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Special Feature: Management of biological invasions in China

Clonal functional traits favor the invasive success of alien plants into native communities

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Abstract

Functional traits are frequently proposed to determine the invasiveness of alien species. However, few empirical studies have directly manipulated functional traits and tested their importance in the invasion success of alien species into native plant communities, particularly under global change. We manipulated clonal integration (a key clonal functional trait) of four alien clonal plants by severing inter-ramet connections or keeping them intact and simulated their invasion into native plant communities with two levels of species diversity, population density and nutrient availability. High community diversity and density impeded the invasion success of the alien clonal plants. Clonal integration of the alien plants promoted their invasion success, particularly in the low-density communities associated with low species diversity or nutrient addition, which resulted in a negative correlation between the performance of alien plants and native communities, as expected under global change. Thus, clonal integration can favor the invasion success of alien clonal plants into degraded resident communities with a high degree of disturbance and eutrophication. Our findings confirm the role of clonal functional traits in facilitating alien plant invasions into native plant communities and suggest that clonal functional traits should be considered to efficiently restore degraded communities heavily invaded by alien clonal plants.

KEYWORDS
eutrophication, functional traits, invasiveness, multispecies comparison, physiological integration, plant invasion, Special Feature: Management of biological invasions in China

INTRODUCTION

At global scales, habitat destruction induced by human activities and the introduction of alien plant species is contributing to declines in biodiversity, ecosystem functioning, and economic development (Callaway & Aschehoug, 2000; Diagne et al., 2021; Diamond, 1989; Pyšek et al., 2020;

Richardson et al., 2007; van Kleunen et al., 2015). Habitat degradation as a result of human activities has caused a decrease in the abundance and diversity of locally endemic flora and fauna (Diamond, 1989; Sax et al., 2002), which may decrease the resistance of communities and ecosystems to invasion by alien plants (Elton, 1958; Levine & D'Antonio, 1999; Richardson et al., 2007).

Human activities, such as human-mediated disturbances, can also alter resource availability in environments, which often occurs in concert with or acts as triggers for the introduction, spread, and invasion of alien plants (Melbourne et al., 2007; Sax et al., 2002; Sher & Hyatt, 1999). Thus, plant invasion is the outcome of complex interactions of both biotic factors, such as the abundance and diversity of plant species (Levine & D'Antonio, 1999; van Kleunen et al., 2011; Zhao et al., 2020), and abiotic factors, such as eutrophication and resource availability in particular environments (Davis et al., 2000; Funk & Vitousek, 2007; Melbourne et al., 2007).

The resident plant species in communities differ markedly in their susceptibility to plant invasion owing to their community characters (Adomako et al., 2019; Fargione & Tilman, 2005; Levine, 2000; Michelan et al., 2013; Parepa et al., 2013; van Ruijven et al., 2003). The biotic resistance hypothesis (Elton, 1958) postulates that diversity is a significant characteristic of a resident community that can provide resistance against plant invaders partly due to complementary effects that enable species of diverse communities to occupy more niche spaces and fully exploit the available resources (Dostál, 2011; Elton, 1958; Fargione & Tilman, 2005; van Ruijven et al., 2003). Moreover, diverse communities also possess variable functional groups, such as grasses, forbs and legumes, a more complex food web, a high diversity of allelopathic compounds, and stronger allelopathy, thereby increasing the stability and decreasing the invasibility of communities compared with less diverse ones (Adomako et al., 2019; Emery & Gross, 2007; Fargione & Tilman, 2005; Pearson et al., 2018). In addition, diverse communities could have a greater probability of containing competitively superior species to effectively suppress invasive species by a sampling (selection) effect (Petruzzella et al., 2018; Wardle, 2001).

Plant density is another significant community character that enhances the intensity of competition and efficiency at utilizing resources and space (Brown & Fridley, 2003; Michelan et al., 2013; Naeem et al., 2000; Vojik & Boublik, 2018), leaving fewer resources and less space for potential invaders (Dostál, 2011; Michelan et al., 2013). Furthermore, dense communities with a high or undisturbed canopy closure could effectively inhibit the growth and regeneration of invasive alien plants (Emery & Gross, 2007; Pearson et al., 2018) and are also less likely to be invaded by alien plants compared with disturbed open-canopy communities (Davis et al., 2000; Sun et al., 2015).

Environmental resource availability is likely to modify the outcome of competition between alien and native plants and thus determine the vulnerability of a native community to invasion (Alpert et al., 2000; Chen et al., 2019; Liu et al., 2019; Parepa et al., 2013). A release

in nutrient constraints, such as nutrient loading by nitrogen deposition and fertilizers added to agricultural and other areas, may promote the invasion of alien plants into native communities (Dukes & Mooney, 1999; Vitousek et al., 1997). Studies have shown that invaders that can capitalize on the increased nutrient availability in disturbed systems may outcompete native species that are adapted to previously low nutrient conditions (Vitousek et al., 1997). This suggests that invasive plants can take up and utilize nutrients more effectively than most natives when there is a high supply of nutrients. Therefore, we need to determine whether nutrient availability alters the outcome of competition between invasive alien and native plants in a degraded resident community with low species diversity and low population density.

It is frequently proposed that functional traits contribute significantly to the invasion success of alien plants (Baker, 1965; Drenovsky et al., 2012; Elton, 1958; Fried et al., 2019; Gallien & Carboni, 2017; Ordonez & Olff, 2013; Song et al., 2013; van Kleunen et al., 2010). For instance, invasive species are commonly associated with a high growth rate, strong competitive ability, greater resource utilization efficiency, and high capability of clonal integration (Song et al., 2013; Wang et al., 2017). However, most of these studies tested the correlational relationship between functional traits and performance of invasive plants; very few empirical studies have directly manipulated the functional traits of invasive species and tested their roles in the invasion success in native plant communities.

In this study, we directly manipulated the absence versus presence of clonal integration, a key clonal functional trait, of four alien clonal plants by severing inter-ramet connections versus keeping them intact and simulated their invasion into native plant communities with two levels of species diversity, population density and nutrient availability. We used clonal plants as our target invasive species and manipulated clonal integration because many of the world's worst invasive plant species are capable of clonal growth (Liu et al., 2006; Lowe et al., 2000; Pyšek, 1997; Song et al., 2013; Yu et al., 2009), and clonal integration is one of the most important functional traits of clonal invasive plants (Bittebiere et al., 2020; Chen et al., 2019; Roiloa et al., 2010; Wang et al., 2017; Yu et al., 2009). We predicted that (1) clonal integration would increase the biomass and biomass proportion of alien species, that is, increase their invasion success, regardless of native community diversity, population density and nutrient availability, and (2) the effect of clonal integration on the invasion success of alien plants would be stronger in native communities with low species diversity, low population density, and high nutrient availability.

MATERIALS AND METHODS

Species selection and cultivation

The species were selected based on a field investigation of the dominant alien invasive and native plant species in the wetlands and moist grasslands in the Nanshuihu National Wetland (24°47′16″ N, 113°120′23″ E), Guangdong Province, China, in 2016. We chose four alien clonal plant species (i.e., *Alternanthera philoxeroides*, *Sphagneticola trilobata*, *Hydrocotyle vulgaris*, and *Trifolium repens*) as the target species, which were dominant in the investigated habitats and co-occurred in subtropical and tropical wetlands or grassland habitats in China (Ma, 2014, 2020; Ma & Li, 2018). We chose six plant species commonly found and dominant in the wetlands and grasslands that were investigated to construct native plant communities (Appendix S1: Table S1). To balance the functional diversity in communities, the six native species belonged to different functional groups of grasses (two) and forbs (four). All 10 of the selected herbaceous species co-occur in the field (Appendix S1: Table S1).

The species used in the experiment were collected from field sites in Guangdong Province in China. We collected ramets for target clonal alien species and seeds for native species (Appendix S1: Table S1). The collected ramets were cultivated in a greenhouse at Huazhong Agricultural University (Wuhan, China) to produce enough new clonal fragments for the experiment. The seeds were germinated in potting soil in the greenhouse to produce enough seedlings/plants. In 2016, we selected 96 similarly sized four-ramet clonal fragments for each alien species and 768 seedlings/plants for each native species for the experiment described in what follows. Each fragment consisted of four rooted, similarly sized ramets interconnected by a single stolon internode. Each plant had two to three leaves and some roots.

Experimental design

The experiment consisted of four fully crossed factors: (a) clonal integration (without vs. with, by severing the inter-ramet stolon connections or not), (b) native community density (low vs. high, with six or 18 plants), (c) native community diversity (low vs. high, with two or six species), and (d) nutrient addition (with vs. without). Community diversity and density were designed based on the previously described investigations (i.e., there were two to 12 species/m^2 and 80 to 300 plants/m^2 in the field).

On 11 April 2016, we planted each fragment of the target invasive alien species in the central area of a plastic pot (30 cm diameter × 20 cm high) filled with 9.5 L of a 1:1 (v/v) even mixture of sand and local soil. The soil mixture was relatively low in nutrients. The total N was 0.23 ± 0.03 g kg^{-1}, the total P 0.32 ± 0.04 g kg^{-1}, and the total K 14.27 ± 1.25 g kg^{-1} (mean $\pm$ SE, $n = 10$).

For the low- and high-community-diversity treatments, each pot was respectively planted with two and six native species surrounding a central area where a clonal fragment of the target alien species was planted (Appendix S1: Figure S1). Seven different composition combinations were produced at two levels of diversity: six combinations of low diversity and one combination of high diversity. For the low-diversity combinations, the species were randomly selected, with the restriction that each species was part of an equal number of combinations per diversity category (Appendix S1: Table S2). There were six replicates of each diversity level. For the low- and high-community-density treatments, six or 18 plants were arranged at equal intervals in a hexagonal design around the central area of the pot, with six plants in the middle hexagon or each of six plants in the inner, middle, and outer hexagon (Appendix S1: Figure S1). The soil of half of the pots was mixed with 2.0 g L^{-1} slow-release fertilizer (Osmocote, N-P-K:15-9-12, which lasts for 5–6 months), and no fertilizer was added to the other half. During the experiment, the total amount of nutrients added to the treatment in which nutrients were added corresponded to the current level of nutrient enrichment in the grasslands investigated. After allowing the plants to recover for 2 weeks (on 25 April 2016), the connection between the middle two ramets in each four-ramet fragment of target alien species was either severed in the middle or left intact (Appendix S1: Figure S1). There were 384 pots in total (4 target alien species × 2 community diversity × 2 community density × 2 clonal integration × 2 nutrient addition × 6 replicates).

The experiments were conducted in a greenhouse at Huazhong Agricultural University, Wuhan, China. We initiated the experiment 10 days after fragment severing (on 5 May 2016), and no plant died during this time. The plants were watered regularly throughout the experiment. The pots were positioned randomly and rearranged every 2 weeks to avoid the potential effects of microenvironments. The light intensity in the greenhouse during the experiment was $77.2 \pm 4.7\%$ of natural light, and the mean temperature and mean relative humidity in the greenhouse were 27.4°C and 70.1%, respectively, which were measured by a TR-74Ui-S (T&D Corporation, Nagano, Japan). The experiment ran 112 days (16 weeks) and was terminated on 25 August 2016.

Measurements and analysis

We harvested the aboveground and belowground biomass of the target alien species and total biomass of the native plant community separately in each pot. All samples were dried at 80°C for at least 72 h and then weighed. We calculated the biomass proportion of the target alien species as the proportion of the total biomass of the alien target plant species to the total biomass of the whole community (alien target species plus native plant community) of each pot. The biomass of the native community was the sum of the biomass of the six native species in a pot.

We used linear mixed models to analyze the data (biomass and the proportion of target alien species and biomass of native plant community) with the nlme package in R (Pinheiro et al., 2015; R Core Team, 2020). In these models, clonal integration (intact vs. severed connection), native community diversity (low vs. high), native community density (low vs. high), nutrient addition (with vs. without), and their interactions were treated as fixed terms, and the identity of the alien species and species composition of the native communities were included as random terms. Log-likelihood ratio was used

to evaluate the significance differences of the fixed factors, and a χ^2 distribution of the calculated log-likelihood ratios was exhibited in the linear mixed models (Zuur et al., 2009). The data were transformed to the square root to meet the assumption of normality. An effect was considered significant if $p < 0.05$. All analyses were conducted using R software (version 4.0.2; R Core Team, 2020).

RESULTS

Averaged across nutrient availability, community diversity, and community density, clonal integration significantly increased the biomass and biomass proportion of the target alien species and decreased the biomass of native communities (Table 1, Figures 1 and 2). More importantly, in the low-density treatment, the positive effect of clonal integration on the biomass of alien species was significantly greater in the low-diversity than in the high-diversity treatment, whereas in the high-density treatment, this was not the case (significant interaction of community diversity $[D_i] \times$ community density $[D_e] \times$ clonal integration $[I]$ in Table 1 and Figure 1a). In the low-density treatment, clonal

TABLE 1 Effects of native community diversity (low vs. high), native community density (low vs. high), nutrient addition (with vs. without), clonal integration (with vs. without), and their interactions on biomass and proportion of alien species and biomass of native community.

Fixed effect	Biomass of alien species[a]			Proportion of alien species[b]			Biomass of native community[c]		
	df	χ^2	p	df	χ^2	p	df	χ^2	p
Community diversity (D_i)	1	**11.9**	**<0.001**	1	**12.6**	**<0.001**	1	**20.7**	**<0.001**
Community density (D_e)	1	**79.3**	**<0.001**	1	**420.9**	**<0.001**	1	**249.7**	**<0.001**
Nutrient (N)	1	**183.7**	**<0.001**	1	3.5	0.063	1	**277.3**	**<0.001**
Integration (I)	1	**38.7**	**<0.001**	1	**104.9**	**<0.001**	1	**10.4**	**0.001**
$D_i \times D_e$	1	<0.1	0.993	1	**8.9**	**0.003**	1	**71.4**	**<0.001**
$D_i \times N$	1	**4.2**	**0.042**	1	2.1	0.150	1	**8.4**	**0.004**
$D_i \times I$	1	2.9	0.09	1	**6.2**	**0.013**	1	1.9	0.169
$D_e \times N$	1	**139.5**	**<0.001**	1	0.7	0.405	1	**43.9**	**<0.001**
$D_e \times I$	1	0.1	0.743	1	**4.2**	**0.040**	1	**4.5**	**0.034**
$N \times I$	1	**22.3**	**<0.001**	1	**4.0**	**0.044**	1	**19.7**	**<0.001**
$D_i \times D_e \times N$	1	0.3	0.591	1	0.6	0.444	1	1.4	0.227
$D_i \times D_e \times I$	1	**4.6**	**0.032**	1	0.5	0.486	1	**9.6**	**0.002**
$D_i \times N \times I$	1	0.4	0.530	1	1.0	0.307	1	1.0	0.326
$D_e \times N \times I$	1	**11.1**	**<0.001**	1	**11.3**	**<0.001**	1	2.7	0.102
$D_i \times D_e \times N \times I$	1	<0.1	0.961	1	0.1	0.771	1	0.1	0.724

Note: All data were square-root transformed. Values are in bold when $p < 0.05$.
[a]Random effect: alien species, SD = 0.185; native community, SD = 0.025; residual, SD = 0.207. Marginal $R^2 = 0.838$, conditional $R^2 = 0.911$.
[b]Random effect: alien species, SD = 0.108; native community, SD = 0.022; residual, SD = 0.109. Marginal $R^2 = 0.629$, conditional $R^2 = 0.817$.
[c]Random effect: alien species, SD = 0.064; native community, SD = 0.040; residual, SD = 0.207. Marginal $R^2 = 0.958$, conditional $R^2 = 0.963$.
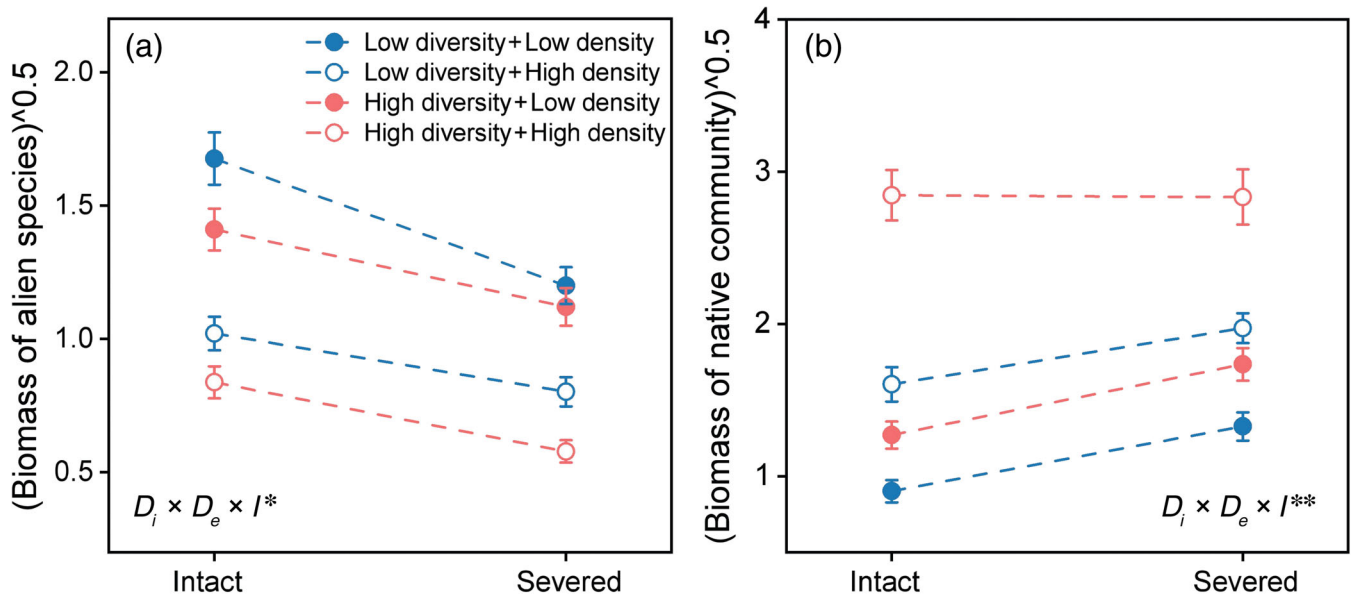
FIGURE 1 (a) Biomass of alien species and (b) biomass of native communities with fragments of target alien clonal plants intact or severed, with low or high diversity and with low or high plant density. Mean $\pm$ SE are given. ^0.5 indicates square-root transformed. D_i, community diversity; D_e, community density; I, integration. $*p < 0.05$, $**p < 0.01$.
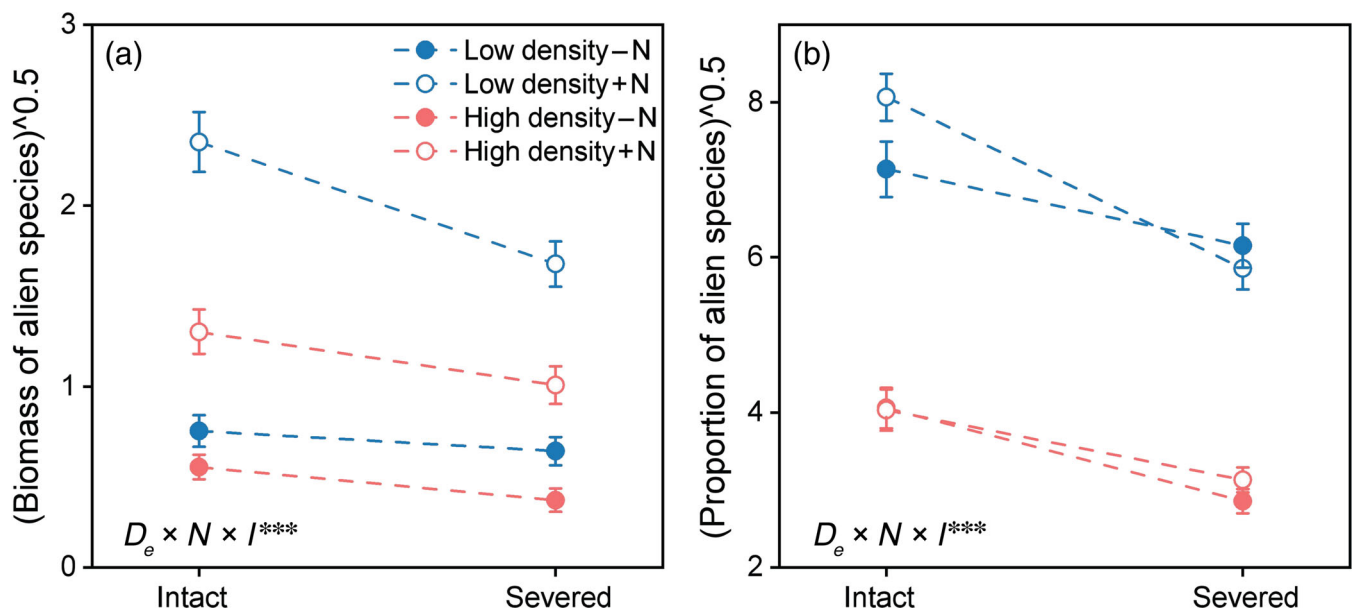

FIGURE 2 (a) Biomass and (b) proportion of alien species with their fragments intact or severed and in native communities with low or high density and with or without nutrient addition ($+N$ or $-N$). Mean $\pm$ SE are given. ^0.5 means square-root transformed. D_e, community density; N, nutrient addition; I, integration. $***p < 0.001$.

integration decreased the biomass of the native community in both the high-diversity and low-diversity treatments, but in the high-density treatment, integration decreased the biomass only in the low-diversity treatment and the decrease disappeared in the high-diversity treatment (significant interaction of $D_i \times D_e \times I$ in Table 1, Figure 1b). The biomass and biomass proportion of the target alien species were greater with than without the

addition of nutrients (Table 1, Figure 2a). In the low-density treatment, the positive effects of clonal integration on these parameters were significantly greater with than without the addition of nutrients, whereas these differences disappeared in the high-density treatment (significant interaction of $D_e \times$ nutrient addition $[N] \times I$ in Table 1, Figure 2a,b). The negative effect of high diversity on the proportion of biomass of the alien species was

significantly greater in the high-density than in the low-density treatment (significant interaction of $D_i \times D_e$ in Table 1, Appendix S1: Figure S2a).

DISCUSSION

We found that clonal integration substantially improved the growth and dominance of target alien plants in the native community, particularly in the low-density community associated with low species diversity or the addition of nutrients, which led to a sharp suppression of the biomass of the alien species on the native species. These results indicate that clonal integration can favor the successful invasion of alien plants into degraded resident communities characterized by a relatively low species diversity and density caused by, for example, global change factors.

Effects of clonal integration on plant invasion

Clonal integration improved the growth of target invasive alien species and decreased the growth of the native communities (Table 1, Figure 1), consistent with previous findings observed in both heterogeneous and homogeneous resource conditions (Chen et al., 2019; Wang, Xu, et al., 2021; Xi et al., 2019; Yu et al., 2009). A potential mechanism for the substantial benefits of clonal integration is the translocation of resources between older (larger) and younger (smaller) ramets, which can promote the performance of the whole clone of the invasive plants in homogeneous environments (Dong et al., 2015; Wang, Alpert, & Yu, 2021). Another potential mechanism could be the developmentally programmed division of labor, such as specializing in the acquisition of belowground resources or aboveground expansion for the connected ramets, which facilitates the clonal expansion of invasive plants (Xi et al., 2019).

Considering individual species, the positive effect of clonal integration was significant in *A. philoxeroides*, *S. trilobata*, and *H. vulgaris*, but not in *T. repens* (Appendix S1: Figures S6 and S7). This difference is likely because *A. philoxeroides*, *S. trilobata*, and *H. vulgaris* depend mainly on clonal propagation to spread their populations in introduced ranges (Ma, 2020; Wang et al., 2020; Zhu et al., 2015), whereas *T. repens* can also spread its populations via seeds (Ma, 2020). Thus, the relative importance of clonal propagation and sexual reproduction might influence the role of clonal traits in the invasion success of alien clonal plants. Overall, our findings suggest that clonal integration of alien clonal species can mediate their effects on native community structure and the performance of individual species within communities.

Effects of community traits on plant invasion under global change

The proportion of the biomass of alien species decreased significantly in the high-diversity and high-density communities (Table 1, Appendix S1: Figure S2a). This result is consistent with previous findings showing that species-rich and canopy-closed (undisturbed) communities are less vulnerable to alien plant invasions (Adomako et al., 2019; Brown & Fridley, 2003; Elton, 1958; Kempel et al., 2013; Petruzzella et al., 2018; Turnbull et al., 2010; Vojik & Boublik, 2018). This is because, owing to species complementarity or selection effects, communities that are richer in species or denser can make better use of available resources and so leave fewer resources for invasive species (Adomako et al., 2019; Fargione & Tilman, 2005; van Ruijven et al., 2003).

Interestingly, the benefits of clonal integration to the invasive alien species were greater in the low-diversity and low-density communities (Table 1, Figure 1). The low-diversity and low-density communities in our study had less opportunity to possess species that had a high ability to compete, efficiently use resources, and resist competitive suppression, leaving abundant resources and niche spaces for invasive species. Thus, under the incomplete exploitation of resources and space (niche opportunities) and the relatively low competitive suppression in native communities, the higher benefit of clonal integration could be that invasive clonal plants are better able to translocate resources and share between their connected ramets under such conditions. Global human activities can cause habitat degradation, resulting in a decrease in species diversity and coverage or density in native communities, which are more likely to be invaded by alien plants (Davis et al., 2000; Elton, 1958; Levine & D'Antonio, 1999; Sun et al., 2015). Therefore, clonal integration of alien plants can promote their invasion in the degraded resident community mediated by relatively low species diversity and density.

Effects of nutrient availability on plant invasion under global change

Not surprisingly, a supply of nutrients increased the growth of alien species and native communities (Table 1, Figure 2, Appendix S1: Figure S3). However, in the low-density community, the positive effect of clonal

integration on the growth and dominance of alien species was significantly greater with than without the addition of nutrients (Table 1, Figure 2). This is consistent with a conceptual model showing that clonal integration can increase the performance of clonal plant in a homogeneous environment when there is a large supply of external resources but not in a homogeneous environment when the supply of external resources is low (Dong et al., 2015). Moreover, the amounts of resources were more available for utilization in high resource environments and in low-density communities. Thus, the connected ramets of invasive clonal plants could take up, utilize, and translocate nutrients more efficiently than native plants in competitive conditions, suggesting that clonal integration can increase the ability of a whole clone of alien plants to compete against other species, at least partly resulting in their invasion success (Alpert, 1995; Chen et al., 2019; Wang et al., 2016, 2019; Wang, Alpert, & Yu, 2021; Zobel et al., 2010).

However, in communities with high diversity and density, the positive effect of nutrient addition on plant invasion disappeared. These results might stem from increased resource-use efficiency as a result of increasing plant species diversity, leading to reduced niche space to support the establishment and growth of alien plants (Adomako et al., 2019; Fargione & Tilman, 2005). In addition, denser native communities possess a greater degree of canopy closure or biomass production when nutrient availability is high, which can greatly inhibit the growth of alien plants by shading (Brown & Fridley, 2003; Kempel et al., 2013).

Potential limitations

One caveat that must be pointed out with regard to this study is that our high-diversity treatment used only one fixed set of native plant species, so that random distinction scenarios of the diversity effect were not considered (Abernathy et al., 2016; Liao et al., 2015; Qin et al., 2020). Another caveat is that the study was conducted in a greenhouse and lasted for a relatively short time, so attempts to extrapolate its findings should be made with caution. Finally, although clonal integration of invasive alien species played a significant role in their successful invasions into native plant communities, the effects of species diversity and density of native plant communities and the effect of nutrient addition were much stronger (Appendix S1: Figure S8). Despite these limitations, our results do indicate that clonal integration can increase the ability of at least some invasive alien clonal species to establish and dominate in degraded communities with low diversity and density but high soil nutrient contents.

CONCLUSIONS

Clonal functional traits, such as clonal integration, can promote the invasion success of alien clonal plants into degraded native plant communities with a high degree of disturbance and eutrophication. Most of the world's worst invasive plant species are clonal (Lowe et al., 2000; Pyšek, 1997; Song et al., 2013), as are most of the worst invasive plants in China (Liu et al., 2006). Thus, to efficiently control the spread of alien invasive clonal plants and restore degraded native plant communities heavily invaded by alien clonal plants, clonal functional traits should be considered. For instance, management measures could be taken to prevent clonal integration among ramets to eliminate its potential positive effects on alien plants and negative effects on native plant communities. These measures should be combined with measures that can help increase native species diversity and density and decrease soil available nutrients.

AUTHOR CONTRIBUTIONS
Yong-Jian Wang and Fei-Hai Yu designed the experiment. Yong-Jian Wang and Duo Chen performed the experiment. Yong-Jian Wang and Yuan-Yuan Liu conducted the statistical analysis. Yong-Jian Wang wrote the first draft of the manuscript. Fei-Hai Yu, Dao-Lin Du, and Heinz Müller-Schärer contributed substantially to the revisions.

CONFLICT OF INTEREST
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data and code (Wang et al., 2022) are available in Dryad at https://doi.org/10.5061/dryad.qjq2bvqk5.

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SUPPORTING INFORMATION

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