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Soil fauna may buffer the negative effects of drought on alien plant invasion

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Abstract

Assessing how climate change affects the potential invasion risk of alien plants has garnered considerable interest in ecology. Although many studies have tested the direct effects of drought on alien plant invasion, less is known about how drought affects alien plant invasion indirectly via other groups of organisms such as soil fauna. To test for such indirect effects, we grew single plant of nine naturalized alien target species in pot mesocosms with a native community of five native grassland species under four combinations of two drought (well-watered *vs* drought) and two soil-fauna (with *vs* without) treatments. We found that drought decreased the absolute and the relative biomass production of the alien target plants, and thus reduced their invasion success in the native community. Inoculation with a soil fauna increased the biomass of the native plant community and thereby decreased the relative biomass production of the alien species. The increased invasion resistance due to soil fauna tended (p = 0.09) to be stronger for plants growing under well-watered conditions than under drought. Our multispecies experiment shows for the first time that soil fauna might help native resident communities to resist alien plant invasions, but that this effect might be diminished by drought.

Key words: alien-native competition, biological invasion, climate change, exotic, plant-environment interactions, soil animals

INTRODUCTION

With the rapid globalization, more and more plant species have been introduced to new regions outside their native range (van Kleunen et al. 2015; Seebens et al. 2018; van Kleunen et al. 2018). Some of these alien plants have become invasive, which could decrease native species diversity, change nutrient cycles, and thereby affect ecosystem functions (Hejda et al. 2009; Vilà et al. 2011; Pyšek et al. 2012; Linders et al. 2019; Pyšek et al. 2020). Forecasts show that the number of alien plant species per continent may increase on average by 18% from 2005 to 2050 (Seebens et al. 2020), indicating that the impacts of plant invasions on ecosystems may become even more serious. However, as there are many potential drivers of invasions, there are many uncertainties about how invasions and their impacts will develop in the future (Essl et al. 2020). In this regard, particularly the potential effects of ongoing climate change on plant invasions have garnered interest (Liu et al. 2017; Bartz and Kowarik 2019).

In many places, climate change is characterized by more frequent and more intense drought events (Dai 2013; Diffenbaugh et al. 2015; Yoon et al. 2015; Spinoni et al. 2018). Droughts do not only reduce water availability to the plants, but also decreases the nutrient absorption (da Silva et al. 2011; Bueno et al. 2020). Consequently, drought might affect the competition between alien and native plants (Werner et al. 2010; Manea et al. 2016; Bueno et al. 2020), and thereby affect invasion success of alien plants (Ahanger et al. 2016; Mohammad et al. 2016; Haeuser et al. 2019; Bueno et al. 2020). For example, Manea et al. (2016) found that drought could reduce biomass production of native grasses, and consequently enhance the establishment success of alien plants. However, many other studies also found that invasive plants may suffer more from drought than native species, indicating that drought could also suppress alien plant invasion (Werner et al. 2010; Copeland et al. 2016; Liu et al. 2017; LaForgia et al. 2018; Valliere et al. 2019; Kelso et al. 2020). One of the reasons for the mixed findings could be that most studies only considered direct effects of drought on alien plant invasion (Copeland et al. 2016; Liu et al. 2017; Pintó-Marijuan et al. 2017; Valliere et al. 2019). Much less is known about the indirect effects, i.e. how drought affects alien plant invasion via other trophic levels.

Soil fauna include several important belowground trophic levels, which are increasingly recognized to affect plant competition (Wardle et al. 2004; Bardgett et al. 2005; Eisenhauer and Scheu 2008; Eisenhauer et al. 2010). On the one hand, soil fauna could enhance nutrient mineralization, and thereby increase plant nutrient uptake (Smith and Steenkamp 1992; Marinissen and de Ruiter 1993; Bardgett and Chan 1999; Xu et al. 2003; Cole et al. 2004; Barot et al. 2007; Eisenhauer et al. 2010). Given that invasive plants frequently respond more positively to nutrient enrichment than native plants (Liu et al. 2017; Liu et al. 2018), the higher nutrient availability caused by soil fauna may increase the invasion success. On the other hand, soil fauna can also change alien-native competition via herbivory effects (Bonkowski et al. 2009; Korell et al. 2019). The enemy-release hypothesis poses that alien plants are released from most of their native enemies (Keane and Crawley 2002, Mitchell and Power 2003, Vilà et al. 2005, Liu and Stiling 2006). Following this logic, alien plants would be damaged less than natives by herbivorous soil fauna, and therefore soil fauna would promote alien plant invasion. However, until now very few studies have tested how soil fauna affects alien plant invasion into resident communities (Bonkowski et al. 2009; Korell et al. 2019).

It has often been found that indirect effects of altered biotic interactions due to climate change on species populations are more pronounced than their direct effects (Ockendon et al. 2014). For example, empirical studies indicated that belowground trophic interactions could alter the plant responses to drought (Erb et al. 2011; Guyer et al. 2018; Franco et al. 2020; Wilschut and van Kleunen 2021). Consequently, it is likely that drought might indirectly affect alien plant invasion in resident communities via effects on soil fauna. Indeed, drought can reduce the abundance and diversity of soil fauna (Makkonen et al. 2011; Eisenhauer et al. 2012; Guyer et al. 2018; Aupic-Samain et al. 2020; Wilschut and Geissen 2020). Given that soil fauna, in particular some of the root herbivores might affect competition between native and alien plants, indirect effects of drought on alien plant invasion in resident community would occur via the cascading effect of drought suppression on soil fauna (Bonkowski et al. 2009; Korell et al. 2019). However, it has not been tested yet how drought could indirectly, via effects on soil fauna, affect plant invasion.

To test the direct and indirect effects (i.e. via soil fauna) of drought on alien plant invasion into a native resident community, we performed a mesocosm-pot experiment. We grew single plants of nine alien target species in a community of five native grassland species under four combinations of two drought (well-watered *vs* drought) and two soil-fauna (with *vs* without) treatments. By comparing the absolute aboveground biomass production of the alien target species as well as their biomass production relative to the biomass production of the native competitors, we addressed the following specific questions: (1) Does drought suppress the absolute and relative biomass of alien species? (2) Does the presence of soil fauna promote or suppress the absolute and relative biomass of alien species? (3) Does the presence of soil fauna change the effect of drought on the absolute and relative biomass of alien species?

MATERIAL AND METHODS

Study species

To test the effects of drought, the presence of soil fauna, and their interaction on alien plant invasion in a native grassland community, we chose nine naturalized alien species as targets and five native species as competitors from the herbaceous flora of China (see Supporting Information Table S1). We classified the species as naturalized alien or native to China based on information in the book “The Checklist of The Naturalized Plants in China” (Yan et al. 2019) and the Flora of China database (www.efloras.org). To cover a wide taxonomic breadth, the nine alien species were chosen from eight genera of four families. The five native species, used to create the native community, included two forbs and three grasses that are all very common and do co-occur in grasslands in China. Seeds of all species, except one whose seeds were bought from a commercial seed company, were collected from natural populations growing in grasslands (Table S1).

Soil-fauna collection

To provide a live soil-fauna community as inoculum for the pot mesocosms, we collected soil fauna from a grassland site at the Northeast Institute of Geography and Agricultural Ecology, Chinese Academy of Sciences (125°24'30"E, 43°59'49"N) on 21 July 2020. In the grassland, we removed aboveground plant materials from each of 100 sampling locations (30cm × 30cm), and then collected from each location a soil sample of 1-L (10cm × 10cm× 10cm) using a shovel. Each sampling location was at least 10m apart from the others. Then, we brought the 100 soil samples back to the laboratory, where we extracted the soil fauna communities of each soil sample separately using the Macfadyen method (Macfadyen 1962). In brief, we put all soil samples on top of 100 stainless steel soil-sieves with a 2mm mesh size, and then waited 12 days so that many of the soil organisms would fall through the holes, via stainless steel funnels, into plastic bottles filled with 50 ml potting soil (Pindstrup Plus, PindstrupMosebrug A/S, 103Denmark; pH 6; 120 mg/L N; 12 mg/L P; 400 mg/L K; 28 mg/L Mg; 0.4 mg/L B; 2.0 mg/L Mo; 1041.7 mg/L Cu; 2.9 mg/L Mn; 0.9 mg/L Zn; 8.4 mg/L Fe). On 2 August 2020, we finished the soil-fauna-community collection. We then randomly chose ten of the 100 soil-fauna communities for soil-fauna investigation (see Supporting Information Table S2), and used the remaining 90 soil-fauna communities for inoculating of the soil in the experimental pot mesocosms.

Experimental set-up

To compare the growth performance of alien plants when growing in a resident native grassland community under different drought and soil-fauna treatments, we did a mesocosm-pot experiment in a greenhouse of the Northeast Institute of Geography and Agricultural Ecology, Chinese Academy of Sciences. We grew each of the nine alien species in the centre of a matrix of the native community under two water availabilities (well-watered *vs* drought) and two soil fauna treatments (with *vs* without).

Form 15 May to 5 July 2020, we sowed the seeds of each species separately into plastic trays (195 × 146 × 65 mm) filled with the same potting soil as used for soil-fauna collection. As previous experiments had shown that the time required for germination differs among the species, we sowed the species on different dates (Table S1) to get similarly sized seedlings at the start of the experiment. On 3 August 2020, we filled 180 2.5-L circular plastic pots (top diameter × bottom diameter × height: 18.5 × 12.5 × 15 cm, Yancheng Tengle Plastics Co., Ltd, China) with the same potting soil as used for germination. To avoid nutrient limitation during plant growth, we mixed each pot with 5 g slow-release fertilizer (Osmocote® Exact Standard; 15% N + 9.0%

P_2O_5 + 12% K_2O + 2.0% MgO + 0.02% B + 0.05% Cu + 0.45% Fe + 0.09% chelated by EDTA + 0.06% Mn + 0.02% Mo + 0.015% Zn, Everris International B.V., Geldermalsen, The Netherlands). To create the native community, we selected similarly sized seedlings from each of the five native species, and transplanted one seedling of each native species at equal distance in a circle (diameter = 11 cm) around the centre of each pot. We then planted into the centre of each pot one seedling of one of the alien species. For each of the nine alien species, we had 20 pots.

After transplanting, we randomly assigned 2 pots of each alien species to each of ten plastic cages (150 cm × 90 cm × 100 cm). The ten cages were covered with nylon nets (mesh size: 0.15 × 0.15 mm) to keep out small soil fauna. We put a plastic dish under each pot, and regularly watered the pots before starting the drought treatment to ensure that none of the plants were water limited. On 3 August 2020, we inoculated each pot in five of the ten cages (i.e. 90 pots) with 50 ml of potting soil that contained the soil-fauna communities we had collected. As a control for adding potting soil, we also added 50 ml of potting soil to each pot of the remaining five cages. We assigned the cages with and without soil-fauna inoculations to alternating positions that were at least 0.5 m apart from each other (Fig. S1). On 30 August 2020 (i.e. 27 days after the start of the experiment), we started the drought treatment. One of the two pots of each alien target species in each cage served as a control, which was watered regularly to keep the substrate moist throughout the entire experiment, while the other pots did not receive water unless the plants had wilted. We daily checked all pots of the drought treatment, and when some plants of the community in a pot had wilted (i.e. had lost leaf turgor), we supplied the pot with 50 ml of water. So, for each of the nine alien species, we had five replicates of each of the four drought × soil-fauna treatment combinations, resulting in a total of 180 pots (9 alien species × 2 soil-fauna treatments [with *vs* without] × 2 drought treatments [well-watered *vs* drought] × 5 replicates [i.e. cages]).

On 28 September 2020, 10 weeks after the start of the drought treatments, we harvested the experiment. For each pot, we separately harvested the aboveground biomass of the alien target species and of each of the five native competitor species. As the roots of the plants were too much intertwined, we could not harvest the belowground biomass. All aboveground biomass was dried for at least 72 h at 65 °C, and then weighed. Based on the aboveground biomass of the alien and native species, we calculated the biomass proportion of the alien target species (the biomass of the alien target species / [biomass of the alien target species + biomass of the five native competitor species]) as a proxy of the dominance of the alien target species (for a similar approach, see Parepa et al. 2013 and Liu et al. 2018). We also calculated the aboveground biomass of the native community by summing the biomass of the five native species.

Statistical analysis

To analyze the effects of drought, soil-fauna addition and their interactions on performance of the alien plants in the native community, we fitted linear mixed-effects models using the lme function of the ‘nlme’ package (Pinheiro et al. 2020) in R 4.0.3 (R Core Team 2020). Aboveground biomass production of the alien target species, the native competitor species and biomass proportion of the alien target species in each pot (i.e. target aboveground biomass/total aboveground biomass) were the response variables. To meet the assumption of normality, biomass production of the alien target species and the native competitor species were natural-log-transformed, and biomass proportion of the target species was logit-transformed. We included drought treatment (i.e. well-watered *vs* drought), soil-fauna treatment (i.e. with *vs* without addition) and their interactions as fixed effects in all models.

To account for non-independence of individuals of the same alien plant species and for phylogenetic non-independence of the species, we included identity of the target species nested within family as random factors in all models. In addition to account for non-independence of plants within the same cage, we also included cage identity as random factor in all model. As the homoscedasticity assumption was violated in all models, we also included variance structures to model different variances per species or per cage (based on model selection) using the "*varIdent*" function in the R package 'nlme' (Pinheiro et al. 2020). We used log-likelihood ratio tests to assess significance of the fixed effects drought treatment, soil-fauna treatment and their interaction (Zuur et al. 2009). These tests were based on comparisons of maximum-likelihood models with and without the terms of interest, and the variance components were estimated using the restricted maximum-likelihood method of the full model (Zuur et al. 2009).

RESULTS

Averaged across the nine alien target species, drought significantly decreased the aboveground biomass production of alien target species (-58.6%; Table 1; Figure 1a), and the native community (-51.5%; Table 1, Figure 1b). As the biomass of the aliens decreased more strongly in response to drought than the biomass of the natives did, the biomass proportion of the alien target species in each pot decreased (-11.6%; Table 1; Figure 1c). Inoculation with soil fauna had no significant effect on aboveground biomass of the alien target plants (-30.8%), but had a significant positive effect on aboveground biomass of the native community (+40.1%; Table 1; Figure 1b). Consequently, the aboveground biomass proportion of the alien target species was decrease in the presence of soil fauna (-41.9%; Table 1; Figure 1c). Moreover, as the native community benefitted more from the presence of soil fauna under well-watered conditions (+44.0%) than under drought conditions (+32.5%; Table 1; Figure 1b), the negative effect of soil-fauna inoculation on biomass proportion of the alien target species tended to be stronger under well-watered conditions (-49.7%) than under drought conditions (-32.0%; marginally significant S × D interaction in Table 1, $p = 0.09$; Figure 1c).

DISCUSSION

Our multispecies experiment found that drought limited the absolute and the relative biomass production of the alien target plants. This means that drought suppressed the invasion succession of the alien species in the native community. In addition, we found that the presence of soil-fauna communities benefited the native community and resulted in a decreased biomass proportion of the alien species. In other words, the soil fauna promoted the resistance of the native community against invasion by the alien species. Moreover, the suppressive effect of drought on biomass proportion of the alien plants disappeared (although this effect was only marginally significant; $p = 0.09$) in the presence of soil fauna. This suggests that the presence of soil-fauna communities might mediate the negative effect of drought on alien plant invasion into a resident community.

While drought is well known to inhibit plant performance overall (Beierkuhnlein et al. 2011, Zlatev and Lidon 2012, Gupta et al. 2020), recent studies found that growth and reproduction were more strongly affected for invasive than for native plant species (Liu et al. 2017; Valliere et al. 2019; Kelso et al. 2020). Our results are consistent with these previous findings (see also the total biomass production per pot in Fig. S2), and suggest that the native competitors were more tolerant to drought than the invasive alien species (Werner et al. 2010; Copeland et al. 2016; Liu et al. 2017; LaForgia et al. 2018; Valliere et al. 2019; Kelso et al. 2020). On the other hand, it could also indicate that the invasive alien plants took more advantage of the well-watered conditions than the native species did. This would be in line with the idea that invasive plants show higher phenotypic plasticity, and capitalize more strongly on benign conditions than native plants do (i.e. the Master-of-some strategy *sensu* Richards et al. 2006). In any case, the negative effect of drought on the biomass proportion of the alien plants suggests that the competitive balance between invasive alien plants and native plants could be changed by drought in favour of the resident community. Another recent study, however, showed that alien species that are not invasive yet could benefit from drought (Haeuser et al. 2019), which could imply a turn-over in invasive alien species with ongoing climate change.

Inoculation with soil fauna significantly increased the biomass production of the native community. It is often suggested that soil fauna, such as collembolans and mites in present study (Table S2), could enhance soil nutrient mineralization and consequently nutrient absorption of plants (Bardgett and Chan 1999, Lussenhop and Bassirirad 2005). As a consequence, soil fauna frequently have positive effects on plant performance (Lussenhop and Bassirirad 2005, Partsch et al. 2006, Mehring and Levin 2015). However, we found that soil-fauna inoculation had a slightly negative, though not statistically significant, effect on growth of the alien target plants. Therefore, it is unlikely that soil fauna promoted native plant growth solely by increasing nutrient availability, as we would have expected the invasive alien species to benefit from it. The most likely explanation for this is that although the invasive alien species may have been released from their native specialist enemies (Blossey and Notzold 1995; Chun et al. 2010), they may – in contrast to the native plant species – be largely naïve to the generalist herbivorous soil fauna in their new ranges (Parker et al. 2006; Verhoeven et al. 2009). As a result, a possible advantage due to an increase in soil-nutrient availability by the soil fauna might have been negated by negative effects of herbivorous soil fauna. As this would be less the case for the native species, this could explain why the soil fauna suppressed the dominance (i.e. biomass proportion) of alien target plants. While it has been shown before that soil fauna affects the composition of plant communities (Wardle et al. 2004; Bonkowski et al. 2009; Eisenhauer et al. 2010), this is one of the first studies to document the ability of the soil fauna to provide resistance against alien plant invasion.

Although numerous studies have shown that climate change could affect interactions of plants with aboveground organisms at other trophic levels (de Sassi and Tylianakis 2012; Eisenhauer et al. 2012; Nooten and Hughes 2014; Meza-Lopez and Siemann 2020), only few studies have addressed how climate change may affect interactions of plants with belowground organisms at other trophic levels (Eisenhauer et al. 2012; Classen et al. 2015; Guyer et al. 2018; Wilschut and van Kleunen 2021). To the best of our knowledge, no studies have addressed how resident soil fauna might affect the interactions between native and invasive plant species. We found that the growth promotion of native plants induced by soil fauna was stronger under well-watered condition than under drought condition. This may be because drought could decrease the abundance and diversity of soil arthropods (Lindberg 2003; Kardol et al. 2010; Makkonen et al. 2011; Eisenhauer et al. 2012; Guyer et al. 2018; Aupic-Samain et al. 2020), and thus the increase of soil-nutrient availability induced by soil fauna is stronger under well-watered condition than under drought conditions. Interestingly, we found tentative evidence that the decrease in dominance of alien target plant caused by drought was larger in the absence of soil fauna than in its presence. In other words, the presence of soil fauna might buffer against the negative effects of drought on alien plant invasion in resident communities. Therefore, previous pot experiments that did not include soil fauna might have overestimated the effects of drought on alien plant invasion. Therefore, future studies testing effects of climate change on alien plant invasion should also consider the role of other trophic levels, and especially the role of belowground trophic levels.

CONCLUSIONS

The findings of our multi-species experiment are in line with results of previous studies that drought can inhibit alien plant invasion into a native resident community. However, to the best of our knowledge, we here show for the first time that the presence of soil fauna might help the resident plant community to resist alien plant invasions. This soil-fauna mediated resistance, however, may be partly negated by drought. This implies that with ongoing climate change, and more frequent droughts, invasive plants might be more likely to overcome the resistance provided by soil fauna.

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AUTHOR CONTRIBUTIONS

YL conceived the idea and designed the experiment. HJ and LC performed the experiment. HJ and YL analyzed the data. HJ and YL wrote the first draft of the manuscript, with further inputs from MvK and LC.

DATA ACCESSIBILITY

Should the manuscript be accepted, the data supporting the results will be archived in Dryad and the data DOI will be included at the end of the article.

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Table 1

Table 1 Results of linear mixed-effects models testing the effects of drought (well-watered *vs* drought), soil fauna (with *vs* without) and their interactions on aboveground biomass production of the alien target plants, native competitor species, and biomass proportion of the alien target species in each pot. Significant effects ($p < 0.05$) are bold.

	Aboveground biomass production of the alien target species (natural-log-transformed)			Aboveground biomass production of the native competitor species (natural-log-transformed)			Aboveground biomass proportion of the target species in each pot (logit-transformed)		
Fixed effects	**Df**	χ^2	***P***	**Df**	χ^2	***P***	**Df**	χ^2	***P***
Soil fauna (S)	1	2.4990	0.1139	1	4.7722	**0.0289**	1	7.0803	**0.0078**
Drought (D)	1	63.8413	**<0.0001**	1	164.1043	**<0.0001**	1	5.6339	**0.0176**
S × D	1	0.1512	0.6974	1	5.6304	**0.0177**	1	2.8297	0.0925
Random effects		***SD***			***SD***			***SD***	
Family		0.004			0.002			0.004	
Species		0.970*			0.086			1.057*	
Cage		0.004			0.267*			0.187	
Residual		0.586			0.126			0.555	
		Marginal *R*^{2}	**Conditional *R*^{2}**		**Marginal *R*^{2}**	**Conditional *R*^{2}**		**Marginal *R*^{2}**	**Conditional *R*^{2}**
R^2 of the model		0.138	0.770		0.641	0.940		0.063	0.802

* Standard deviations for individual alien species or individual cage random effects for the saturated model are found in Table S3.

Figure 1

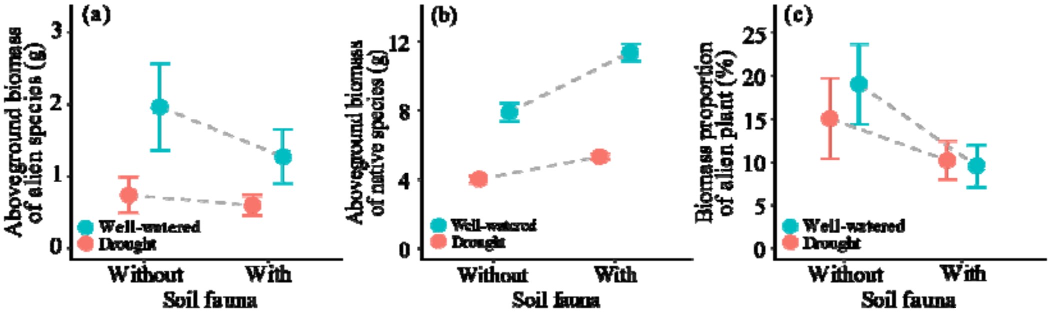

Figure 1 Mean values (± SE) of aboveground biomass of the alien target species (a), aboveground biomass production of the native competitor species (b), and biomass proportion of the alien target species in each pot (c) under different drought (well-watered *vs* drought) and soil-fauna (with *vs* without) treatments.

SUPPORTING INFORMATION

Table S1 Details of the study species used in the experiment.

Species	**Family**	**Status**	**Seed sources**	**Sowing data**
Bidens frondosa L.	Asteraceae	Alien	Zhejiang, China	26/6/2020
Bidens pilosa L.	Asteraceae	Alien	Zhejiang, China	26/6/2020
Erigeron canadensis L.	Asteraceae	Alien	Jilin, China	26/6/2020
Hibiscus trionum L.	Malvaceae	Alien	Jilin, China	5/7/2020
Lolium perenne L.	Poaceae	Alien	Greenwood flower seed industry, China	26/6/2020
Medicago sativa L.	Leguminosae	Alien	Nei Mongol, China	26/6/2020
Paspalum notatum Flüggé	Poaceae	Alien	Zhejiang, China	15/5/2020
Solidago canadensis L.	Asteraceae	Alien	Zhejiang, China	26/6/2020
Xanthium strumarium L.	Asteraceae	Alien	Nei Mongol, China	26/6/2020
Chloris virgata Sw.	Poaceae	Native	Nei Mongol, China	26/6/2020
Digitaria sanguinalis (L.) Scop.	Poaceae	Native	Jilin, China	26/6/2020
Echinochloa crus-galli (L.) P.Beauv.	Poaceae	Native	Jilin, China	26/6/2020
Lepidium apetalum Willd.	Brassicaceae	Native	Jilin, China	26/6/2020
Plantago asiatica L.	Plantaginaceae	Native	Nei Mongol, China	26/6/2020

541 **Table S2** Soil-fauna taxa found in the soil used to inoculate the pot mesocosms.

Species	**Taxonomy groups**
Allonychiurus songi	Collembola
Entomobrya koreana	Collembola
Folsomia sp1	Collembola
Folsomides sp1	Collembola
Homidia phjongiangica	Collembola
Hypogastrura sp1	Collembola
Isotomiella minor	Collembola
Isotomodes sp1	Collembola
Orchesellides sinensis	Collembola
Proisotoma sp1	Collembola
Sminthurides sp1	Collembola
Thalassaphorura macrospinta	Collembola
Acrotritia ardua (Koch, 1841)	Mites
Antennoseius alexandrovi Bregetova, 1977	Mites
Galumna changchunensis Wen, 1987	Mites
Mesostigamata sp.1	Mites
Mesostigamata sp.2	Mites
Mesostigamata sp.3	Mites
Mesostigamata sp.4	Mites
Mesostigamata sp.5	Mites
Mesostigamata sp.6	Mites
Mesostigamata sp.7	Mites
mites nymph	Mites
Nothrus anauniensis Canestrini & Fanzago, 1877	Mites
Oppiella nova (Oudemans, 1902)	Mites
Prostigamata sp.1	Mites
Prostigamata sp.2	Mites
Scheloribates fimbriatus Thor, 1930	Mites
Tectocepheus velatus (Michael, 1880)	Mites
Trichogalumna nipponica (Aoki, 1966)	Mites
Veigaia slonovi Bregetova, 1961	Mites
Zygoribatula exilis (Nicolet, 1855)	Mites
Zygoribatula truncata (Aoki, 1961)	Mites
Araneae	Others
Chilopoda	Others
Coleoptera adult	Others
Coleoptera larvae	Others
Diptera larvae	Others
Formicidae	Others
Homoptera larvae	Others
Phytophthira	Others
Protura	Others
Scutigerellidae	Others

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Table S3 Standard deviations for individual alien species or individual cage random effects for metrics analyzed with models with a Gaussian error distribution. The standard deviations given refer to the first species and cage respectively. For each species and cage, these should be multiplied by the multiplication factors. The names of the alien species in the table are abbreviated using the first letter of the genus and species epithet.

Metric	Species Standard Deviation	Multiplication factor standard deviation								
		LP	EC	HT	PN	SC	BF	BP	MS	XS
Aboveground biomass production of the alien target species	0.970	1.000	0.778	0.626	0.820	1.078	1.935	2.600	1.890	1.778
Aboveground biomass proportion of the target species in each pot	1.057	1.000	0.879	0.920	0.942	1.179	2.164	2.958	1.905	1.815

Metric	Cages Standard Deviation	Multiplication factor for standard deviation									
		Cage1	Cage2	Cage3	Cage4	Cage5	Cage6	Cage7	Cage8	Cage9	Cage10
Aboveground biomass production of the native competitor species	0.267	1.000	2.461	2.603	3.751	1.531	1.725	2.090	1.302	3.503	2.590

Figure S1

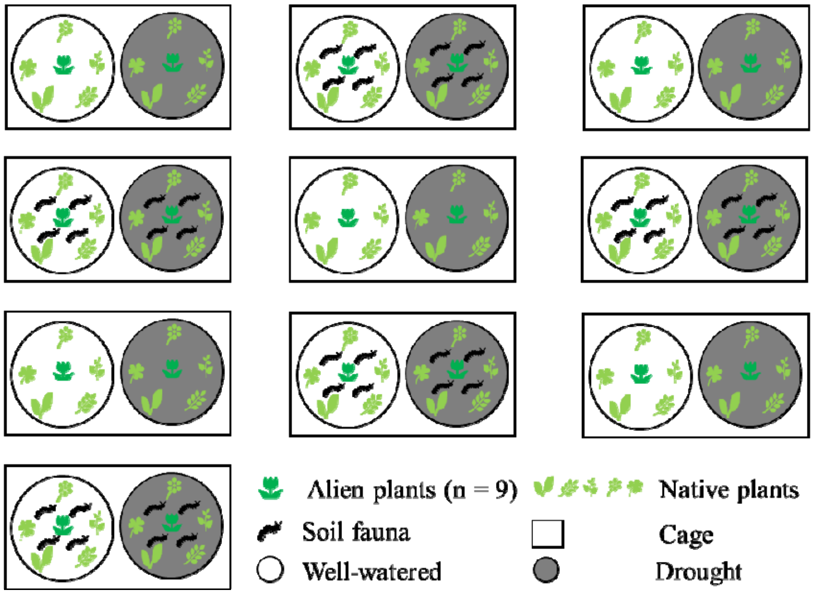

Figure S1 Graphical illustration of the experimental design.

Figure S2

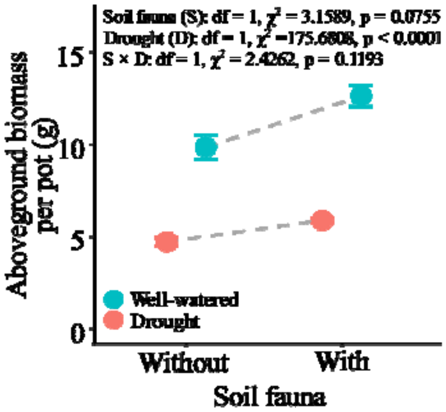

Figure S2 Mean values (± SE) of the aboveground biomass production per pot under different drought (well-watered *vs* drought) and soil fauna (with *vs* without) treatment.