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Research Article

Contrasting effects of herbivory on responses of a native and an alien plant to soil nutrient heterogeneity

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Abstract

Soil nutrient heterogeneity can influence the performance of both native and alien plants. However, such effects may be modified by native generalist herbivores and this modification may differ between native and alien plants due to differences in co-evolutionary histories with the herbivores. In a greenhouse experiment, we grew two native and two alien plants either alone or in native-alien pairs in homogeneous or heterogeneous soils, with or without the native generalist herbivore *Spodoptera litura*. Total biomass of the native plant *Alternanthera sessilis* and the alien plant *Celosia argentea* was lower in the heterogeneous than in the homogeneous soils, indicating an overall negative effect of soil nutrient heterogeneity. Although the heterogeneity × herbivory interaction was not significant, post-hoc comparisons revealed species-specific patterns. For *A. sessilis*, the lowest total biomass occurred in heterogeneous soils under herbivory, whereas the other treatment combinations did not differ significantly. In contrast, for *C. argentea*, total biomass differences between homogeneous and heterogeneous soils were evident only in the absence of herbivores. Belowground biomass analyses suggest that the contrasting responses were likely to result from species-specific, herbivore-induced trade-offs between the benefits and costs of root foraging precision in heterogeneous soils. These effects, however, were not observed for the native plant *Achyranthes bidentata* or the alien plant *Amaranthus retroflexus*. Competition with alien plants reduced aboveground biomass of both native plants, whereas the alien plants were unaffected by competition with natives. Competition did not alter the effects of soil heterogeneity or herbivory. These results indicate that soil nutrient heterogeneity and native generalist herbivores may jointly shape the performance of native and alien plants in a species-specific manner, regardless of competition between them.

Key words: Foraging behaviour; herbivore insect; interspecific competition; plant invasion; spatial heterogeneity

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Introduction

Soil nutrient heterogeneity is a common feature of terrestrial ecosystems (García-Palacios et al. 2011, 2012; Xue et al. 2023). It refers to spatial variation in nutrient availability within soil, which can occur over a range of scales from fine root-level microsites to community-level nutrient patches (Hutchings et al. 2003; Hodge 2004; Stein et al. 2014). Soil nutrient heterogeneity plays an important role in

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influencing plant performance at both individual species and community levels (Hutchings et al. 2003; Stein et al. 2014; Wang et al. 2022). At the species level, soil nutrient heterogeneity can affect individual plant biomass production (Zhou et al. 2023), biomass allocation between root and shoot (Liu et al. 2021) and the spatial distribution of roots (Liu et al. 2017b). At the community level, soil nutrient heterogeneity can alter community productivity and diversity by modifying the competitive interactions amongst species (Xue et al. 2019, 2021, 2023). These effects may vary depending on the relative size of plant root systems and the grain size of soil nutrient heterogeneity (Hutchings et al. 2003; Liu et al. 2019; Xue et al. 2019). Plants can only respond to soil nutrient heterogeneity when the size of their root systems matches the grain (patch) size of the soil nutrient heterogeneity, i.e. the root system should not be much larger or smaller than the grain size of soil nutrient heterogeneity (Hutchings et al. 2003; Adomako et al. 2021b; Huang et al. 2023).

Plants can respond to soil nutrient heterogeneity by allocating more roots and/or shoots into nutrient-rich patches within a spatially variable environment, which is known as foraging behaviour (Hutchings and de Kroon 1994; Fransen and de Kroon 2001; McNickle et al. 2009; Li et al. 2024). Alien plants generally have greater phenotypic plasticity and higher growth rates than native plants, allowing them to exploit high-quality patches more rapidly and precisely (i.e. with higher foraging precision; Drenovsky et al. (2008); James et al. (2009); van Kleunen et al. (2010); Davidson et al. (2011); Keser et al. (2015); Chen et al. (2019)). Consequently, soil nutrient heterogeneity may differentially influence alien and native plants, thereby altering interspecific interactions between them. Under competitive conditions, alien plants may benefit more from soil nutrient heterogeneity and eventually outcompete native plants (Liang et al. 2020; Wei and van Kleunen 2022, 2024).

The effects of soil nutrient heterogeneity on alien and native plants may be modified by aboveground herbivores (Bardgett and Wardle 2003; Liu et al. 2017a; Zhang et al. 2020). When an alien plant is introduced into a new region, it may face challenges from native generalist herbivores (Levine et al. 2004; Meijer et al. 2016; Shan and Hou 2024). Increased growth of alien and native plants due to soil nutrient heterogeneity may lead to a higher likelihood of being attacked by native generalist herbivores (Pérez-Harguindeguy et al. 2003; Adler et al. 2006; Cherif and Loreau 2013). Therefore, the presence of a native generalist herbivore may reduce the positive effects of soil nutrient heterogeneity on both alien and native plants. In the field, alien plants often co-exist with native plants in local invaded communities. When native generalist herbivores attack alien plants more than native plants due to the lower resistance of the alien plants (i.e. the biotic resistance hypothesis; Levine et al. (2004); Allen et al. (2021); Guo et al. (2024)), their presence will reduce the growth benefit that alien plants gain from soil nutrient heterogeneity more than that of native plants. By contrast, when native generalist herbivores attack native plants more than alien plants due to enemy release (i.e. the enemy release hypothesis; Liu and Stiling (2006); Schultheis et al. (2015); Brian and Catford (2023)), the growth benefit from soil nutrient heterogeneity will be reduced more in native plants than in alien plants. However, we still know little about how native generalist herbivores influence the performance of alien and native plants in heterogeneous soils.

Here, we conducted a greenhouse experiment to test how soil nutrient heterogeneity and the presence of a native generalist herbivore influence the performance of both alien and native plants grown alone and in competition. Specifically, we

tested the following hypotheses: (1) both alien and native plants grow better in heterogeneous than in homogeneous soils, due to higher precision of root foraging behaviour; (2) the positive effects of soil nutrient heterogeneity are reduced by the presence of a native generalist herbivore; (3) these effects vary depending on whether the alien and native plants are grown alone or together.

Materials and methods

Experimental design

The experiment had two levels of soil nutrient heterogeneity treatments (homogeneous vs. heterogeneous soil), two levels of competition treatments (absence vs. presence of interspecific competition between a native and an alien plant), fully crossed with two levels of herbivore treatment (with vs. without herbivores). In the heterogeneous soil treatment, we divided each experimental pot (10 cm × 10 cm × 9 cm) into four quadrats and filled each quadrat with a 2:1:1 (volume ratio) mixture of peat (Klasmann-Deilmann, China; N: 0.14 g l^{-1}; P: 0.10 g l^{-1}; K: 0.18 g l^{-1}), sand and field soil. We randomly selected two opposite quadrats within each pot and made a hole (1-cm diameter, 4-cm deep) at the centre of each selected quadrat (Fig. 1). We then added 1 g of slow-release fertiliser (Everris International B.V., The Netherlands; N:P:K = 14:14:14; effective for 3–4 months) to each hole and refilled the hole using the soil in the pot (Fig. 1). In the homogeneous soil treatment, we evenly mixed 2 g of slow-release fertiliser into each pot, so that the total nutrient content was equal in the heterogeneous and homogeneous soil treatments.

We used two plant species native to China (*Alternanthera sessilis* L. and *Achyranthes bidentata* Blume) and two alien species introduced to China (*Celosia argentea* L. and *Amaranthus retroflexus* L.) in the experiment. All species belong to the family Amaranthaceae. On 15 July 2022, we evenly sowed seeds of each species separately into trays filled with peat and watered them daily. On 22 July 2022, similar-sized seedlings were selected and transplanted into the homogeneous and heterogeneous soils. In the treatment without competition, one seedling of each species was planted at the centre of a pot (Fig. 1), with 10 pots per species for each soil treatment, resulting in 80 pots in total (4 species × 2 soils × 10 pots). In the competition treatment, we randomly selected one seedling of the native plants and one seedling of the alien plants (in a total of four different combinations) and planted them together in the centre of a pot (Fig. 1); two pots were planted for each combination under each soil treatment, resulting in 16 pots in total (4 combinations × 2 soils × 2 pots). Dead seedlings were replaced during the first two weeks of the experiment.

On 8 October 2022, we caged each pot individually using hanging mesh cages (size: 20 cm in diameter and 100 cm in height) and introduced four second-instar larvae of *Spodoptera litura* into half of the pots. *S. litura* is a nocturnal moth in the family Noctuidae. Its larvae feed voraciously on plants, often leaving leaves completely destroyed by the larvae. We selected this species because it is a common native herbivore in China and can cause severe damage to many crops and wild plants. On 15 October 2022, after one week of feeding, we removed all caterpillars and harvested the plants. During the experiment, the mean air temperature and relative humidity were 27.9 °C and 76.2%, respectively.

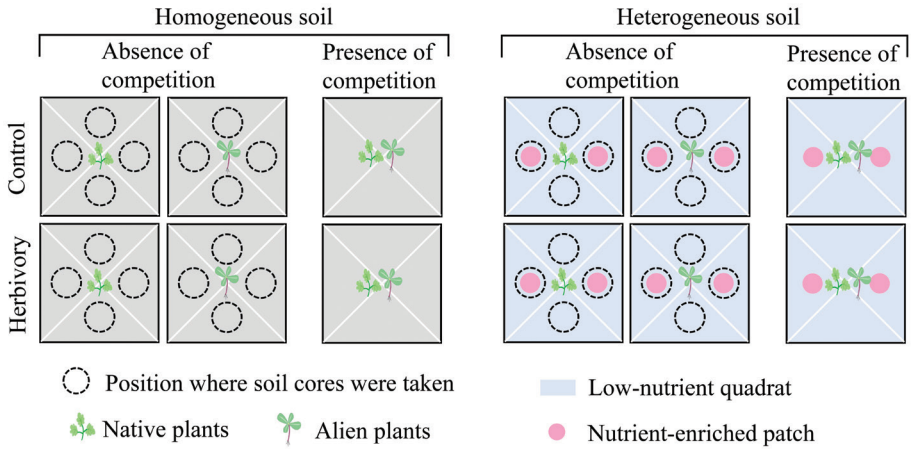


Figure 1. Schematic diagram of the experimental design. Plants were grown alone (i.e. absence of competition) or in a mixture of one alien plant and one native plant (i.e. presence of competition) in homogeneous soil where soil nutrients were evenly distributed or in heterogeneous soil where soil nutrients were enriched in two circular patches (pink circle) located at the centre of two opposite quadrats. Pots were assigned to the treatment with or without herbivores. Dashed circles mark the positions where soil cores were taken at the end of the experiment.

Harvest and measurements

At the end of the experiment, we harvested aboveground biomass of each plant separately in each pot. In the heterogeneous soil treatment, we took a soil core (2.5 cm in diameter) from the centre of each quadrat within a pot (Fig. 1). The two soil cores from the two opposite quadrats were combined, such that belowground biomass from the two nutrient-enriched patches was pooled separately from that of the two low-nutrient patches. In the homogeneous soil treatment, we took soil cores in the same sampling regime as in the heterogeneous soils. All remaining belowground materials in each pot were then harvested. This was done only for heterogeneous and homogeneous soil treatments in the absence of competition. In the competition treatment, all belowground materials were harvested together in each pot as it is not possible to separate belowground biomass of each plant species. All belowground materials were washed using a 0.5 mm mesh. All plant materials were dried at 70 °C for at least 48 hours.

Data analysis

At the pot level, we analysed total, aboveground and belowground biomass of each plant species from the whole pot. We used three-way ANOVAs to examine the effects of soil nutrient heterogeneity (homogeneous vs. heterogeneous soil), herbivory (with vs. without herbivores) and competition (absence vs. presence of interspecific competition between a native and an alien plant) on aboveground biomass of each plant species separately. We used two-way ANOVAs to examine the effects of soil nutrient heterogeneity and herbivory on total and belowground biomass of each plant species separately; competition was excluded from the model because it is not possible to separate the belowground biomass and, thus, the total biomass of individual plant species in the competition treatment. Tukey's post-hoc tests were performed for multiple comparisons using the *emmeans* function (version 1.10.2) when a significant effect ($P < 0.05$) was detected.

At the patch level, we analysed belowground biomass per soil core from homogeneous soils and from nutrient-enriched and low-nutrient patches within the heterogeneous soils, considering only plants grown in the absence of competition. In some soil cores taken from patch centres, no roots were detected. These observations do not represent missing samples or plant mortality, but indicate the absence of roots at that spatial location; therefore, belowground biomass for these cores was recorded as zero rather than coded as NA. We used linear mixed-effects models, implemented with the *nlme* package (version 3.1-164), to test the effects of herbivory and patch type (homogeneous soil vs. nutrient-enriched patches vs. low-nutrient patches) on belowground biomass per soil core for each plant species separately. In these models, herbivory, patch type and their interactions were included as fixed effects; pot identity was included as a random effect to account for the non-independence of measurements from different patches within the same pot. Tukey's post-hoc test were performed to compare belowground biomass per soil core amongst different soil patch types under each herbivory treatment when a significant effect ($P < 0.05$) was detected.

All analyses were performed in R (version 4.4.0; http://www.r-project.org). For all ANOVAs and mixed-effects models, residuals of all variables were checked graphically for normality and homogeneity of variance before analysis.

Results

Effects on native plant growth at the pot level

Total biomass of the native plant *Alternanthera sessilis* was significantly affected by soil heterogeneity, with lower total biomass in heterogeneous than in homogeneous soils (Fig. 2A; Table 1: A). However, post-hoc comparisons did not detect significant differences between soil treatment within either herbivory level (Fig. 2A). Similarly, aboveground biomass of *A. sessilis* was significantly lower in heterogeneous than in homogeneous soils (Fig. 2B; Table 1: A), whereas post-hoc comparisons revealed no significant differences between soil treatments within any herbivory × competition combination (Fig. 2B). Aboveground biomass was also significantly reduced when *A. sessilis* grew in competition with alien species compared with when grown alone (Fig. 2B; Table 1: A). In contrast, herbivory had no significant main effect on aboveground biomass of *A. sessilis* and no significant interactions amongst factors were detected (Table 1: A). Additionally, soil nutrient heterogeneity, herbivory and their interaction had no significant effects on belowground biomass of *A. sessilis* (Fig. 2C; Table 1: A).

Soil nutrient heterogeneity, herbivory and their interaction did not significantly affect the total, aboveground or belowground biomass of the native plant *Achyranthes bidentata* (Fig. 2D–F; Table 1: B). The aboveground biomass of *A. bidentata* tended to be lower when grown in competition with alien plants compared to when it was grown alone, regardless of soil nutrient heterogeneity and herbivory (Fig. 2E; Table 1: B), but post-hoc comparisons did not detect significant pairwise differences.

Effects on alien plant growth at the pot level

Soil heterogeneity also significantly affected the total biomass of the alien plant *Celosia argentea*, with lower biomass in heterogeneous than in homogeneous soils

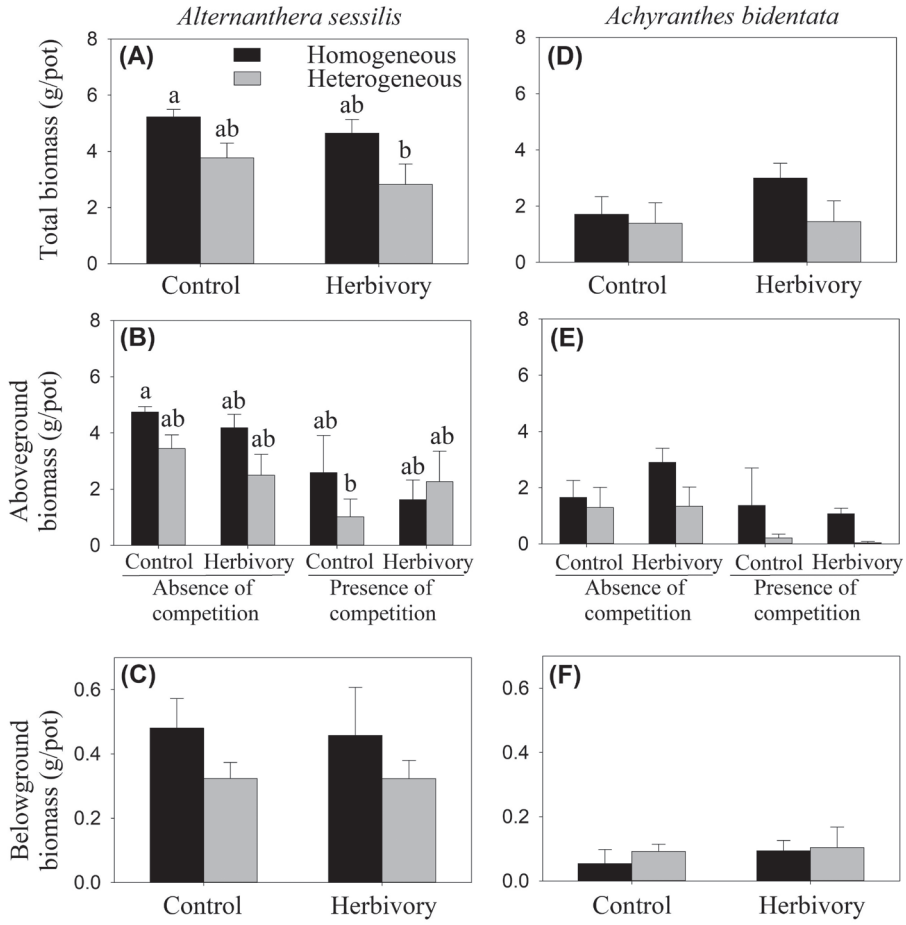


Figure 2. Total biomass (**A, D**), aboveground biomass (**B, E**) and belowground biomass (**C, F**) of the native plants *Alternanthera sessilis* and *Achyranthes bidentata* under different treatments. Competition was excluded from the top and bottom panels because it is not possible to separate the belowground biomass and, thus, the total biomass of individual plant species in the competition treatment. Letters (a, b) represent significant difference ($P < 0.05$) amongst the treatments.

(Fig. 3A; Table 2: A). Post-hoc comparisons indicated that total biomass of *C. argentea* was significantly lower in heterogeneous than in homogeneous soils under control conditions, whereas no significant difference between soil treatments was detected under herbivory (Fig. 3A). Soil heterogeneity further had a significant effect on aboveground biomass and a marginal effect on belowground biomass of *C. argentea*; however, post-hoc pairwise comparisons revealed no significant differences amongst specific treatment combinations (Fig. 3B, C; Table 2: A).

In contrast, none of the growth measures of the alien plant *A. retroflexus* was affected by soil nutrient heterogeneity, herbivory, competition (when applicable) or their interactions (Fig. 3D–F; Table 2: B).

Effects on native and alien plant growth at the patch level

Under no-herbivore control conditions, belowground biomass per soil core of the native plant *A. sessilis* was significantly greater in nutrient-enriched than in low-nutrient patches, whereas no difference was found between homogeneous soil and nutrient-enriched or low-nutrient patches (Table 3: A; Fig. 4A). In contrast,

Table 1. Effects of soil nutrient heterogeneity, herbivory and competition on total biomass, aboveground biomass and belowground biomass of the native plants (A) *Alternanthera sessilis* and (B) *Achyranthes bidentata.* Competition was excluded from the model because it is not possible to separate the belowground biomass, and thus the total biomass of individual plant species in the competition treatment.

Effects	(A) *Alternanthera sessilis*						(B) *Achyranthes bidentata*					
	Total biomass		Aboveground biomass		Belowground biomass		Total biomass[1]		Aboveground biomass		Belowground biomass	
	$F_{1,16}$	*P*	$F_{1,20}$	*P*	$F_{1,16}$	*P*	$F_{1,13}$	*P*	$F_{1,17}$	*P*	$F_{1,13}$	*P*
Heterogeneity (H)	9.40	**0.007**	7.00	**0.015**	2.34	0.145	1.69	0.216	3.49	***0.079***	0.31	0.587
Herbivory (B)	2.03	0.173	1.19	0.289	0.02	0.904	0.66	0.430	0.47	0.504	0.32	0.580
Competition (C)			13.54	**0.001**					3.77	***0.070***		
H × B	0.12	0.739	0.16	0.698	0.01	0.906	0.71	0.416	0.57	0.460	0.10	0.762
H × C			1.05	0.318					0.02	0.890		
B ×C			0.80	0.382					0.63	0.438		
H × B × C			1.68	0.209					0.34	0.567		

[1]data were root-squared transformed. Values are in bold italic when $P < 0.1$, Values are in bold when $P < 0.05$.

Table 2. Effects of soil nutrient heterogeneity, herbivory and competition on total biomass, aboveground biomass and belowground biomass of the alien plants (A) *Celosia argentea* and (B) *Amaranthus retroflexus*. Competition was excluded from the model because it is not possible to separate the belowground biomass, and thus the total biomass of individual plant species in the competition treatment.

Effects	(A) *Celosia argentea*						(B) *Amaranthus retroflexus*					
	Total biomass		Aboveground biomass		Belowground biomass		Total biomass		Aboveground biomass		Belowground biomass	
	$F_{1, 16}$	*P*	$F_{1, 20}$	*P*	$F_{1, 16}$	*P*	$F_{1, 16}$	*P*	$F_{1, 20}$	*P*	$F_{1, 16}$	*P*
Heterogeneity (H)	6.52	**0.021**	5.49	**0.030**	4.23	***0.056***	0.06	0.813	0.15	0.699	0.18	0.674
Herbivory (B)	0.43	0.519	1.01	0.327	0.07	0.796	0.46	0.505	0.38	0.546	0.16	0.693
Competition (C)			0.07	0.791					1.42	0.248		
H × B	2.44	0.138	2.02	0.171	1.43	0.249	0.04	0.841	0.77	0.391	0.17	0.689
H × C			1.13	0.301					1.45	0.243		
B ×C			0.05	0.832					0.12	0.732		
H × B × C			0.50	0.488					0.78	0.389		

Values are in bold italics when $P < 0.1$. Values are in bold when $P < 0.05$.

Table 3. Effects of herbivory and patch type (homogeneous soil vs. nutrient-enriched patches vs. low-nutrient patches) within pot on belowground biomass per soil core of the native plants (A) *Alternanthera sessilis* and (B) *Achyranthes bidentata***,** and the alien plants (C) *Celosia argentea* and (D) *Amaranthus retroflexus* when grow alone.

Effects		(A) *Alternanthera sessilis*[1]		(B) *Achyranthes bidentata*[1]		(C) *Celosia argentea*[1]		(D) *Amaranthus retroflexus*	
	DF	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Herbivory (B)	1	0.26	0.618	0.09	0.771	2.33	0.144	0.66	0.428
Patch (P)	2	7.81	**0.021**	1.46	0.335	4.44	***0.066***	0.67	0.548
B × P	2	0.38	0.700	0.41	0.691	1.93	0.226	0.39	0.691

[1]data were root-squared transformed. Values are in bold italic when $P < 0.1$, Values are in bold when $P < 0.05$.

under herbivory, post-hoc comparisons revealed no significant differences in belowground biomass per soil core amongst patch types (Fig. 4A).

For the native plant *A. bidentata* and the alien plants *C. argentea* and *A. retroflexus*, belowground biomass per soil core was not significantly affected by herbivore, patch type or their interaction (Table 3: B–D, Fig. 4B–D).

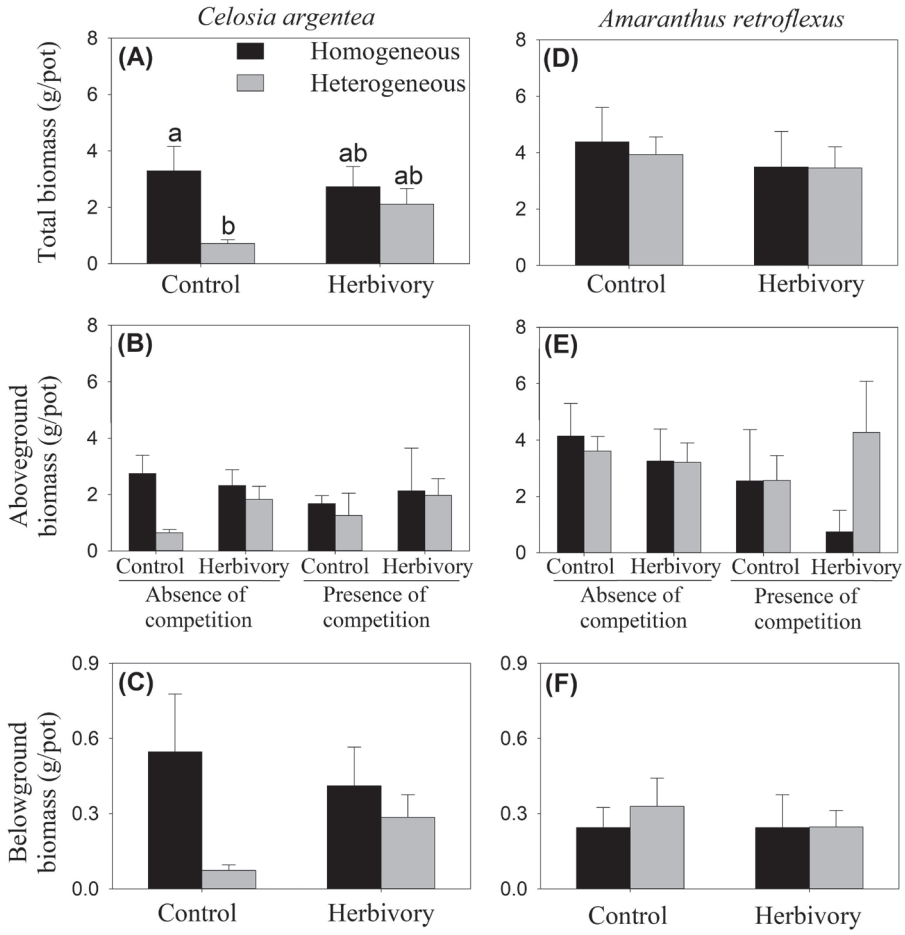


Figure 3. Total biomass (**A, D**), aboveground biomass (**B, E**) and belowground biomass (**C, F**) of the alien plants *Celosia argentea* and *Amaranthus retroflexus* under different treatments. Competition was excluded from the top and bottom panels because it is not possible to separate the belowground biomass and, thus, the total biomass of individual plant species in the competition treatment. Letters (a, b) represent significant difference ($P < 0.05$) amongst the treatments.

Discussion

Our results showed that soil nutrient heterogeneity significantly reduced the growth of the native plant *A. sessilis* and the alien plant *C. argentea*. Although the interaction between soil nutrient heterogeneity and herbivory was not significant, post-hoc comparisons revealed species-specific patterns in the expression of heterogeneity effects across herbivory treatments. Specifically, at the plot level, total biomass differences between homogeneous and heterogeneous soils were most evident for *C. argentea* in the absence of herbivores, whereas for *A. sessilis*, no significant differences between soil treatments were detected within either herbivory level. At the patch level, belowground biomass per soil core of *A. sessilis* was significantly greater in nutrient-enriched than in low-nutrient patches within heterogeneous soils only in the absence of herbivores, whereas for *C. argentea*, no significant differences between patch types were detected within either herbivory level. In contrast, neither soil nutrient heterogeneity nor herbivory affected the growth of the native plant *A. bidentata* or the alien plant *A. retroflexus*. Moreover, competition with alien plants reduced the growth of both native plants, whereas competition with native plants did not affect the growth of the two alien plants. We found no evidence that

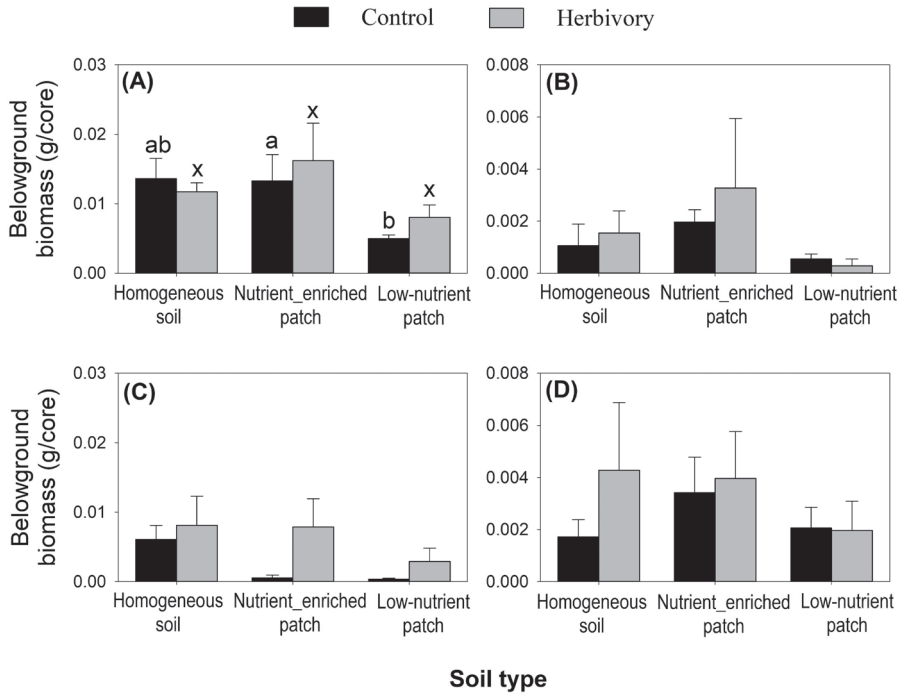


Figure 4. Belowground biomass per soil core of the native plants **A**. *Alternanthera sessilis* and **B**. *Achyranthes bidentata* and the alien plants; **C**. *Celosia argentea* and **D**. *Amaranthus retroflexus* in homogeneous soil, as well as the nutrient-enriched and low-nutrient patches within the heterogeneous pots where they grow alone. Letters (a, b; x) represent significant difference ($P < 0.05$) amongst the three soil types within each level of herbivory treatments.

competition modified the effects of soil nutrient heterogeneity or herbivory. These results indicate that the expression of plant responses to soil nutrient heterogeneity depends on both native generalist herbivores and species identity.

In contrast to our first hypothesis, soil nutrient heterogeneity exerted a negative main effect on the total biomass of the native plant *A. sessilis* and the alien plant *C. argentea*. Similar negative responses to nutrient heterogeneity have been reported for *Leymus chinensis* (Adomako et al. 2021a), *Lolium perenne* (Nakamura et al. 2008) and *Plantago lanceolata* (Tsunoda et al. 2014). Generally, plants are expected to benefit from soil nutrient heterogeneity by preferentially allocating roots to high-nutrient patches, thereby enhancing resources acquisition and whole-plant growth (Dong et al. 2015; Liu et al. 2017b; Chen et al. 2019). Consistent with this expectation, the native plant *A. sessilis* produced and the alien plant *C. argentea* tended to produce greater belowground biomass in nutrient-enriched than in low-nutrient patches within the heterogeneous soils. However, this localised root foraging did not translate into increased total biomass, suggesting that the costs of exploiting fine-scale nutrient patches outweighed the benefits. Unlike the common checkerboard design used in previous studies (e.g. Xue et al. (2019, 2021); Yao et al. (2021)), we created nutrient heterogeneity by adding slow-release fertiliser to a small spatially discrete patch (1 cm in diameter). As a result, plants may have spent more energy exploiting the nutrient-enriched patches, but gained fewer benefits, resulting in reduced whole-plant growth under heterogeneous conditions.

Post-hoc comparisons revealed species-specific patterns in the expression of soil nutrient heterogeneity effects. The contrasting responses of the native plant *A. sessilis* and the alien plant *C. argentea* may reflect differences in their belowground

foraging strategies and associated costs under herbivore pressure. In heterogeneous soils, *A. sessilis* exhibited clear root foraging behaviour in the absence of herbivores (Fig. 4A), suggesting that herbivory constrained its capacity to exploit nutrient-enriched patches. As a result, *A. sessilis* may have experienced both reduced nutrient uptake and simultaneous aboveground damage, resulting in particularly low biomass in heterogeneous soils under herbivory. In contrast, the lack of strong root foraging responses in *C. argentea* (Fig. 4C) may have limited the costs associated with exploiting fine-scale nutrient heterogeneity. This strategy could allow *C. argentea* to maintain growth under herbivory pressure, thereby diminishing the effects of soil heterogeneity in the presence of herbivores. This pattern may also reflect the generally greater environmental tolerance of alien plants compared with natives, including higher resistance or compensatory ability to damage caused by generalist herbivores (Alpert et al. 2000; Keane and Crawley 2002; Fornoni 2011).

Another possible explanation relates to the distinct co-evolutionary histories between the native generalist herbivore and the native versus alien plants. Native plants may experience stronger or more maladaptive responses to herbivory due to long-term co-evolution, whereas alien plants may suffer less damage from native generalist herbivores due to their shorter co-evolutionary history (Kirichenko et al. 2013; Yoon and Read 2016; Ameline et al. 2023). Consequently, the presence of the native generalist herbivore may largely eliminate the benefits native plants gain from heterogeneous soils, but not affect alien plants in the same way. These results suggest that local native generalist herbivores can alter the expression of soil nutrient heterogeneity effects on plant performance in a species-specific manner, by reshaping how individual species balance the costs and benefits of belowground foraging under herbivore pressure.

When competing, aboveground growth of both native plants was reduced compared to when they were grown alone, but competition did not affect the growth of the alien plants. This is consistent with previous studies showing that alien plants can generally outcompete native plants due to rapid growth strategies (Leishman et al. 2014), allelopathic effects (Yuan et al. 2021) and positive plant-soil feedbacks (Yuan et al. 2025). These processes may also have occurred in our study, but further research is needed to explore their relative contributions to the distinct responses of native and alien plants to competition. However, we did not find evidence that competition altered the effects of soil nutrient heterogeneity or herbivory. This may be because the effects of competition overwhelmed those of soil nutrient heterogeneity and herbivory. In our study, competition-induced reductions in aboveground growth were 49.6 ± 9.1% and 62.2 ± 11.4% for the native plants *A. sessilis* and *A. bidentata*, respectively, while heterogeneity-induced reductions were 31.6 ± 6.8% and 33.1 ± 7.9%, respectively. Herbivory induced a 14.3 ± 6.1% reduction in *A. sessilis* growth, but contributed to a 25.1 ± 9.3% increase in *A. bidentata* growth. These results indicate that direct competition may be more important than soil nutrient heterogeneity and herbivory in regulating the performance of the native and alien plants.

Conclusions

We conclude that soil nutrient heterogeneity can suppress the growth of the native plant *A. sessilis* and the alien plant *C. argentea*, whereas the native *A. bidentata*

and the alien *A. retroflexus* were largely insensitive to spatial variation in soil resources. Although the interaction between soil nutrient heterogeneity and herbivory was not statistically significant at the pot level, post-hoc comparisons revealed species-specific patterns in the expression of plant responses to heterogeneous soils: *A. sessilis* tended to show its lowest growth in heterogeneous soils under herbivory, whereas for *C. argentea* the suppressive effect of soil heterogeneity was most evident in the absence of herbivores. Competition between native and alien plants did not modify plant responses to either soil nutrient heterogeneity or herbivory. Collectively, these findings highlight that the effects of soil nutrient heterogeneity and native generalist herbivores on plant growth are contingent on individual species identity.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

Wei Xue conceived the idea and designed methodology. Xiao-Yan Na, Yin-Ni Wu and Lin Huang conducted the experiment and collected the data. Xiao-Yan Na performed the analysis with guidance of Wei Xue. Xiao-Yan Na wrote the first version of the manuscript with the input of Wei Xue. Kai Ou-Yang has taken the lead in revising and resubmitting this manuscript. All authors discussed the results, revised the manuscript, contributed substantially to the draft and gave final approval for publication.

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Data availability

Raw data supporting the findings of this study are available from the corresponding author upon request.

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