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Effects of Soil Nutrient Heterogeneity on the Growth and Invasion Success of Alien Plants: A Multi-Species Study

*Fang-Lei Gao [1,2], Qiao-Sheng He [2], Yi-Dan Zhang [2], Jia-Hui Hou [2] and Fei-Hai Yu [2]**

[1] Shandong Key Laboratory of Eco-Environmental Science for the Yellow River Delta, Binzhou University, Binzhou, China,
[2] Institute of Wetland Ecology & Clone Ecology; Zhejiang Province Key Laboratory of Plant Evolutionary Ecology and Conservation, Taizhou University, Taizhou, China

Spatial heterogeneity in soil nutrient availability can influence performance of invasive plant species under competition-free environments. However, little was known about whether invasive plants perform better under heterogeneous than under homogeneous soil nutrient conditions in competition with native plant communities. We conducted a multi-species greenhouse experiment to test the effect of soil nutrient heterogeneity on the growth and invasion success of alien plants in a native plant community. We grew ten alien invasive plant species that are common in China under a homogeneous or heterogeneous environment alone or together with a community consisting of six native plant species from China. Compared with the homogeneous soil condition, the heterogeneous soil condition significantly increased aboveground biomass of the invasive plants. However, soil nutrient heterogeneity did not affect the relative abundance of the invasive species, as measured by the ratio of aboveground biomass of the invasive species to total aboveground biomass of the whole community. There were no significant interactive effects of soil nutrient heterogeneity and competition from the native community on aboveground biomass of the invasive plants and also no significant effects of soil nutrient heterogeneity on its relative abundance. Our results indicate that soil nutrient heterogeneity has a positive effect on the growth of invasive plants in general, but do not support the idea that soil nutrient heterogeneity favors the invasion success of exotic plant species in native plant communities.

Keywords: biological invasion, environmental heterogeneity, invasibility, invasiveness, multi-species

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Correspondence:
Fei-Hai Yu
feihaiyu@126.com

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INTRODUCTION

Soil nutrients are generally spatially heterogeneously distributed in nature, and such soil nutrient heterogeneity occurs at different scales relevant to plant growth and distribution (Jackson and Caldwell, 1993a; Stein et al., 2014; Brezina et al., 2019). Soil nutrient heterogeneity may affect plant population dynamics, community structure and ecosystem function (Day et al., 2003a,b; Wijesinghe et al., 2005; Gazol et al., 2013; Tamme et al., 2016; Xi et al., 2017) as it can modulate intra- and interspecific competition owing to the different responses of plant species to nutrient heterogeneity (Mommer et al., 2011, 2012; Roiloa et al., 2014; Tsunoda et al., 2014; Xue et al., 2018). Alien plant invasions can directly reduce the diversity of native plant communities due to their greater competitive advantages compared with native ones (Vilà et al., 2011; Zhang et al., 2019). Soil nutrient heterogeneity, particularly at fine scales, may influence the invasion success of alien plants by shifting the competitive balance between native plants and invaders (Chen et al., 2017; Liu et al., 2017).

Plant species frequently perform better in environments with a heterogeneous than with a homogenous soil nutrient supply, even though the total amount of nutrients are the same in the two environments (Cahill et al., 2010; Zhou et al., 2012; Liu et al., 2020). This is because plants have a foraging response and can capture more resources from resource-rich patches in heterogeneous environments (Robinson et al., 1999; James et al., 2009; Gao et al., 2012). Invasive exotic non-clonal plant species typically have a stronger root-foraging ability than non-invasive species or natives (Rajaniemi and Reynolds, 2004; Drenovsky et al., 2008; Keser et al., 2015). Alternatively, some invasive clonal plants have a higher ability of selectively placing nutrient-acquisition organs in high-resource patches and translocating more resources between interconnected ramets than native clonal plants, which benefit their ramets in nutrient-poor patches and thus promote the performance of the whole clone (Keser et al., 2014; Wang et al., 2017; Chen et al., 2019). Since invasive plants can benefit more from environmental heterogeneity than natives (Wang et al., 2017; Chen et al., 2019), we hypothesized that environmental heterogeneity can increase the competitive ability of invasive species more than that of native species so that it can promote the invasion success of exotic plants in native plant communities.

Although soil nutrient heterogeneity has the potential to promote the growth of invasive plants, most previous studies testing the heterogeneity effects on the invasion success consisted of only two species, i.e., one target species of invasive plants and one species of competing native plants (Chen et al., 2017; Liang et al., 2020). In addition, experiments on invasive plants with an assembled community were conducted mostly in a homogenous environment (Kennedy et al., 2002; Heckman and Carr, 2016). Thus, little is known about whether soil nutrient heterogeneity affects the invasion success of exotic plant species in native communities consisting of multiple plant species.

To assess the effects of soil nutrient heterogeneity and competition from the native community on the growth and invasion success of alien plant species, we conducted a greenhouse experiment using ten invasive plant species that are common in southeast China and a synthetic community that consisted of six native plant species. We grew the ten invasive plants alone (without competition) or with a synthetic community (with competition) in a homogenous or heterogeneous environment. Specifically, we addressed the following two questions. (1) Does soil nutrient heterogeneity generally increase the growth of invasive species in competition with the native plant community, as measured by aboveground biomass of the invasive species? (2) Does soil nutrient heterogeneity generally promote the invasion success of invasive plant species in the native plant community, as measured by the ratio of aboveground biomass of the invasive species to that of the whole community (native and invasive plants together)?

MATERIALS AND METHODS

Plant Species and Cultivation

We used ten alien invasive plant species in China (**Table 1**). Ramets of *A. philoxeroides*, *W. trilobata*, and *H. vulgaris* were collected from five locations spaced at least 500 m apart to increase the likelihood of sampling ramets from different genets, i.e., genotypes. Then, they were propagated vegetatively in a greenhouse in Taizhou University, Taizhou, China, for at least 1 year before use. Seeds of *S. canadensis* and the six non-clonal species were collected from 3 to 5 populations spaced at least 1.5 km apart in Taizhou. Seeds of six native plant species were collected in Taizhou (**Table 1**) and used to construct native plant communities. We chose these six native species as they are widely distributed in China and also co-occur with the invasive species used in the experiment.

On May 18, 2019, seeds of the native species and the alien invasive species were sown separately in 13 trays (20 × 12 × 5 cm) filled with a mixture of equal amounts of peat, vermiculite and sand. On May 25, 2019, we planted 90 one-node stem fragments of each of *A. philoxeroides*, *W. trilobata*, and *H. vulgaris* in three plastic containers (71 × 45.5 × 18 cm) filled with the same soil mixture. A total of 32 similarly sized individuals of each alien invasive species and 160 similarly sized individuals of each native species were selected for use in our experiment.

Experimental Design

Each of the ten invasive species was subjected to two soil nutrient treatments (homogeneous or heterogeneous) crossed with two competition treatments (native community present or absent), with four replicates. For the heterogeneous treatment, each pot (24 cm in diameter and 20 cm in height) was divided into four equal quadrants, two of which were filled with a high nutrient soil and the other two with a low nutrient soil, arranged in a checkerboard pattern. For the homogeneous treatments, the four quadrants of the pot were each filled with an equal mixture of the low and the high nutrient soils. The high and the low nutrient soils were an equal mixture of peat, sand and vermiculite with 7.2 and 0.8 g L^{-1} slow-release fertilizer (14:14:14 N:P:K, Osmocote Exact Standard 3–4 M; Scotts, Marysville, Ohio, USA), respectively. There were no physical barriers between the quadrants, so the plant roots could grow across different quadrants.

For the treatment without competition, two plants of an invasive species were grown in the center of a pot, and no plants of native species were grown in the pot (**Figure 1**). For the treatment with competition, two plants of an invasive species were grown in the center of a pot, and two plants of each of the six native species (a total of 12 plants) were grown in the pot (**Figure 1**). The 12 plants of the native species were randomly assigned to the 12 planting positions along the four border lines of the four quadrants with three positions along each line (**Figure 1**). There were a total of 160 pots (10 invasive species × 2 soil treatments × 2 competition treatments × 4 replicates). The pots were randomly arranged on a bench in a greenhouse at Taizhou University.

TABLE 1 | Information on the ten alien invasive plant species (A) and the six native plant species (B) used in this experiment.

Species	Family	Life form	Clonality	Collection site
(A) Alien invasive species				
Ageratum conyzoides L.	Asteraceae	Annual	No	Taizhou city
Alternanthera philoxeroides (Mart.) Griseb.	Amaranthaceae	Perennial	Yes	Taizhou city
Bidens frondosa L.	Asteraceae	Annual	No	Taizhou city
Bidens pilosa L.	Asteraceae	Annual	No	Taizhou city
Celosia argentea L.	Amaranthaceae	Annual	No	Taizhou city
Erigeron annuus (L.) Cronq.	Asteraceae	Annual	No	Taizhou city
Hydrocotyle vulgaris L.	Umbelliferae	Perennial	Yes	Taizhou city
Sesbania cannabina (Retz.) Poir.	Fabaceae	Annual	No	Taizhou city
Solidago canadensis L.	Asteraceae	Perennial	Yes	Taizhou city
Sphagneticola trilobata (L.) Pruski	Asteraceae	Perennial	Yes	Guangzhou city
(B) Native species				
Achyranthes bidentata Blume.	Amaranthaceae	Perennial	No	Taizhou city
Artemisia argyi Lévl. et Van.	Asteraceae	Perennial	No	Taizhou city
Arthraxon hispidus (Trin.) Makino	Poaceae	Perennial	No	Taizhou city
Bellis perennis L.	Asteraceae	Perennial	No	Taizhou city
Patrinia scabiosaefolia Fisch. ex Trev.	Valerianaceae	Perennial	No	Taizhou city
Plantago asiatica L.	Plantagonaceae	Perennial	No	Taizhou city

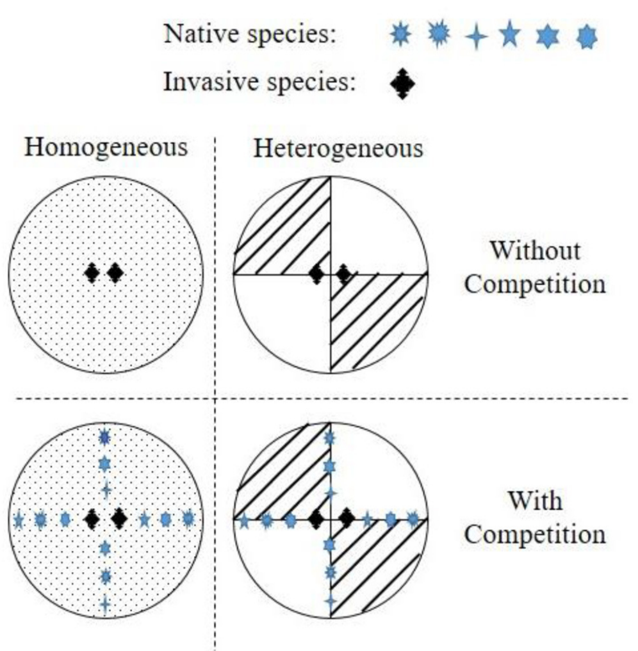

FIGURE 1 | Schematic representation of the experimental design. Two plants of each ten invasive species were grown alone in the center of a pot under soil homogeneous condition or were grown together with 12 native plants (two plants of each of six native species) under heterogeneous soil environment. The total amount of soil nutrients in a pot was the same in all the treatments. Black filled pattern represents invasive species and blue filled different patterns indicate six native species.

The experiment started on June 19, 2019, ended on August 13, 2019, and lasted for 52 days. The mean temperature in the greenhouse was 27.3°C, and mean relative humidity was 80.1% during the experiment. The light intensity inside the greenhouse was ∼70% of the natural light outside the greenhouse.

Harvest and Measurements

We measured initial height of each invasive plant in each pot at the beginning of the experiment. At the end of the experiment, we harvested aboveground part of the invasive species for the treatment without competition and the aboveground part of the invasive species and of each of the native species for the treatment with competition in each pot. All the plant materials were dried at 70°C in ovens for 72 h and weighed to obtain aboveground biomass. Total aboveground biomass per pot was the sum of aboveground biomass of the invasive species and that of the six native species in a pot. The relative abundance of the invasive species in a pot was calculated by dividing aboveground biomass of the invasive species in the pot by total aboveground biomass of all the species in pot (Parepa et al., 2013).

Data Analysis

Since we were preferentially interested in the generality of the effect of soil nutrient heterogeneity on the growth and invasion success of exotic plant species, we analyzed all ten invasive species jointly. Aboveground biomass and the relative abundance of the alien species were analyzed with a linear mixed model using the *lme* function in the R package *nlme* (Pinheiro et al., 2016). In this model, we included competition with native species (with or without), soil nutrient heterogeneity (heterogeneous or homogeneous), and their interactions as fixed terms. We accounted for differences in the initial size of the exotic alien species by including initial height as a covariate in the model. We accounted for variation among the different species by including species as random terms. To improve the normality of residuals, we tried different transformations and achieved the best residual

TABLE 2 | Results of linear mixed effect models to test the effects of soil nutrient heterogeneity and competition on (A) aboveground biomass and (B) the relative abundance of invasive plant species in plant communities.

	(A) Aboveground biomass			(B) Relative abundance		
Effect	**df**	**F**	***P***	**df**	**F**	***P***
Initial height	1,145	29.35	**<0.0001**	1.67	1.97	0.1647
Heterogeneity (H)	1,145	3.98	**0.0479**	1.67	0.70	0.4061
Competition (C)	1,145	453.37	**<0.0001**			
H × C	1,145	0.05	0.8320			

Species was included as a random effect. Values are in bold when P < 0.05.

distributions with a square root transformation of aboveground biomass and the relative abundance of exotic alien species. Since the homoscedasticity assumption was violated, we also included variance structures that modeled different variances per species in the models using the "*varIdent*" function in the R package *nlme* (Zuur et al., 2009; Pinheiro et al., 2016).

We were also interested in the effect of soil nutrient heterogeneity on aboveground biomass, the Shannon–Wiener diversity index ($H^{'}$) and evenness of the native community. $H^{'}$was calculated as $-\sum p_i \ln p_i \, (i = 1, 2, \ldots, S)$, where S is number of species in a community, and p_i is aboveground biomass of species i divided by total biomass of all species in the community (Kent and Coker, 1992). Evenness (J) was derived as $J = H^{'}/H^{'}_{\max} = H^{'}/\ln S$ (Kent and Coker, 1992). These data were also analyzed with a liner mixed model using the package *nlme* (Pinheiro et al., 2016). In these models, soil nutrient heterogeneity was acted as fixed terms and species as random terms. To improve the normality of residuals, we tried different transformations and achieved the best residual distributions with a natural-log transformation for aboveground biomass of the native community and with the square root transformation for $H'$and J. To account for the heterogeneity of variance, we used the "*varIdent*" variance structure implemented in the *nlme* function to allow for different variances for each combination of species and soil nutrient heterogeneity treatment. All the analyses were implemented in R 3.6.1 (R Core Team, 2019).

RESULTS

Soil nutrient heterogeneity significantly increased aboveground biomass of invasive species (**Table 2**, **Figure 2**), but had no significant effect on the relative abundance (**Table 2**, **Figure 3**), suggesting that it promote the growth but not the invasive succession of invasive species in native plant communities. Not surprisingly, competition from the native communities decreased aboveground biomass of invasive species (**Table 2**, **Figure 2**). There was no interactive effect of soil nutrient heterogeneity and competition from the native community on aboveground biomass of invasive species (**Table 2**). Soil nutrient heterogeneity did not significantly affect aboveground biomass, but marginally significantly increased species diversity and evenness of the native community (**Figure 4**).

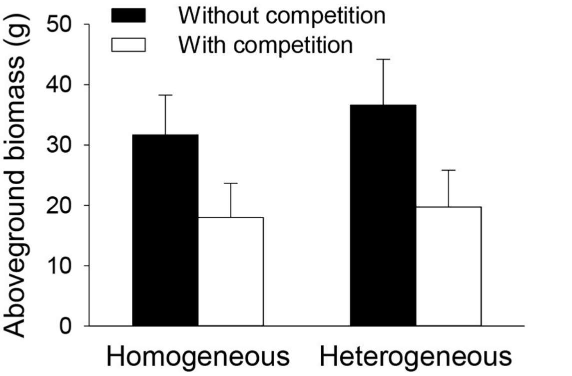

FIGURE 2 | Aboveground biomass (mean + SE) across the ten invasive plant species in the homogeneous or heterogeneous soil nutrient treatment with or without competition from the native community.

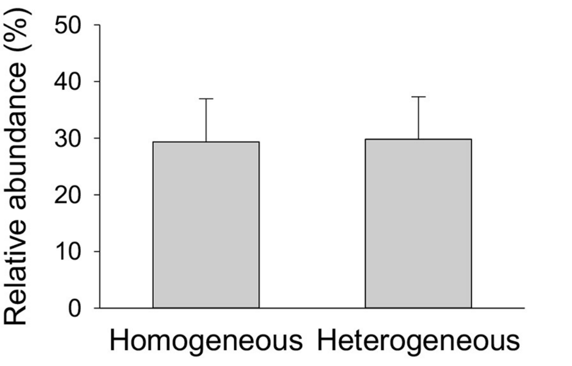

FIGURE 3 | Mean relative abundance (mean + SE) across the ten invasive species in the homogeneous and heterogeneous soil nutrient treatments.

DISCUSSION

Spatial heterogeneity of environmental factors are common in nature (Jackson and Caldwell, 1993b; Alpert and Mooney, 1996; Liu et al., 2003; Liang et al., 2007; Gao et al., 2021), and may influence exotic plant invasions (Keser et al., 2015; Chen et al., 2017; Wang et al., 2017; Liang et al., 2020). However, previous studies testing effects of soil heterogeneity on invasive

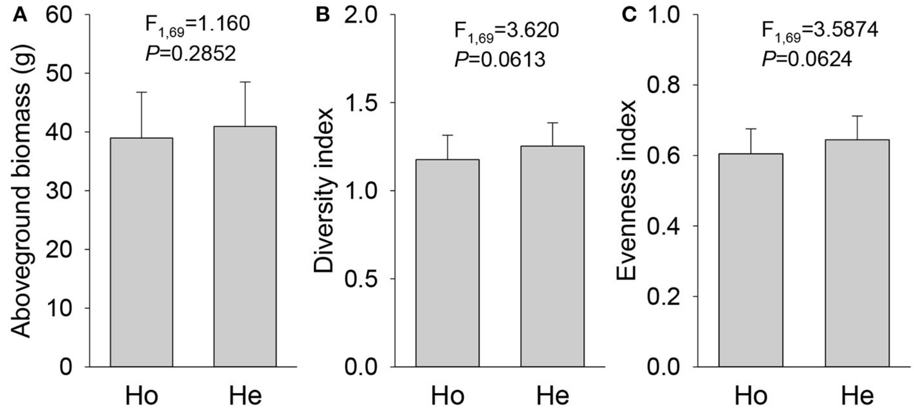

FIGURE 4 | (A) Aboveground biomass, **(B)** species diversity, and **(C)** species evenness of the native community under the homogeneous (Ho) and heterogeneous (He) soil nutrient treatment.

plants were conducted mostly under competition-free conditions (Keser et al., 2014, 2015; Dong et al., 2015; Wang et al., 2017), and its effects on the invasion success of exotic plant has not been adequately addressed (Liang et al., 2020). Our results suggest that, although soil heterogeneity increased the performance of invasive plant species in the presence of native plant communities, it did not increase the final invasion success of exotic plant species.

We found that biomass of invasive plant species was generally greater in heterogeneous than in homogeneous soil nutrient conditions (**Table 2**; **Figure 2**). This result is in line with a recent study showing that biomass of the invasive plant *A. philoxeroides* was significantly higher in heterogeneous nutrient treatment than in the homogeneous nutrient treatment, and such an effect did not depend on whether the invasive plant was grown alone or with the native plant *A. sessilis* (Liang et al., 2020). One potential mechanism is that plants usually capture more nutrients in nutrient-rich patches in heterogeneous environments, and thus promote the performance by selectively proliferating roots or concentrating other resource-acquiring organs in nutrient-rich patches (Robinson et al., 1999; Zhou et al., 2012; Gao et al., 2014; Roiloa et al., 2014). The heterogeneity-mediated increase in plant performance suggests that soil nutrient heterogeneity has the potential to improve the invasiveness of alien plant species.

However, we found that soil nutrient heterogeneity had no effect on the invasion succession of exotic plants (**Table 2**; **Figure 3**), suggesting that heterogeneous soil condition did not significantly shift the competitive balance between alien plants and natives toward the invaders. This is not consistent with previous studies showing that the competitive effects of the invasive species on some native species was greater in heterogeneous than homogeneous soils (Chen et al., 2017; Liang et al., 2020). This discrepancy might be attributed to the differences in the diversity of native competitors (Stachowicz et al., 1999; Kennedy et al., 2002), as previous studies demonstrated that native biodiversity can suppress the success of plant invasion owing to increased resource use, i.e., complementarity of resource use between species results in lower levels of available resources at high diversity (Kennedy et al., 2002; Fargione and Tilman, 2005). The native communities in our experiment, consisting of six different native species, have more species diversity than the previous studies. Thus, the effects of soil nutrient heterogeneity on the competitive ability of invasive species may be more complex and unpredictable for the native community with diverse native species.

One caveat is that the effect of soil nutrient heterogeneity on the invasion success of exotic plant may depend on the scale of soil spatial nutrient heterogeneity considered. In our study, the patch scale of soil heterogeneity may be too fine to induce a significant effect on the invasion success of exotic plants. Thus, experiments involving larger scales of soil nutrient heterogeneity should be considered in future studies. Also, the interaction between native species diversity and soil nutrient heterogeneity should also be considered to fully understand the effect of soil nutrient heterogeneity on exotic plant invasions.

We conclude that soil nutrient heterogeneity has a positive effect on the growth of invasive plants in general, but do not support the idea that soil nutrient heterogeneity favors the invasion success of exotic plant species in native plant communities. However, we cannot exclude the possibilities that soil nutrient heterogeneity plays a roles in exotic plant invasions under other scales of soil heterogeneity and different levels of native plant diversity. Further studies should be conducted to test these new hypotheses.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

F-LG and F-HY designed the study and analyzed the data. Q-SH, Y-DZ, and J-HH performed the research and collected the data. F-LG drafted the manuscript. F-HY revised the manuscript.

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