reached 52°C. Therefore, the Ezhou greenhouse experienced extremely high temperatures.

The common garden experiment had a split-plot design, with the experimental site (Ezhou, Ezhou greenhouse and Xinmi) as the whole-plot factor and the culture type (monoculture or mixed culture) and herbivory treatment (no herbivory or herbivory by specialist enemies) as subplot factors within the whole-plot factor (experimental sites). At each site, 36 aquariums (100 cm length × 65 cm width × 70 cm height) were used as the experimental containers. To simulate the natural shoreline of a waterbody, washed sand was used as the sediment to form a slope; more details of the experimental setup are provided in Figure S1. The total nitrogen (TN); total phosphorus (TP) in the drinking water of Ezhou = 0.71±0.04 mg/L; the TN: TP in the water of Xinmi = 0.56±0.04 mg/L. We added 50 g slow-release Osmocote fertilizer (Osmocote Exact, SCOTTS, USA., containing 16 g TN, 9 g P2O5, 12 g K2O5, 2 g MgO, 0.02 g B, 0.05 g Cu, 0.03 g Fe, 0.02 Mo and 0.014 Zn per 100 g) to the sediment to ensure that sufficient nutrients were available to support plant growth and to eliminate nutrient limitations. The fertilizer was evenly spread on the surface of the sand in each aquarium. The containers were randomly assigned to six treatments: (1) control (no herbivory), A. philoxeroides monoculture; (2) control (no herbivory), E. crassipes monoculture; (3) control (no herbivory), mixed culture of A. philoxeroides + E. crassipes; (4) herbivory (two newly mated pairs of A. hygrophila), A. philoxeroides monoculture; (5) herbivory (four newly mated pairs of N. eichhorniae), E. crassipes monoculture; and (6) herbivory (two newly mated pairs of A. hygrophila and four newly mated pairs of N. eichhorniae), mixed culture of A. philoxeroides + E. crassipes (Figure S2). To examine the effects of extremely high temperatures, the same experimental set-up was established in the Ezhou greenhouse. Each treatment combination had six replicates.

In June 2018, approximately 300 shoots of A. philoxeroides and 300 clonal ramets of E. crassipes were collected from Liangzi Lake and cultivated at the National Field Station of Freshwater Ecosystems of Liangzi Lake, Hubei Province, China (30°50′–30°180′N, 114°210′–114°390′E). From 13 to 18 July 2018, when the biomass of the two plant species was similar, 72 plants of A. philoxeroides of similar height and weight (dry weight: 2.11 ± 0.48 g) and 72 plants of E. crassipes of similar size (dry weight: 1.93 ± 0.3 g) were taken to the three experimental sites and planted in each aquarium according to the experimental design (Method S1). In each aquarium, groups of plants of one or both species were planted next to each other in the centre of the aquarium in 5 cm of water (Figure S3). After 32 days, the herbivory treatment (with the presence or absence of specialist enemies) was applied. Two newly mated pairs of A. hygrophila were released into each aquarium assigned to the A. philoxeroides herbivory treatments (both the monoculture and the mixed culture), and four newly mated pairs of N. eichhorniae were released into each aquarium assigned to the E. crassipes herbivory treatment (both the monoculture and the mixed culture). More specialist enemies were added to the E. crassipes treatment than to the A. philoxeroides treatment because the biomass and ramet number of E. crassipes were approximately twice as high as those of A. philoxeroides at that point in the experiment (Figure S2). The experiment ended after 40 days of herbivory by the specialist enemies and lasted 72 days. During the experiment, all aquariums were covered with white nylon nets (120 mesh, light intensity of ≥95%). The temperature and light intensity were monitored in the field at the three sites at 30-min intervals with a HOBO MX2202 sensor (Onset, USA).
At the end of the experiment, the larvae and adults of *A. hygrophiła* and *N. eichhorniae* in each aquarium were counted. Then, the defoliation of *A. philoxeroides* and *E. crassipes* in herbivory treatments was measured by the method used in the field surveys. Last, the plants were harvested, and the dead ramets of each species in each aquarium were counted. All plants were then washed and dried at 70°C for more than 48 hr. Their biomass was then determined, and the relative growth rate (RGR) was calculated as \[\frac{\ln (\text{total biomass}) - \ln (\text{initial biomass})}{\text{days}}\] (Pérez-Harguindeguy et al., 2013).

### 2.4 Data analysis

For field surveys, we used generalized linear mixed models in the lme4 Package in R to analyse how the average air temperature influenced the biomass, coverage and defoliations of both invasive plants *A. philoxeroides* and *E. crassipes* and nested habitat type within quadrat as a random effect. Because the defoliation and coverage are the ratio data of the range from 0 to 1, and we chose the binomial distribution for the response variable of coverage and defoliation. The biomass value is positive real numbers; we chose Gamma distributions for the biomass of both invasive plants. Then, we applied smooth functions to demonstrate the trends of the biomass, coverages and defoliations of *A. philoxeroides* and *E. crassipes* to average air temperature in ggplot2 Package in R. Then, ANOVA was used to diagnose the differences in biomass between *A. philoxeroides* and *E. crassipes* growing together and in monoculture in each field quadrat, and Duncan tests were used to compare levels within factors for significance (\(p < .05\)).

The common garden experiments were performed in a split-plot design, with the experimental site (Xinmi, Ezhou and Ezhou greenhouse) as a whole-plot factor and the culture type (monoculture or mixed culture) and the herbivory treatment (no herbivory or herbivory by specialist enemies) as subplot factors within the whole-plot factor (the experimental site). At each experimental site, all aquariums were randomly assigned to each treatment combination. Then, mixed ANOVAs were applied to test the effects of the experimental site (whole-plot factor), culture type (subplot factor), herbivory treatment (subplot factor) and their interactions on the biomass and RGR of *E. crassipes* and *A. philoxeroides*. When significant interactive effects were detected, Duncan tests were used to compare levels within factors for significance (\(p < .05\)). Before data analysis, the biomass data were transformed using a Ln (x) function. As all leaves

![Figure 1](image)

**Figure 1** Average daily temperature (a) and daily accumulated light intensity (c) at two common garden experiment sites and the temperature difference (b) and mean temperature difference at different times of day (d) inside and outside of the Ezhou greenhouse.
were intact and no ramet death occurred in the control treatments (no herbivory), the defoliation and mortality of each plant species and the abundance of each herbivore were analysed only within the herbivory treatments. We used the Kruskal function within "agricolae" package conducting two-factor nonparametric test to determine the effects of the combination of the experimental site (whole-plot factor), culture type (subplot factor) and their interaction on the number of \( E.\ crassipes \) dead ramets and \( E.\ crassipes \) and \( A.\ philoxeroides \) defoliation.

To identify the mechanisms underlying the direct and indirect impacts of the combination of herbivory and different of temperature rises on the relationship of both noxious invasive plants and their specialist enemies, a structural equation model (SEM) was developed to specifically test for how specialist enemies mediate the interaction between invasive plants under climate warming or extremely high temperatures. The SEM for climate warming used the data from the Xinmi and Ezhou experimental sites, while the SEM for extremely high temperatures used the data from the Xinmi and Ezhou greenhouse experimental sites. All analyses were performed using R v3.4.2 (R Core Team, 2017).

3 | RESULTS

3.1 | Field surveys

In total, we surveyed 191 locations (Figure 2) and established 1866 quadrats. Of these locations, \( A.\ philoxeroides \) and \( E.\ crassipes \) were present at 158 and 93 locations, respectively. Along the latitudinal gradient, \( A.\ philoxeroides \) was distributed in areas ranging from 18.5°N to 39.7°N, while \( E.\ crassipes \) was distributed in areas ranging from 19.9°N to 31.7°N. Within areas where the ranges of the two species overlapped, there were 98 locations where only \( A.\ philoxeroides \) was present, 33 locations where only \( E.\ crassipes \) was present, and 60 locations where both \( E.\ crassipes \) and \( A.\ philoxeroides \) were present (Figure 2). These results demonstrated that \( A.\ philoxeroides \) and \( E.\ crassipes \) co-occur frequently in the field. In these field surveys, \( A.\ hygrophila \) occurred in areas ranging from 19°N to 33.5°N and \( N.\ eichhorniae \) occurred in areas ranging from 18°N to 23.6°N along the latitudinal gradient (Figure 2).

In the field, with the increase in the average air temperature, the population biomass \( \left( R^2 = 0.228, p < .01 \right) \) and coverage \( \left( R^2 = 0.11, p < .01 \right) \) of \( A.\ philoxeroides \) showed downward trends overall and were low between 20°C and 25°C (north of 32°N). Both the population biomass \( \left( R^2 = 0.0121, p < .01 \right) \) and coverage \( \left( R^2 = 0.031, p < .01 \right) \) of \( E.\ crassipes \) showed significant increasing trends with the rising of average air temperature. Furthermore, the trends in the total biomass of \( A.\ philoxeroides \) and \( E.\ crassipes \) with average air temperature within their distribution ranges were not significant \( \left( R^2 = 0.003, p = .06 \right) \). In the distribution area where the two plant species co-occur, the population coverage and biomass of \( E.\ crassipes \) were consistently higher than those of \( A.\ philoxeroides \) (Figure 3a,b and Figure 4). Moreover, we also found that the biomass in the plots with only \( E.\ crassipes \) was significantly higher than that in the plots with only \( A.\ philoxeroides \) (Figure 4). In areas where \( E.\ crassipes \) was absent, the coverage and biomass of \( A.\ philoxeroides \) were higher than those in other regions (Figure 3a,b). Meanwhile, with the increase in the average air temperature, the defoliation of \( A.\ philoxeroides \) showed a gradually rising trend \( \left( R^2 = 0.085, p < .01 \right) \), while the defoliation of \( E.\ crassipes \) was consistently low and did not show an obvious change trend \( \left( R^2 = 0.011, p = .493 \right) \).

3.2 | Common garden experiment

The experimental site, culture type and herbivory had significant effects on the biomass and RGR of both plant species (Table 1). The biomass and RGR of \( E.\ crassipes \) and \( A.\ philoxeroides \) were both higher in Ezhou than in Xinmi. However, extremely high temperatures (Ezhou greenhouse) reduced the biomass and RGR of \( E.\ crassipes \), while it increased the biomass and RGR of \( A.\ philoxeroides \) (Figure 5a,b). The biomass and RGR of \( A.\ philoxeroides \) were both lower in the mixed-culture and herbivory treatments than in the control treatments (Figure 5a,b). The significant interaction effects of culture type and experimental site and of herbivory and experimental site on the biomass and RGR of \( E.\ crassipes \) suggest that the effects of the culture type and herbivory on \( E.\ crassipes \) differed in the different scenarios of temperature rise (Table 1). Mixed culture and herbivory significantly reduced the biomass of \( E.\ crassipes \) in the extreme high-temperature environment (Ezhou greenhouse) (Figure 5a,b). The significant interaction effects of culture type and herbivory on the biomass and RGR of \( A.\ philoxeroides \) suggest that the effect of herbivory on \( A.\ philoxeroides \) differed between the monoculture and mixed-culture treatments (Table 1). In the monoculture treatments, herbivory reduced the biomass and RGR of \( A.\ philoxeroides \) more intensely than in mixed-culture treatments (Figure 5a,b). Additionally, the biomass and RGR of \( E.\ crassipes \) were higher than those of \( A.\ philoxeroides \) in all treatments (Figure 5a,b), which indicates that \( E.\ crassipes \) has an advantage in competition with \( A.\ philoxeroides \).

The abundances of \( N.\ eichhorniae \) and \( A.\ hygrophila \) differed at the different experimental sites (Table 2). The abundances of \( N.\ eichhorniae \) and \( A.\ hygrophila \) increased with increasing temperature (daily average temperature in Xinmi < Ezhou < Ezhou greenhouse). We found that the differences between the abundances of \( N.\ eichhorniae \) and \( A.\ hygrophila \) in Xinmi and Ezhou were not statistically significant (Figure 6a,b).

Moreover, there were no significant differences in the abundances of \( N.\ eichhorniae \) and \( A.\ hygrophila \) in the monoculture and mixed-culture treatments (Table 2, Figure 6a,b). The defoliation of \( E.\ crassipes \) at the three experimental sites differed, but all the values were quite low; the average defoliation of \( E.\ crassipes \) plants in each treatment was lower than 4% (Table 2, Figure 7a). In contrast, there were no differences in the defoliation of \( A.\ philoxeroides \) among the three experimental sites; all values were relatively high, and the
average *A. philoxeroides* defoliation values in all treatments were ≥34.0% (Table 2, Figure 7b). Moreover, no significant differences in the defoliation of either plant species were detected between the monoculture and mixed-culture treatments at each site (Table 2, Figure 7a,b). In the herbivory treatments, *E. crassipes* mortality varied among experimental sites (Table 2). *E. crassipes* ramet mortality in the Ezhou greenhouse was significantly higher than that in Xinmi and Ezhou (Figure 7c). No *E. crassipes* ramets in the control treatments or *A. philoxeroides* ramets in any treatment died during the experiment.

The SEM indicated that in environments experiencing climate warming, the climate warming significantly improved the performance of *E. crassipes* and *A. philoxeroides*; the abundance of *A. hygrophi*a, the combination of *A. hygrophi*a herbivory and competition from *E. crassipes* negatively affected *A. philoxeroides* (Figure 8a). In the extreme high-temperature environment, the relationships were similar to those in the SEM for climate warming. Notably, with the increase in temperature, the effect of temperature on the performance of *E. crassipes* changed from positive to negative. However, under extremely high temperature, the effect of temperature on the performance of *E. crassipes* was non-significant (Figure 8b).

4 | DISCUSSION

4.1 | Distribution patterns of the two plants

In the field, with the increase in the average air temperature, the population performances of *A. philoxeroides* and *E. crassipes* showed opposing trends. The population coverage and biomass of *A. philoxeroides* decreased gradually, but the population coverage and biomass of *E. crassipes* increased gradually. Climate could explain the distribution pattern of *E. crassipes*, but it could not directly explain the distribution pattern of *A. philoxeroides* because the performances of the two plants were better in a subtropical climate than in a warm temperate climate in our common garden experiments, which shows that both plants are warmth-demanding species. However, climate indirectly determines the distribution pattern of *A. philoxeroides*. The
abundance of *A. hygrophila* is high at low latitudes (Lu et al., 2013). Therefore, the defoliation of *A. philoxeroides* is high, and its performance is limited. *A. philoxeroides* allocates more resources to growth or reproduction and fewer resources to defence due to its release from specialist enemies at high latitudes (Yang et al., 2021). In addition, our study showed that *E. crassipes* restricted the population expansion of *A. philoxeroides* in warmer ranges where both invasive plant species co-occur. A previous study also found *E. crassipes* can decrease the growth of *A. philoxeroides* and have a negative effect on its invasion success (Wundrow et al., 2012). Both now and in the future, most of the distribution areas of *A. philoxeroides* and *E. crassipes* in the world overlap (Hallstan, 2005), and they also frequently overlapped in the field in this study. Therefore, when studying and predicting the distribution and effects of *A. philoxeroides*, attention must be paid to the interaction between *A. philoxeroides* and *E. crassipes* and not only to climate, natural enemies, environmental conditions or resource availability.

4.2 | Effects of herbivory on the growth performances of the two plants and their interactions

Both in the fields where the specialist beetle *A. hygrophila* occurred and in the *A. hygrophila* herbivory treatment in the common garden experiments, the defoliation of *A. philoxeroides* was quite high. *A. hygrophila* affects the growth of *A. philoxeroides* not only by damaging its organs and tissues and reducing its photosynthetic area but also by decreasing the nitrogen concentrations and photosynthetic activity of the remaining intact tissue (Yu & Fan, 2018). Therefore,
**TABLE 1** The effects of culture type, herbivory, experimental site and their interactions on the biomass and RGR of *Eichhornia crassipes* and *Alternanthera philoxeroides*

| Resource | Effect                  | df | Biomass F  | p   | RGR F  | p   |
|----------|-------------------------|----|------------|-----|--------|-----|
|          |                         |    | (p<.05)    |     | (p<.05)|     |
| E. crassipes | Culture type           | 1  | 31.282     | .001| 15.147 | .001|
|          | Herbivory               | 1  | 14.242     | .001| 6.576  | .013|
|          | Site                    | 2  | 140.249    | .001| 111.161| .001|
|          | Culture type ×Herbivory | 1  | 2.269      | .138| 2.017  | .161|
|          | Culture type ×Site      | 2  | 10.624     | .001| 2.766  | .071|
|          | Herbivory ×Site         | 2  | 4.768      | .012| 3.954  | .025|
|          | Culture type ×Herbivory ×Site | 2 | 2.245 | .115| 2.718  | .075|
| A. philoxeroides | Culture type          | 1  | 19.119     | .001| 18.090 | .001|
|          | Herbivory               | 1  | 10.563     | .002| 19.012 | .001|
|          | Site                    | 2  | 68.188     | .001| 71.437 | .001|
|          | Culture type ×Herbivory | 1  | 4.413      | .040| 6.760  | .012|
|          | Culture type ×Site      | 2  | 1.800      | .836| 0.317  | .730|
|          | Herbivory ×Site         | 2  | 1.009      | .371| 2.330  | .107|
|          | Culture type ×Herbivory ×Site | 2 | 2.485 | .092| 1.845  | .168|

Note: Significant results are shown in bold.

**FIGURE 5** Plant biomass (a) and relative growth rate (b) (mean ± SE) of *Eichhornia crassipes* and *Alternanthera philoxeroides* with and without biological control agents growing in monocultures or mixed cultures at different experimental sites. Means with the same letters were not different according to Duncan tests (p > .05). The biomass data were transformed using a ln(x) function.

*A. hygrophila* can effectively control the population of *A. philoxeroides* in China (Lu et al., 2013). In addition, many generalist herbivores in China feed on *A. philoxeroides* (Li et al., 1990, 2008). Although these generalists cause less morphological and physiological damage to *A. philoxeroides* than co-evolved specialists, they can also limit the population spread of *A. philoxeroides* and eliminate the competitive advantage of *A. philoxeroides* over native plants (Fan, Liu, et al., 2013; Fan et al., 2016; Yu & Fan, 2018).

The defoliation of *E. crassipes* was low in the field even in the areas where the specialist *N. eichhorniae* occurred. In the natural environment of the common garden experiment, the defoliation and mortality of *E. crassipes* ramet caused by *N. eichhorniae* were also relatively low. Notably, the distribution area of the specialist in China is much smaller than that of its host plant, *E. crassipes*. Although studies have reported that *N. eichhorniae* can control *E. crassipes* (Ding et al., 2001; Julien, 2001; Reddy et al., 2019), the control effects...
depend on the water nutrient quality, winter temperatures and interference from herbicide operations (Coetzee et al., 2011). Some generalist enemies in China can feed on *E. crassipes*, but the population of *E. crassipes* cannot be well controlled by these enemies (Dong et al., 2008). The higher leaf nitrogen content and thinner foliage of *A. philoxeroides* result in its palatability being higher than those of *E. crassipes* (Fan, Yu, et al., 2013; Fan, Liu, et al., 2013; Yu & Fan, 2018), and generalist enemies will prefer *A. philoxeroides* over *E. crassipes* (Zhao et al., 2014). In addition, *E. crassipes* exhibits high tolerance to herbivory and can fully or even excessively compensate for light defoliation by improving its photosynthetic rates and changing its resource allocation strategy. Simulated herbivory experiments have confirmed that only heavy defoliation (80% clipping leaf) can reduce the growth performance of *E. crassipes* (Lyu et al., 2016; Soti & Volin, 2010). Based on our field observation, the natural enemies could not produce such the heavy defoliation, only caused approximately 2% defoliation. In the native range of *E. crassipes*, herbivory also has minimal effects on the coverage and biomass of *E. crassipes* and its ability to maintain growing populations (Adis & Junk, 2003; Franceschini et al., 2010; Gutiérrez et al., 2001). Our study speculate that herbivory facilitates the *E. crassipes* suppressed the population of *A. philoxeroides*, and the enemy release hypothesis cannot effectively explain the success of *E. crassipes* invasions, and our research also confirmed the speculations of other studies (Lolis et al., 2020).

In systems with multiple exotic species, it is impossible to introduce biocontrol agents for all exotic species. After some invasive plants are controlled by biocontrol agents, they usually become less competitive than the native species. In South Africa, various specialist insects have been introduced as biological control agents to control invasive floating macrophytes. The populations of several invasive plants (e.g. *P. stratiotes, E. crassipes, Salvinia molesta,*...)

---

**TABLE 2** The effects of culture type, experimental site and their interactions on the abundance of *Neochetina eichhorniae* and *Agasicles hygrophila*, the defoliation of *Eichhornia crassipes* and *Alternanthera philoxeroides* and the mortality of *Eichhornia crassipes* due to biological control agents

| Source                          | Effect                      | df  | F value   | p Value |
|---------------------------------|-----------------------------|-----|-----------|---------|
| Abundance of *N. eichhorniae*   | Culture type                | 1.29| 0.415     | .542    |
|                                 | Site                        | 2.29| 17.129    | <.001   |
|                                 | Culture type × Site         | 2.29| 0.339     | .716    |
| Abundance of *A. hygrophila*    | Culture type                | 1.29| 2.349     | .140    |
|                                 | Site                        | 2.29| 14.844    | <.001   |
|                                 | Culture type × Site         | 2.29| 0.041     | .960    |
| Defoliation of *E. crassipes*   | Culture type                | 1.29| 2.911     | .099    |
|                                 | Site                        | 2.29| 4.092     | .027    |
|                                 | Culture type × Site         | 2.29| 0.856     | .435    |
| Defoliation of *A. philoxeroides* | Culture type              | 1.29| 3.557     | .070    |
|                                 | Site                        | 2.29| 0.391     | .680    |
|                                 | Culture type × Site         | 2.29| 0.145     | .866    |
| Mortality of *E. crassipes*     | Culture type                | 1.29| 1.780     | .193    |
|                                 | Site                        | 2.29| 27.202    | <.001   |
|                                 | Culture type × Site         | 2.29| 1.441     | .253    |

Note: Significant results are shown in bold.

**FIGURE 6** Abundance (larvae and adults) (mean ± SD) of *Neochetina eichhorniae* (a) and *Agasicles hygrophila* (b) in monocultures or mixed cultures at different experimental sites. Means with the same letters were not different according to Duncan tests (p >.05)
Myriophyllum aquaticum and Azolla filiculoides) declined after the introduction of these insects; however, the establishment and spread of submerged and emergent invasive plant species increased and still pose significant threats to aquatic ecosystems (Hill et al., 2020). Furthermore, introduced biocontrol agents may also feed on native species (Lu et al., 2015).

4.3 Effects of different scenarios of temperature rise on the growth performances of the two plants and their interactions

In the common garden experiment, the performances of both the plants and the populations of their enemies were better at the subtropical sites than at warm temperate sites, but the interactions among plants and between plants and their enemies were not altered. The overlapping range of the subtropical and warm temperate zones is the same as the northern margin of the distribution of E. crassipes in China, which cannot overwinter in environments with extreme cold temperatures or ice coverage (Madsen et al., 1993; Tyndall, 1982). Over the past decades, winters have become warmer in China, with both the maximum and minimum temperatures increasing (Zhou et al., 2004). In the future, climate warming will continue, especially in winter and at higher latitudes. An increase in temperature in winter can increase the survival rate of E. crassipes (You et al., 2013) and promote the expansion of the distribution of E. crassipes to higher latitudes (Hellmann et al., 2008; Rahel & Olden, 2008). Likewise, climate warming promotes the northward expansion of the distribution of A. philoxeroides (Lu et al., 2013). Hence, we speculate that E. crassipes will replace A. philoxeroides as the dominant species in some communities in warm temperate zones. However, A. philoxeroides will also expand its range farther to the north in response to climate warming.

Extreme high-temperature events can affect competition among plants and trophic interactions, leading to complex responses at the community level (Sentis et al., 2013; White et al., 2001) and facilitating biological invasions (Diez et al., 2012). The influences of extremely high temperatures on aquatic plants are species specific.
Extreme high-temperature environment improved the growth performance of *A. philoxeroides* but reduced that of *E. crassipes*. The reason is that the optimal growth temperatures of *E. crassipes* are 28–30°C, whereas *A. philoxeroides* can still keep a high growth rate at 40°C (Gopal, 1987; Shen et al., 2005), when the air temperature was above 34°C during our experiments, the growth of *E. crassipes* has been decreased. In common garden experiment, the interaction between herbivory and experimental site has broad effect on *E. crassipes* biomass and RGR. This is because the increase in average air temperature leading by experimental site improved the abundances of *N. eichhorniae*. Previous studies investigated that *N. eichhorniae* will not hatch at temperatures below 20°C (Julien, 2001). The increase in average air temperature gradually maintained growing *N. eichhorniae* population, especially extremely high-temperature environment. And, the large number of the specialists had negative effect on its host plant *E. crassipes* (Ding et al., 2001; Julien, 2001). Furthermore, the interaction of herbivory and culture style has significantly affected *A. philoxeroides* biomass and RGR. The reason is that herbivory from *A. hygrophila* have significantly negative on the biomass of *A. philoxeroides*, the result has been proved by other many studies (Lu et al., 2013, 2016). Meanwhile, *E. crassipes* inherent superiority have stronger than that of *A. philoxeroides* (Hua et al., 2012). Hence, *A. philoxeroides* have been suppressed by *E. crassipes* when they co-occurring a habitat (Wundrow et al., 2012).

Additionally, climate warming represents a beneficial development for insect reproduction (Bale & Hayward, 2010; Lehmann et al., 2020), and previous studies have shown that both climate warming and extremely high temperature can facilitate outbreaks of populations of some insects (Ju et al., 2015). In the extreme high-temperature environment in this study, the responses of the biocontrol agent *N. eichhorniae* and the host *E. crassipes* differed. The population of *N. eichhorniae* increased further, and the growth rate of *E. crassipes* decreased. These results imply that *N. eichhorniae* will eventually control the population of *E. crassipes* under continuous extremely high temperature. In addition, in the extreme high-temperature environment, the combination of *N. eichhorniae* herbivory and competition from *A. philoxeroides* reduced the performance of *E. crassipes*. However, *E. crassipes* still dominated when in competition with *A. philoxeroides*. This suggests two conclusions: first, inherent superiority plays a key role in determining the outcome of competition among multiple invasive plants that co-occur in a habitat, and invasive plants do not facilitate each other’s population growth; second, extreme high-temperature events will slow the replacement of *A. philoxeroides* by *E. crassipes* if herbivory occurs, but they will not shift the interaction of the two plants completely.

Finally, in the common garden experiment, temperature rise is beneficial for the biomass of *A. philoxeroides*. But based on the result of field surveys, the biomass decreased with the increase of temperature rise. In other words, our common garden experiments and field surveys showed opposing trends. The reason is that the interaction of many environmental factors determines the distribution of *A. philoxeroides*, not just the temperature and interspecific competition from one species.

### 4.4 Implications for the processes and management of biological invasion

The existence in interspecific competition between invasive plant species demonstrates that invasive plants can resist the invasion of other exotic plants just as native plants do. It also demonstrates that some invasive plants will be replaced by more powerful invasive plants as the dominant species in certain communities. Our study found that not every biological control agent can control its host effectively within the invasion range and that one biological control agent cannot control its host effectively in all areas of the host range. These results indicate that there is a mismatch in the biological distribution of invasive plants and their specialist enemies. Even if some biological control agents of some invasive plants, the affected target plants are more likely to be replaced by other invasive plants than by
natives, especially in communities with multiple invasive plants where biocontrol agents for only few invasive plants have been introduced. Therefore, the introduction of enemies cannot completely eliminate plants invasions in freshwater ecosystems, and a holistic approach to controlling invasive plants will be required (Hill et al., 2020). In addition, our findings imply that predictions of the distribution, performance and effects of invasive plants in the future should be linked to their interactions with enemies and other invasive plants and to climate warming, especially extreme climate events.

ACKNOWLEDGEMENTS

We thank Fei Ma, Yang Li, Xuan Xu, Zhiwei Yan, Chuanxin Cao, Qiankun He, Xiwen Chen, Xianru Dong, Xin Guan, Siqi Yu, Yaping Hong, Huimin Zhou, Shuang Li, Jinghao Zhai, Sulin Fan and Yaqizhou Fan for their valuable work in the field and the laboratory. We also thank our field guides Baobo Zhao and Mingcao Zhai.

CONFLICT OF INTEREST

We have no conflict of interest to disclose.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13406.

DATA AVAILABILITY STATEMENT

The raw data required to reproduce these findings cannot be shared at this time as the data also form part of an ongoing study.

ORCID

Xiaoliang Zhang https://orcid.org/0000-0003-0331-7305
Tian Lv https://orcid.org/0000-0003-2613-6734

REFERENCES

Adis, J., & Junk, W. J. (2003). Feeding impact and bionomics of the grasshopper Conops aquaticum on the water hyacinth Eichhornia crassipes in Central Amazonian floodplains. Studies on Neotropical Fauna and Environment, 38(3), 245-249. https://doi.org/10.1076/snfe.38.3.245.28167
Bale, J., & Hayward, S. A. L. (2010). Insect overwintering in a changing climate. Journal of Experimental Biology, 213(6), 980–994.
Barrett, S. C. H. (1980). Sexual reproduction in Eichhornia crassipes (Water Hyacinth II). Seed production in natural populations. Journal of Applied Ecology, 17, 113–124. https://doi.org/10.2307/2402967
Bellows, T. S. (2001). Restoring population balance through natural enemy introductions. Biological Control, 21(3), 199–205. https://doi.org/10.1006/bcon.2001.0936
Belote, R. T., & Weltzin, J. F. (2006). Interactions between two co-dominant, invasive plants in the understory of a temperate deciduous forest. Biological Invasions, 8(8), 1629–1641. https://doi.org/10.1007/s10530-005-3932-8
Carpenter, D., & Cappuccino, N. (2005). Herbivory, time since introduction and the invasiveness of exotic plants. Journal of Ecology, 93(2), 315–321. https://doi.org/10.1111/j.1365-2745.2005.00973.x
Center, T. D., Van, T. K., Dray, 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. https://doi.org/10.1016/j.biocontrol.2005.02.005
Clay, K., Marks, S., & Cheplick, G. P. (1993). Effects of insect herbivory and fungal endophyte infection on competitive interactions among grasses. Ecology, 74(6), 1767–1777. https://doi.org/10.2307/1939935
Coetzee, J. A., Hill, M. P., Byrne, M. J., & Bownes, A. (2011). A review of the biological programmes on Eichhornia crassipes (C.Mart.) Solms (Pontederiaceae), Salvinia molesta D.S. Mitch. (Salviniacae), Pistia stratiotes L. (Araceae), Myriophyllum aquaticum (Vell.) Verdc. (Haloragaceae) and Azolla filiculoides (Lam.) (Azollaceae) in South Africa. African Entomology, 19, 451–468.
Cornelissen, B., Neumann, P., & Schweiger, O. (2019). Global warming promotes biological invasion of a honey bee pest. Global Change Biology, 25(11), 3642–3655.
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. https://doi.org/10.1111/j.1365-2745.2010.01776.x
Dief, J. M., D’Antonio, C. M., Dukes, J. S., Grosholz, E. D., Olden, J. D., Sorte, C. J. B., Blumenthal, D. M., Bradley, B. A., Early, R., Ibáñez, I., Jones, S. J., Lawler, J. J., & Miller, L. P. (2012). Will extreme climatic events facilitate biological invasions? Frontiers in Ecology and the Environment, 10(5), 249–257. https://doi.org/10.1890/110137
Ding, J., Chen, Z., & Fu, W. (2001). Control Eichhornia crassipes, an invasive aquatic weed in South China with Neochetina echinorhaina. Chinese Journal of Biological Control, 17(3), 97–100.
Dong, Y., Zhao, Y., Chen, Cui, X., & Shang, H. (2008). Inhibitory effect of Rhopalosiphum nymphaeae on the growth of water hyacinth. Journal of Ecology and Rural Environment, 24(3), 55–59.
Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: Observations, modeling, and impacts. Science, 289(5487), 2068–2074.
Fan, S. F., Liu, C. H., Yu, D., & Xie, D. (2013). Differences in leaf nitrogen content, photosynthesis, and resource-use efficiency between Eichhornia crassipes and a native plant Monochoria vaginalis in response to altered sediment nutrient levels. Hydrobiology, 711(1), 129–137. https://doi.org/10.1007/s10750-013-1471-3
Fan, S. F., Yu, D., & Liu, C. H. (2013). The invasive plant Alternanthera philoxeroides was suppressed more intensively than its native congener by a native generalist: Implications for the biotic resistance hypothesis. PLoS One, 8(13), e83619. https://doi.org/10.1371/journal.pone.0083619
Fan, S. F., Yu, H. H., Dong, X., Wang, L. G., Chen, X. W., Yu, D., & Liu, C. H. (2016). Invasive plant Alternanthera philoxeroides suffers more severe herbivory pressure than native competitors in recipient communities. Scientific Reports, 6, 36542. https://doi.org/10.1038/srep36542
Flory, S. L., & Bauer, J. T. (2014). Experimental evidence for indirect facilitation among invasive plants. Journal of Ecology, 102(1), 12–18. https://doi.org/10.1111/1365-2745.12186
Franceschini, M. C., Poi de Neiff, A., & Galassi, M. E. (2010). Is the biomass of water hyacinth lost through herbivory in native areas important? Aquatic Botany, 92(4), 250–256. https://doi.org/10.1016/j.aquabot.2010.01.005
Fu, D. (2007). Studies on feeding preference and growth adaptation of alligatorweed flea beetle (Agasicles hygrophila) to different genotypes of Alligator weed (Alternanthera philoxeroides). MA thesis, Northwest University, Xian, China.
Francis, R. A. (2012). A handbook of global freshwater invasive species. Earthscan.
Gopal, B. (1987). Water hyacinth. Elsevier.
Gutiérrez, E. L., Ruiz, E. F., Uribe, E. G., & Martinez, J. M. (2001). Biomass and productivity of water hyacinth and their application in control programs. In M. H. Julien, M. P. Hill, T. D. Center, & D. Jianqing (Eds.), Biological and integrated control of water hyacinth, Eichhornia crassipes (pp. 109–119), Canberra: ACIAR proceedings No. 102.
Halliday, S. (2005). Global warming opens the door for invasive macrophytes in Swedish lakes and streams. Master’s thesis, Swedish University of Agricultural Sciences.
Hartley, S. E., & Amos, L. (1999). Competitive interactions between *Nardus stricta* L. and *Calluna vulgaris* (L.) Hull: The effect of fertilizer and defoliation on above- and below-ground performance. *Journal of Ecology*, 87(2), 330–340.

He, W. M., Li, J. J., & Peng, P. H. (2012). A congenic comparison shows that experimental warming enhances the growth of invasive *Eupatorium adenophorum*. *PLoS One*, 7(4), e35681. https://doi.org/10.1371/journal.pone.0035681

Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. *Conservation Biology*, 22(3), 534–543. https://doi.org/10.1111/j.1523-1739.2008.01095.x

Hill, M. P., Coe, J. A., Martin, G. D., Smith, R., & Strange, E. F. (2020). Biological control of water hyacinth with arthroba. *Biological & integrated control of water hyacinth*: Patterns, processes, and management implications. *Biological Conservation*, 219(8), 2339–2347. https://doi.org/10.1016/j.biocon.2013.01.009

Lu, X., Siemann, E., He, M., Wei, H., Shao, X., & Ding, J. (2015). Climate warming increases biological control agent impact on a non-target species. *Ecology Letters*, 18(1), 48–56. https://doi.org/10.1111/ele.12391

Lu, X., Siemann, E., He, M., Wei, H., Shao, X., & Ding, J. (2016). Warming benefits a native species competing with an invasive congener in the presence of a biocontrol beetle. *New Phytopathologist*, 211(4), 1371–1381. https://doi.org/10.1016/j.nph.13976

Lu, X., Siemann, E., Shao, X., Wei, H., & Ding, J. (2013). Climate warming affects biological invasions by shifting interactions of plants and herbivores. *Global Change Biology*, 19(8), 2339–2347. https://doi.org/10.1111/gcb.12244

Ma, R. (2001). *Ecological adaptation for the introduced biocontrol agent, Agasicles hygrophila, for alligatorweed*. *Alternanthera philoxeroides*, in China. PhD Thesis, Chinese Academy of Agricultural Sciences, Beijing, China

Madsen, J. D., Luu, K. T., & Gertsinger, K. D. (1993). Allocation of bio- mass and carbohydrates in water hyacinth (*Eichhornia crassipes*): Pond-scale verification. Technical Report A93-3. US Army Corps of Engineers, Waterways Experiment Station, Vicksburg, MS.

Meehl, G. A., & Tebaldi, C. (2004). More intense, more frequent, and longer lasting heat waves in the 21st century. *Science*, 305(5686), 994–997.

Metlen, K. L., Aschehoug, E. T., & Callaway, R. M. (2013). Competitive outcomes between two exotic invaders are modified by direct and indirect effects of a native conifer. *Oikos*, 122(4), 632–640. https://doi.org/10.1111/j.1600-0706.2012.20792.x

Mitchell, C. E., Agrawal, A. A., Bever, J. D., Gilbert, G. S., Hufbauer, R. A., Jepsen, J. U., Kalinkat, G., Neuvonen, S., Niemelä, P., & Terblanche, J. S. (2013). Competitive interactions and plant invasions. *Ecology Letters*, 9(6), 726–740. https://doi.org/10.1111/j.1461-0248.2006.00908.x

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. https://doi.org/10.1111/j.0030-1299.2008.16896.x

Mulder, C. P., & Russ, R. W. (1998). Effects of herbivory on arroygrass: Interactions between geebe, neighboring plants, and abiotic factors. *Ecological Monographs*, 68(2), 275–293.

Parker, J. D., Burkepile, D. E., & Hay, M. E. (2006). Opposing effects of native and exotic herbivores on plant invasions. *Science*, 311, 1459–1461. https://doi.org/10.1126/science.1121407

Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaugueluberry, P., Bret-Harte, M. S., Cornell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., … Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61, 167–234. https://doi.org/10.1071/BT12225

Portela, R., Vicente, J. R., Roloa, S. R., & Cabral, J. A. (2020). A dynamic model-based framework to test the effectiveness of biocontrol targeting a new plant invader: the case of *Alternanthera philoxeroides* in the Iberian Peninsula. *Journal of Environmental Management*, 264, 110349. https://doi.org/10.1016/j.jenvman.2020.110349

Rahel, F. J., & Olden, J. D. (2008). Assessing the effects of climate change on aquatic invasive species. *Conservation Biology*, 22(3), 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x

Liu, Y., Oduor, A. M. O., Zhang, Z., Manea, A., Tooth, I. M., Leishman, M. R., Xu, X., & van Kleunen, M. (2017). Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biology*, 23(8), 3363–3370. https://doi.org/10.1111/gcb.13579

Lolis, L. A., Alves, D. C., Fan, S., Lv, T., Yang, L., Li, Y., Liu, C. H., Yu, D., & Thomaz, S. M. (2020). Negative correlations between native macrophyte diversity and water hyacinth abundance are stronger in its introduced than in its native range. *Diversity and Distributions*, 26(2), 242–253.
Shen, J., Shen, M., Wang, X., & Lu, Y. (2005). Effect of environmental factors on the emergence and vegetative growth of alligatorweed (Alternanthera philoxeroides). Weed Science, 53(4), 471–478.

Siemann, E., Rogers, W. E., & Dewalt, S. J. (2006). Rapid adaptation of in­sect herbivores to an invasive plant. Proceedings of the Royal Society B: Biological Sciences, 273(1602), 2763–2769.

Simberloff, D. (2006). Invasive meltdown 60 years later: Important phenomena, unfortunate metaphor, or both? Ecology Letters, 9, 912–919. https://doi.org/10.1111/j.1461-0248.2006.00939.x

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindige­nous species: Invasive meltdown? Biological Invasions, 1(1), 21–32.

Soti, P. G., & Volin, J. C. (2010). Does water hyacinth (Eichhornia crassipes) compensate Soti for simulated defoliation? Implications for effective biocontrol. Biological Control, 54(1), 35–40.

Tanveer, A., Ali, H. H., Manalil, S., Raza, A., & Chauhan, B. S. (2018). Ecology and management of alligator weed (Alternanthera philoxeroides (Mart.) Griseb): A review. Wetlands, 38(6), 1067–1079.

Telesnicki, M. C., Sosa, A. J., Greizerstein, E., & Julien, M. H. (2011). Cytogenetic effect of Alternanthera philoxeroides (alligator weed) on Agasicles hygrophi­lo (Coleoptera: Chrysomelidae) in its native range. Biological Control, 57(2), 138–142. https://doi.org/10.1016/j.biocontrol.2011.02.003

Tyndall, R. W. (1982). Nuisance aquatic plants and aquatic plant manage­ment programs in the United States, Vol I, Southwestern Region. The Mitre Corporation.

Van, T. K., Wheeler, G. S., & Center, T. D. (1998). Competitive interactions between Hydrilla (Hydrilla verticillata) and Vallisneria (Vallisneria americana) as influenced by insect herbivory. Biological Control, 11(3), 185–192. https://doi.org/10.1006/bcon.1997.0594

Verlinden, M., De Boeck, H. J., & Nijs, I. (2014). Climate warming alters competition between two highly invasive alien plant species and dominant native competitors. Weed Research, 54(3), 234–244. https://doi.org/10.1111/wre.12076

Von Holle, B., Joseph, K. A., Largay, E. F., & Lohnes, R. G. (2006). Facilitations between the introduced nitrogen-fixing tree, Robinia pseudoacacia, and nonnative plant in­vasion in the glacial upland ecosystem of Cape Cod, MA. biodiversity & Conservation, 15(7), 2197–2215. https://doi.org/10.1007/s10531-004-6906-8

Walther, G.-R., Roques, A., Hulme, P. E., Sykes, M. T., Pysek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., & Bugmann, H. (2009). Alien species in a warmer world: Risks and opportunities. Trends in Ecology & Evolution, 24(12), 686–693. https://doi.org/10.1016/j.tree.2009.06.008

White, T. A., Campbell, B. D., Kemp, P. D., & Hunt, C. L. (2001). Impacts of extreme climatic events on competition during grassland invasions. Global Change Biology, 7(1), 1–13. https://doi.org/10.1046/j.1365-2486.2001.00381.x

Wu, H., Ismail, M., & Ding, J. (2017). Global warming increases the ins­ terspecific competitiveness of the invasive plant alligator weed, Alternanthera philoxeroides. Science of the Total Environment, 575, 1415–1422. https://doi.org/10.1016/j.scitotenv.2016.09.226

Wundrow, E. J., Carrillo, J., Gabler, C. A., Horn, K. C., & Siemann, E. (2012). Facilitation and competition among invasive plants: A field experiment with alligatorweed and water hyacinth. PLoS One, 7(10), e48444. https://doi.org/10.1371/journal.pone.0048444

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. https://doi.org/10.1086/657433

Yang, Y., Liu, M., Pan, Y., Huang, H., Pan, X., Sosa, A., Hou, Y., Zhu, Z., & Li, B. (2021). Rapid evolution of latitudinal clines in growth and de­fence of an invasive weed. New Phytologist, 203, 845–856.

You, W., Yu, D., Xie, D., & Yu, L. (2013). Overwintering survival and re­growth of the invasive plant Eichhornia crassipes are enhanced by experimental warming in winter. Aquatic Biology, 19(1), 45–53. https://doi.org/10.3354/ab00519

Yu, H. H., & Fan, S. F. (2018). Differences in physiological traits and resi­stances of Alternanthera philoxeroides after herbivory by gener­alists and specialists. Aquatic Ecology, 52(4), 323–332. https://doi.org/10.1007/s10238-018-9666-3

Zhang, B. L., Zhang, J. E., Dai, X. Y., Peng, L., Peng, H., & Huang, W. J. (2014). Effects of Pomacea canaliculata on aquatic macrophyte community structure in paddy fields. Acta Ecologica Sinica, 34(4), 907–915.

Zhou, L., Dickinson, R. E., Tian, Y., Fang, J., Li, Q., Kaufmann, R. K., Tucker, C. J., & Myreni, R. B. (2004). Evidence for a significant urb­anization effect on climate in China. Proceedings of the National Academy of Sciences, 101(26), 9540–9544. https://doi.org/10.1073/pnas.0400357101

BIOSKETCH

Chunhua Liu is a freshwater ecologist and a professor currently at the Wuhan University. She is mostly working on aquatic in­vasive species and freshwater ecosystems, and often use aquatic macrophytes and related organisms to test ecological concepts on biological invasions and biodiversity, conduct both a series of laboratory and field studies to evaluate the effect biological invasions on native freshwater ecosystem.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Zhang, X., Yu, H., Lv, T., Yang, L., Liu, C., Fan, S., & Yu, D. (2021). Effects of different scenarios of temperature rise and biological control agents on interactions between two noxious invasive plants. Diversity and Distributions, 27, 2300–2314. https://doi.org/10.1111/ddi.13406