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Effects of native species richness on reproduction of invasive *Bidens pilosa* vary with nutrient supply

Fang-Lei Gao¹, Sergio Roiloa², Jiangbao Xia¹, Jiayun Ren³, Meiling Zou³, Ximei Zhao¹ and Fei-Hai Yu^{4*}

Abstract

Background Both increasing native species diversity and reducing nutrient availability can increase the ability of native plant communities to resist alien plant invasions. Furthermore, native species diversity and nutrient availability may interact to influence alien plant invasions. So far, however, little is known about the interactive effect of species diversity and nutrient availability on reproduction of alien invasive plants. We constructed native plant communities with one, four or eight species under low and high nutrient supply and then let them be invaded by the invasive alien plant *Bidens pilosa*.

Results At both high and low nutrient supply, increasing native species richness significantly increased aboveground biomass of the native plant community and decreased aboveground biomass and biomass proportion of the invader *B. pilosa*. Reproductive biomass of *B. pilosa* decreased significantly with increasing native species richness under high nutrient supply, but this effect was not observed under low nutrient supply. Net biodiversity effect on seed mass of *B. pilosa* decreased significantly with increasing native species diversity under high nutrient supply, but not under low nutrient supply. This was mainly because the selection effect became dominant with increasing species richness under high nutrient supply.

Conclusions Our study suggest that native species richness and nutrient supply can interact to influence reproduction of invasive alien plant species and that measures to help maintain a high level of native species richness and to reduce nutrient supply could be useful for efficient invasive plant control.

Keywords Biodiversity effect, Invasibility, Invasive alien plant, Nutrient availability, Species diversity

Introduction

Biological invasions are a global threat as they can cause biodiversity declines, economic losses and human health problems (Wang et al. 2017; Vilà et al. 2011; Rai and Singh 2020; Diagne et al. 2022). Although over 13,000 plant species have successfully naturalized outside their native ranges (van Kleunen et al. 2015), the accumulation of alien species is still expected to increase (Seebens et al. 2021), which dramatically increases the risk of alien plant invasions around the world. Thus, identifying measures that can slow down alien plant invasions is helpful for invasive plant management (Dong et al. 2024).

Maintaining a certain level of native plant species diversity could be one of such measures that can efficiently

*Correspondence:

Fei-Hai Yu
feihaiyu@126.com

¹ Shandong Key Laboratory of Eco-Environmental Science for the Yellow River Delta, Shandong University of Aeronautics, Binzhou 256603, China

² BioCost Group, Department of Biology, Faculty of Science, Universidade da Coruña, 15071 A Coruña, Spain

³ College of Life and Environmental Engineering, Shandong University of Aeronautics, Binzhou 256603, China

⁴ Zhejiang Province Key Laboratory of Plant Evolutionary Ecology and Conservation, Institute of Wetland Ecology & Clone Ecology, Taizhou University, Taizhou 318000, China

slow down or even prevent alien plant invasions (e.g., Levine 2000; Kennedy et al. 2002; Li et al. 2022a). The idea originates from the biotic resistance hypothesis, which predicts that communities with higher species diversity should have greater resistance to biological invasions (Elton 1958). The hypothesis is supported by results of many theoretical and experimental studies (e.g., Kennedy et al. 2002; van Ruijven et al. 2003; Maron and Marler 2008; Wei and van Kleunen 2022). Reducing available resources in a community could be another measure that can slow down or even prevent alien plant invasions (e.g., Davis et al. 2000; Pearson et al. 2018; van der Loop et al. 2020; Gao et al. 2021). This is because native plant communities become more susceptible to alien plant invasions when there is an increase in the amount of unused resources as a result of resource fluctuation, such as after disturbance, herbivory or eutrophication (Davis et al. 2000). A growing body of studies have provided supporting evidence that such resource fluctuation is associated with invasion success of alien species (e.g., Davis and Pelser 2001; Parepa et al. 2013; Tao et al. 2024).

Species diversity and nutrient availability may interact to influence the successful invasion of exotic species into native plant communities (Brown and Rice 2010; Zheng et al. 2020a). One plausible expectation is that the negative effect of native diversity on invasibility is less at higher nutrient supply. Some experimental studies support this prediction (Brown and Rice 2010; Zheng et al. 2020a), but others found that effects of diversity and nutrients on invasion success of invasive plant species were independent (Maron and Marler 2007; Heckman and Carr 2016; Heckman et al. 2017; Li et al. 2022a). Previous studies of the interactive effect of species diversity and nutrient supply have focused mainly on growth measures of invasive alien species (Mattingly et al. 2010; Mattingly and Reynolds 2014; Heckman and Carr 2016; Li et al. 2022a). However, reproductive measures such as seed production are better proxies for fitness, particularly in the case of annual species, and thus for population growth leading to invasion (Simberloff 2009; Correia et al. 2016). One study using reproductive measures showed that ovule numbers of the invader *Centaurea solstitialis* were greater in species-poor than in species-rich communities at a nutrient-rich site but not at a nutrient-poor one (Brown and Rice 2010). More such studies on the interactive effects of native species diversity and nutrient supply on reproduction of invasive alien plant species are needed to develop efficient measures to prevent alien plant invasions.

The complementarity and selection effects are two major mechanisms underlying the biodiversity effect on the resistance of native plant communities to alien

plant invasions (Fargione and Tilman 2005; Wang et al. 2023). The complementarity effect occurs when more diverse communities result in more complementary resource use among species, leaving less resource available for invaders (Adomako et al. 2019; Jing et al. 2021; Xue et al. 2022). The selection effect occurs when native species with higher competitive ability and thus ability to suppress alien plant invasions have a higher probability of being present in more diverse communities (Wang et al. 2022). Both the selection and complementarity effects are potentially important, but their relative importance is likely to change with environmental stress (Wang et al. 2013). The selection effect may be more important than the complementarity effect in benign environments where inter-specific competition is the dominant interaction in plant communities and highly competitive species tend to dominate (Fridley 2001). The complementarity effect may be more important in stressful environments where facilitation is the dominant interaction (Chu et al. 2008). For example, a recent study showed that the complementarity effect increased with increasing drought stress, but the selection effect did not, which caused that the invader *Symphyotrichum subulatum* performed better in native communities under drought conditions but performed worse in well-watered conditions (Wang et al. 2023). However, we still know little about how nutrient supply may influence the relative importance of the complementarity and selection effects in native plant communities on resistance to alien plant invasions.

We constructed experimental native communities with three levels of species richness (one, four, or eight species) under low and high nutrient supply and then let them be invaded by the annual alien plant *Bidens pilosa*. Specifically, we addressed the following questions: (1) Does native plant species richness affect growth and reproduction of *B. pilosa*? We predicted that growth and reproduction of *B. pilosa* would decrease with increasing species richness of the native plant communities. (2) Does nutrient supply affect growth and reproduction of *B. pilosa*? We predicted that growth and reproduction of *B. pilosa* would be higher under higher nutrient supply. (3) Do species richness and nutrient supply interact to influence growth and reproduction of *B. pilosa*? We predicted that the effect of native species richness on growth and reproduction of *B. pilosa* is more pronounced under high than under low nutrient supply. (4) Does the relative importance of the complementarity and selection effects on resistance to alien plant invasion change with nutrient supply? We predicted that the biodiversity effect shifts from complementarity to selection with increasing nutrient supply.

Materials and methods

Plant species and material preparation

Bidens pilosa L. is an annual forb in the Asteraceae native to tropical America (Xu et al. 2012). It is now widely distributed in China and was listed as one of the most noxious invasive alien plants by the Ministry of Ecology and Environment of China in 2014. *B. pilosa* can outcompete native species and easily forms a large area of monocultures in the invaded area, which poses a serious threat to the biodiversity of the invaded area (Arthur et al. 2012; Deng and Zou 2012). The ten native plant species (Table 1) that were used to construct experimental native plant communities are common in China and co-occur with invading *B. pilosa* in natural habitats.

Seeds of all native species and *B. pilosa* were collected in the mountainous areas of Taizhou City, Zhejiang Province, in 2019. These areas are characterized by a subtropical monsoon climate with mean annual precipitation of 1632 mm. The average temperatures in January and August are 8.5 °C and 30 °C, respectively. The naturally occurring soil nutrient content at the collection sites of seeds was not determined. Wang et al. (2022) found that the local soil in the area where seeds of *B. pilosa* were collected, had 620 ± 170 mg kg⁻¹ total nitrogen, and 130 ± 30 mg kg⁻¹ total phosphorus. The seeds were stored at 4 °C until use. On 25 April 2021, seeds of the invasive species and the native plant species were sown in 11 trays (54 cm long × 28 cm wide × 5 cm high) filled with a mixture of equal volumes of peat and vermiculite. We put all trays in a greenhouse at Binzhou University (37° 22′ 59″ N; 117° 58′ 56″ E) in Binzhou City, Shandong Province, China.

Experimental design

We conducted a factorial experiment with two levels of nutrient supply (low or high) crossed with three levels of native species richness (one, four, or eight species).

For the nutrient treatments, the high and the low nutrient soils were made of an equal mixture of peat and vermiculite with 4 and 1 g L⁻¹ slow release fertilizer (15:9:11 N:P:K, Osmocote Exact Standard 8–9 M; Scotts, Marysville, Ohio, USA), respectively. For the treatments with species richness, we had ten monocultures (i.e., one for each native species) for the 1-species treatment and ten different species mixtures for both the 4-species and the 8-species treatments. These species mixtures were randomly chosen from the pool of the ten native species, with the restriction that all native species had equal occurrence in each species richness level (Table S1). Each monoculture and species mixture were considered as one replicate of the diversity level, and thus we had in total ten replicates for each of the three species richness levels. There were a total of 120 pots (3 species richness × 2 soil nutrient treatments × 2 harvest time × 10 replicates).

On 25 May 2021, we selected similarly sized seedlings for each species and transplanted those seedlings into 120 pots (23 cm in upper diameter, 18 cm in bottom diameter, and 22 cm in height). Half of the pots were filled with 6 L of the high-nutrient soil mixture and the other half filled with 6 L of the low-nutrient soil mixture. Each pot was grown with nine seedlings, including eight seedlings of the native plants and one seedling of *B. pilosa*. The seedling of the invader was grown in the center of the pot, and the eight seedlings of the native plants were grown in a circle around the invader. For the monoculture treatment, eight seedlings of the same native species were grown. For the treatment with four native species, two seedlings of each native species were grown in a pot, and for the treatment with eight native species, one seedling of each native species was grown. We replaced any dead seedlings 48 h after transplantation. The 120 pots were completely randomly placed in the greenhouse at Binzhou University. During the experiment, we watered the pots two or three times a week according to the weather conditions. During the experiment, the mean temperature was 26.4 °C and the mean relative humidity was 71.8% in the greenhouse. The light level inside the greenhouse was $1.01 \times 10^5 \pm 5480$ lx and was about 70% of natural light outside the greenhouse ($1.44 \times 10^5 \pm 8410$ lx).

Harvest and measurements

On 5 August 2021, 10 weeks after the experiment was started, we randomly selected half of the replicates (60 pots in total) and harvested the aboveground parts of all the plants. The plant parts in each pot were sorted into species, dried in an oven at 70 °C for at least 72 h and weighed. On 18 December 2021, 30 weeks after the experiment was started, when the seeds of *B. pilosa* were fully mature, all the seeds of *B. pilosa* in each pot

Table 1 Native species used in the study

No.	Species	Family	Life form	Abbreviation
1	<i>Perilla frutescens</i>	Lamiaceae	Annual	Pf
2	<i>Achyranthes bidentata</i>	Amaranthaceae	Perennial	Ab
3	<i>Patrinia scabiosaeifolia</i>	Valerianaceae	Perennial	Ps
4	<i>Artemisia capillaris</i>	Asteraceae	Perennial	Ac
5	<i>Astragalus adsurgens</i>	Fabaceae	Perennial	Aa
6	<i>Solanum nigrum</i>	Solanaceae	Annual	Sn
7	<i>Plantago asiatica</i>	Plantaginaceae	Perennial	Pa
8	<i>Alternanthera sessilis</i>	Amaranthaceae	Annual	As
9	<i>Eleusine indica</i>	Poaceae	Annual	Ei
10	<i>Taraxacum mongolicum</i>	Asteraceae	Perennial	Tm

were harvested, dried in an oven at 35 °C for 1 week and weighed. *B. pilosa* seeds disperse by zoochory and tend not to fall on their own. We did not measure biomass of stems and leaves of the plants during the second harvest because all the leaves had died and fallen off.

Biomass proportion of *B. pilosa* i.e., aboveground biomass of *B. pilosa* in a pot divided by total aboveground biomass of all plants in the pot, was used as a measure of invasion success. We employed the additive partitioning method of Loreau and Hector (2001) to calculate the complementarity effect and the selection effect on seed biomass of *B. pilosa* (Wang et al. 2022, 2023). The net biodiversity effect is the sum of the complementarity effect and the selection effect. The complementarity effect (CE) was calculated as: $CE = N \times \overline{\Delta RY} \times \bar{M}$, where N is the number of species in the mixture, \bar{M} is the mean value of seed biomass of the invader across all monoculture native species, and ΔRY is the mean value of the deviation from expected relative seed biomass of invader in the mixture. The selection effect (SE), $N \times \text{cov}(\Delta RY, M)$, was calculated as the covariance between seed biomass (M) of the invader with native species in monoculture and their change in relative seed biomass in the mixture ($\overline{\Delta RY}$) multiplied by N of the mixture.

Statistical analyses

We used linear mixed models to test the effects of native species richness, nutrient supply and their interaction on aboveground biomass of *B. pilosa*, aboveground biomass of native communities, aboveground biomass proportion of *B. pilosa*, reproductive biomass of *B. pilosa*, and the net biodiversity, complementarity and selection effects. In these models, we treated nutrient supply, native species richness and their interaction as fixed effects and native plant community composition as a random effect. Nutrient supply was defined as a categorical variable and native species richness as a continuous variable. The likelihood ratio test was used to assess the significance of effects. We used the *lme* function of the *NLME* package R version 4.1.2 (R Core Team 2021) for all the analyses. To test whether average values of the net biodiversity effect under each treatment combinations of nutrient supply and diversity levels were significantly higher or lower than zero, we performed one-sample *t*-tests.

Before analysis, we checked the residuals of all response variables for normality and homoscedasticity. To improve the normality or homoscedasticity, we performed cubic-root, square-root and logit transformation for reproductive biomass, aboveground biomass of native communities and aboveground biomass proportion of *B. pilosa*, respectively. In three replicates of the 4-species treatment with low nutrient supply and one replicate of the 1-species treatment with high nutrient

supply, *B. pilosa* died before flowering, and these replicates were excluded from the analysis on reproduction.

Results

Invader biomass

Aboveground biomass of *B. pilosa* was 55–71% higher in the high than in the low nutrient treatment ($\chi^2 = 18.4$, $P < 0.001$), and decreased significantly with increasing species richness of the native plant community ($\chi^2 = 5.3$, $P = 0.021$; Fig. 1a, Table 2). However, there was no significant interactive effect of nutrient supply and species richness of the native plant communities on aboveground biomass of *B. pilosa* ($\chi^2 = 0.4$, $P = 0.52$; Table 2).

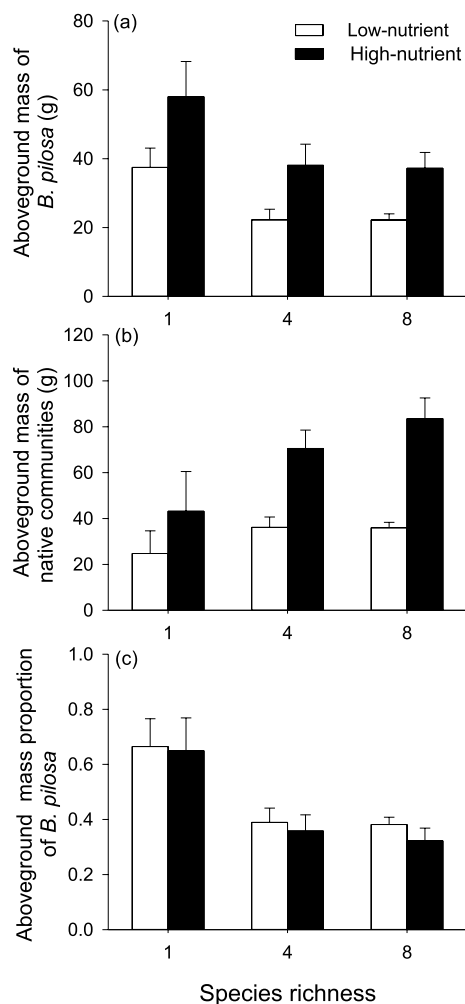


Fig. 1 Effects of nutrient supply and species richness of native communities on aboveground biomass of *B. pilosa* (a), aboveground biomass of the native community (b) and biomass proportion of *B. pilosa* (c). Data shown are mean values + SE

Table 2 Results of linear mixed models of effects of nutrient supply, species richness of native communities and their interaction on aboveground biomass of *B. pilosa*, aboveground biomass of native community, biomass proportion of *B. pilosa* and reproduction biomass of *B. pilosa*

	Aboveground biomass of <i>B. pilosa</i>			Aboveground biomass of native communities			Biomass proportion of <i>B. pilosa</i>			Reproduction biomass of <i>B. pilosa</i>		
	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P
Fixed effect												
Nutrient (N)	1	18.4	<0.001	1	24.6	<0.001	1	0.6	0.447	1	47.5	<0.001
Richness (R)	1	5.3	0.021	1	7.2	0.007	1	7.5	0.006	1	2.5	0.113
N × R	1	0.4	0.518	1	5.4	0.021	1	0.9	0.348	1	4.5	0.033
	SD			SD			SD			SD		
Random effect												
Species composition	13.4			2			1.8			0.1		
Residuals	13.4			1.3			1			0.4		

Values are in bold when $P < 0.05$

Native community biomass

Aboveground biomass of the native plant community was 74–132% higher in the high than in the low nutrient treatment ($\chi^2 = 24.6$, $P < 0.001$) and increased significantly with increasing species richness of the native plant community ($\chi^2 = 7.2$, $P = 0.007$; Fig. 1b, Table 2). However, the effect of species richness on aboveground biomass of the native community was stronger under high than under low nutrient supply (Fig. 1b), as indicated by the significant interaction of nutrient supply and species richness ($\chi^2 = 5.4$, $P = 0.021$; Table 2).

Invader biomass proportion

Increasing species richness of the native plant communities significantly reduced aboveground biomass proportion of *B. pilosa* ($\chi^2 = 7.5$, $P = 0.006$) but did not interact with nutrient treatment ($\chi^2 = 0.9$, $P = 0.35$; Fig. 1c; Table 2). Nutrient supply had no significant effect on aboveground biomass proportion of *B. pilosa* ($\chi^2 = 0.6$, $P = 0.45$; Table 2).

Invader reproduction

Reproductive biomass of *B. pilosa* significantly decreased with increasing species richness of the native plant communities under high but not under low nutrient supply (Fig. 2), as reflected by the significant two-way interaction of nutrient supply and species richness ($\chi^2 = 4.5$, $P = 0.003$; Table 2).

Biodiversity effects on reproduction

The net biodiversity effect was not affected by species richness under low nutrient supply, but decreased with increasing species richness under high nutrient supply,

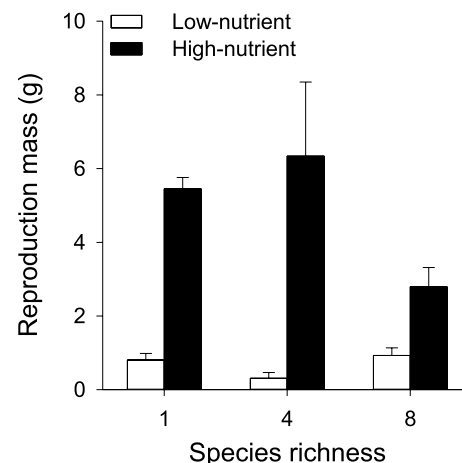


Fig. 2 Effects of nutrient supply and species richness of native communities on the reproductive biomass of *B. pilosa*. Data are shown mean values + SE

as indicated by the significant interaction of species richness and nutrient supply (Fig. 3a; Table 3). The net biodiversity effect did not significantly differ from zero for the 4-species treatment ($t = -2.1$, $P = 0.082$) or the 8-species treatment ($t = 0.9$, $P = 0.37$) under low nutrient supply. Under high nutrient supply, the net biodiversity effect differed significantly from zero for the 8-species treatment ($t = -3.5$, $P = 0.007$) but not for the 4-species treatment ($t = 1.2$, $P = 0.26$).

In both the 4-species and the 8-species communities under both high and low nutrient supply, the values of the complementarity effect were always positive, i.e., reproductive performance of *B. pilosa* was higher in mixed communities than in monocultures of natives.

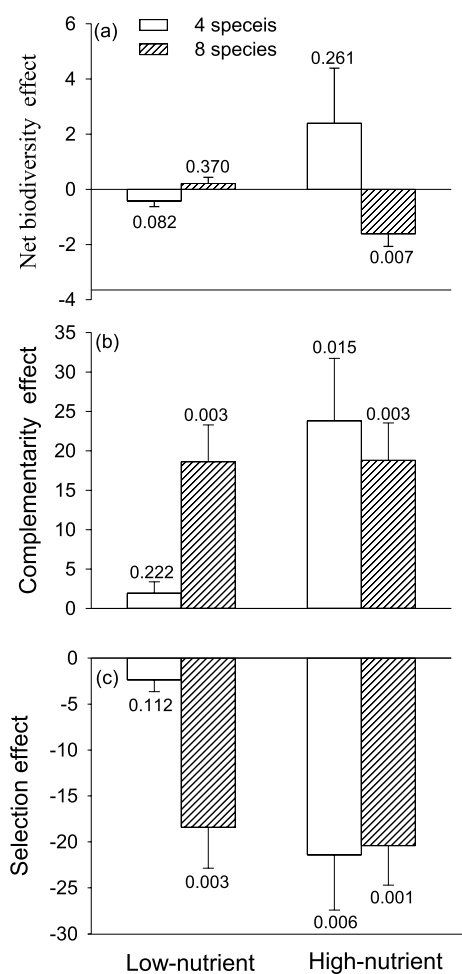


Fig. 3 Effects of nutrient supply and species richness of native communities the net biodiversity effect (a), complementarity effect (b) and selection effect (c) on reproduction of *B. pilosa*. Data show mean values + SE. Numbers above bars give probability that net biodiversity effect differed significantly from zero

In contrast, values of the selection effect were always negative, i.e., reproduction of *B. pilosa* was worse than expected when placed in native mixture communities (Fig. 3b, c). In the 4-species communities under low nutrient supply, neither the complementarity effect nor the selection effect differed significantly from zero. In the 4-species communities under high nutrient supply and the 8-species communities under both high and low nutrient supply, both the complementarity effect and the selection effect differed significantly from zero (Fig. 3b, c; Table 3).

Discussion

Fluctuating resources often promote alien plant invasions (Teixeira et al. 2017; Pearson et al. 2018), and communities poorer in species are commonly less resistant to invasions (Cebrian et al. 2018). There may thus be an interactive effect of resource availability and native species richness on alien plant invasions (Marraffini and Geller 2015; Li et al. 2022b). We found that species richness and nutrient supply interacted to influence reproduction but not growth of *B. pilosa*. This suggests that apparent interactive effects of species richness and nutrient supply on alien plant invasions vary depending on the performance proxies or the stages of plant development that are considered.

Our first prediction was supported by the result that native species richness significantly decreased the aboveground biomass of the invader *B. pilosa* irrespective of nutrient supply (hypothesis 1; Fig. 1a; Table 2). This is consistent with a recent 4-year grassland experiment that demonstrated a negative relationship between native species diversity and community invasibility independent of nutrient addition (Li et al. 2022a). We found that the native species richness also significantly decreased the aboveground biomass proportion of *B. pilosa* within

Table 3 Results of linear mixed models of effects of nutrient supply, species richness of native communities and their interaction on net biodiversity, complementarity and selection effects on reproduction of *B. pilosa*

	Biodiversity effect			Complementarity effect			Selection effect		
	df	χ^2	P	df	χ^2	P	df	χ^2	P
Fixed effect									
Nutrient (N)	1	0.4	0.511	1	3.0	0.084	1	4.0	0.044
Richness (R)	1	2.3	0.127	1	0.7	0.399	1	2.0	0.159
N×R	1	6.2	0.013	1	3.8	0.050	1	3.4	0.064
	SD			SD			SD		
Random effect									
Species composition	3.7			<0.1			<0.1		
Residuals	1.8			17.2			14.3		

Values are in bold when $P < 0.05$ and are in italics when $0.05 \leq P < 0.1$

the community (hypothesis 1; Fig. 1c; Table 2), indicating that biodiversity can reduce invasion success. These results support the biotic resistance hypothesis and show that biodiversity may serve as a barrier against biological invasion (Kennedy et al. 2002; Levine et al. 2004). Our results also showed that high nutrient supply significantly increased the aboveground biomass of *B. pilosa* (hypothesis 2; Fig. 1a; Table 2). This is in line with previous findings that invasive species benefit more from high resource availability (Davidson et al. 2011; Liang et al. 2020). A plausible explanation for this outcome may be that plant invaders have a superior ability to capture resources in rich but not poor habitats (Wang et al. 2017; Hu et al. 2019). In addition, invasive species usually show a higher nutrient use efficiency than their native congeners (Pyšek and Richardson 2007). However, despite the higher aboveground biomass of *B. pilosa* in the high than in the low nutrient supply treatment, our results did not indicate that high nutrients promoted the invasion success of *B. pilosa*, because we did not find a significant effect of nutrient supply on the proportion of biomass that *B. pilosa* represents in relation to the whole community (Fig. 1c; Table 2). This result is not in accordance with previous studies. Gao et al. (2021) found that high nutrient supply increased the proportional biomass of *B. pilosa* within an invaded community, suggesting that the increase in nutrients favored invasion success. On the other hand, a meta-analysis by Liu et al. (2017) reported that invasive plants showed a slightly more positive response to nutrient supply than native species. A plausible reason that would explain our result could be that the positive effect of high nutrient supply on invasive *B. pilosa* was similar to the benefit gained by native species, and therefore does not cause a significant difference in proportional biomasses (Fig. 1c; Table 2).

Our third prediction (i.e. stronger effect of species richness under high than under low nutrients) was supported by the fact that *B. pilosa* produced more reproductive biomass in species-poor communities than in species-rich ones under high nutrient supply but not in the low nutrient treatment (Fig. 2; Table 2). However, our results did not detect an interactive effect of nutrient supply and native species richness on the growth of *B. pilosa* (Fig. 1a; Table 2). This result is particularly interesting, indicating that the interactive effect of native community diversity and resource availability (nutrients in this case) can vary depending on the performance measures being tested. Thus, while the effect of species diversity on growth was independent of nutrient supply, the effect on reproduction was affected by nutrient levels, with a significant reduction in the reproductive capacity of the invasive species driven by native community diversity only under conditions of high nutrients. We propose three potential

mechanisms that could explain the interactive effect of native diversity and nutrient supply on *B. pilosa* reproduction. First, low nutrient supply in the environment caused a reduction in growth (Fig. 1a), which was accompanied by a significant, strong reduction in reproductive biomass (Fig. 2). Reproductive biomass was so low that the effect of diversity on this variable in the low nutrient supply treatment was imperceptible. It is logical to expect that, due to its high energetic cost, reproduction would suffer a significant reduction as a consequence of plants being restricted by low nutrient supply. Second, the resistance of native communities to invasion success depends on their competitive ability, and this ability varied with physical and biotic stress (Valliere et al. 2020; Zheng et al. 2020b; Azeem et al. 2021). According to the stress gradient hypothesis, plant interactions in communities shift from competition to facilitation with increasing stress (Bertness and Callaway 1994; He et al. 2013). The competitive intensity of native communities on invaders may decrease with decreasing nutrient supply such the net interaction between natives and invaders is negative under high but neutral under low nutrient supply. Consistent with this explanation, the biodiversity effect on reproduction of *B. pilosa* changed from negative to neutral with increasing nutrient supply (Fig. 3a; Table 3). Third, the differences between growth and reproduction of *B. pilosa* in our study could be due to time. Growth was measured after 10 weeks and reproduction after 30 weeks. It is possible that growth would also have shown significant differences after 30 weeks. Previous work has shown that the resistance of native communities to invasion can vary over time (Delory et al. 2019; Ferenc et al. 2021). For example, as native plant species establish with time, the competitive intensity of native communities on invaders can become stronger (Chen and van Kleunen 2022).

The complementarity effect and the selection effect are two major components of the net biodiversity effect (Loreau and Hector 2001; Clark et al. 2019). While the complementary effect arises from niche differentiation or facilitation between species, the selection effect indicates processes such as interspecific competition that lead to dominance of species with more competitive traits. The relative importance of these two effects can vary with environmental stress (Wang et al. 2013, 2023). Our fourth hypothesis that the net biodiversity effect shifts from complementarity to selection with increasing nutrient supply was supported by results showing that the selection effect became dominant with increasing diversity in conditions of high nutrient supply (Fig. 3; Table 3). This indicates that the presence of highly competitive native species such as *Solanum nigrum* rather than complementary use of resources among native species led to

the lower reproductive performance of invader *B. pilosa* in high nutrient conditions.

Even though our results include interesting and novel information on how resource supply and diversity of a native community can affect invasibility, some limitations must be acknowledged and future lines of research proposed. First, all species in our study began treatment at the same time as seedlings. This simulates invasion after severe disturbance that removes all vegetation but not invasion into established communities of natives. It would be interesting to test interactive effects of resources and native diversity on invading species when natives are already fully grown. Future research designs could also include growing native communities without the invader as a control. Second, only two nutrient levels were used. This constrains our understanding on how diversity affects invasibility of native communities along environmental gradients. In the future, we recommend that serial nutrient gradients should be used in diversity-invasibility experiments. Third, the species pool we used for constructing native communities was relatively small ($n = 10$). The assemblages we created were similar to each other, especially in the 8-species richness treatment. In the future, we recommend that larger species pools and more diversity levels should be used to test how diversity affects invasibility. Finally, we used just one invasive plant species. This limits the generality of our results. Studies that test the interactive effects of resources and native diversity on invasion by multiple species should be conducted in the future.

Conclusion

The present study demonstrates that the ability of greater species richness to reduce reproduction of invasive plants can be greater when nutrient levels are higher. However, apparent effects of diversity on invasibility can differ between different measures of invasion. At least when nutrient levels are high, competitiveness of individual native species may play a bigger role than niche differentiation or resource partitioning in biological resistance to invasion. Conserving the richness of native communities may help them resist alien plant invasions, especially as global eutrophication accelerates.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-024-00527-3>.

Supplementary Material 1.

Acknowledgements

We thank two anonymous reviewers for their valuable comments on an earlier version of the manuscript, and Professor Peter Alpert (from University

of Massachusetts) for editing the manuscript of grammar, spelling, and syntax, and Jing-Jie Dou, Yu Zhang and Xiao-Yu Zhou for assistance with laboratory work.

Author contributions

FLG: conceptualization, methodology, data curation, visualization, writing—original draft, Funding acquisition. SR: data curation, writing—review and editing. JX: conceptualization, investigation, data curation. JR: investigation, data curation. MZ: investigation. XZ: investigation. FHY: conceptualization, writing—review and editing, supervision.

Funding

This study was supported by the National Natural Science Foundation of China (32001302), a Startup Project for Doctor's Scientific Research of Binzhou University (2019Y35) and the Innovation and Training Program of University Students of Shandong Province in 2021 (S202110449140).

Availability of data and materials

Data are available on reasonable request from the corresponding author.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

All authors consent to the publication of the manuscript and supplementary material.

Competing interests

The authors declare that they have no conflicts of interests.

Received: 29 February 2024 Accepted: 29 May 2024

Published online: 06 June 2024

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