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RESEARCH ARTICLE

Herbivory may mediate the effects of nutrients on the dominance of alien plants

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Abstract

1. Numerous studies have highlighted the roles of nutrient availability and fluctuations therein for invasion success of alien plants. Many others also highlighted the role of herbivores in invasion success. However, how herbivory and the level and fluctuations in nutrient availability interact in driving alien plant invasion into native communities remains largely unexplored.

2. We grew eight invasive alien species as target species in pot-mesocosms with five different synthetic native communities in a three-factorial design with two levels of nutrient availability (low vs. high), two levels of nutrient fluctuation (constant vs. pulsed) and two levels of above-ground insect herbivory (with vs. without herbivores). As natural communities have both specialist and generalist herbivores, we simulated this using both a generalist and a specialist herbivorous grasshopper.

3. The relative biomass production of the alien target plants to the total biomass production (i.e. alien biomass/total biomass) decreased in response to an increase in nutrient availability, but increased in response to the presence of herbivores. Furthermore, we found indications that the dominance of the alien target species may depend on interactions of herbivory with changes in nutrient availability and nutrient fluctuations, although these interactions were only marginally significant.

4. Our multi-trophic multi-species experiment suggests that herbivory could mediate the interactive effect of nutrient enrichment and variability in nutrient supply on invasion of alien plants into native communities. Therefore, we recommend that studies testing the effects of resources on plant invasion should also consider interactive effects of other trophic levels.

KEYWORDS
biological invasions, exotic plants, global change, plant–herbivore interactions, resource variability, trophic level

1 | INTRODUCTION

Invasion by alien plants could reduce native biodiversity, influence ecosystem functions and degrade ecosystem services (Vilà et al., 2011). Due to rapid globalization, the increase in the number of naturalized alien plant species does not yet show any sign of saturation, and it was recently predicted that their numbers may increase on average by 18% from 2005 to 2050 (Gippet & Bertelsmeier, 2021; Seebens et al., 2017, 2020). Therefore, a major research objective in the field of ecology is to identify the mechanisms that underlie alien plant invasion (Catford et al., 2009; Enders et al., 2020; Liu & van Kleunen, 2019; Schultheis et al., 2015; Speißer et al., 2021).

It has frequently been suggested that an increase in soil-nutrient availability is one of the most important drivers of alien plant invasion (Bradley et al., 2010; Davis et al., 2000; Enders et al., 2020). As successful alien plant species are often introduced from anthropogenic, nutrient-rich environments, they might be more likely to be pre-adapted to the high-nutrient environments they invade (Dostál et al., 2013; Kalusová et al., 2017). Indeed, both a recent meta-analysis (Liu et al., 2017) and a globally replicated study on 64 grasslands (Seabloom et al., 2015) showed that successful alien plants respond more strongly to nutrient enrichment than most native plants do. However, so far, empirical studies that tested how soil-nutrient changes affect alien plant invasion mainly focused on changes in the mean nutrient level (Heckman et al., 2017; Jia et al., 2016; Kelso et al., 2020; Liu & van Kleunen, 2017; Manea & Leishman, 2015; Pyšek et al., 2012; Sardans, Bartrons, et al., 2017). Due to increasing occurrences of extreme events (i.e. droughts, floodings, heat waves, fires), soil-nutrient changes also include changes in their variability, and this may affect alien plant invasions (Liu & van Kleunen, 2017; Parepa et al., 2013). Therefore, it is important to test how changes in soil-nutrient levels, as well as fluctuations in nutrient availability over time, drive alien plant invasion in resident communities.

The fluctuating resource hypothesis proposes that temporal fluctuations in nutrient supply could promote alien plant invasion in resident communities (Davis et al., 2000). However, empirical studies testing the hypothesis found mixed results. For example, in line with predictions, Parepa et al. (2013) found that a pulsed nutrient supply, compared to a constant nutrient supply, increased the dominance of the invasive plants *Fallopia japonica* and *F. × bohemica* in experimental plant communities. In contrast, Liu et al. (2018) showed that a pulsed nutrient supply decreased the dominance of invasive alien plants. Thus, more studies are needed to test the fluctuating resources hypothesis, and why the results might vary. One reason could be variation in the background nutrient level. Most studies that tested the effect of temporal changes in nutrient availability did so under overall nutrient-rich conditions. Under more nutrient-limiting conditions, however, the effect of temporal fluctuations may be even stronger. In other words, mean nutrient availability might interact with temporal fluctuations in nutrient availability to affect alien plant invasion into resident communities. However, very few studies have tested whether this expectation holds (but see Gao et al., 2021).

Although the fluctuating resource hypothesis has become a key theory in invasion ecology, previous tests only used study systems consisting of a single trophic level (i.e. only considered plant–plant interactions). Plant growth, however, can be strongly regulated by other trophic levels, such as herbivores. This might be relevant for the fluctuating resource hypothesis as alien species are likely to be released from most of their native enemies, particularly from specialists, and thus should suffer less herbivory than native species in their introduced regions (Blumenthal, 2006; Keane & Crawley, 2002; Zhang et al., 2018). Following this logic, the presence of herbivores, as well as increases in resource availability and fluctuations therein (Dawson, Rohr, et al., 2012; Liu & van Kleunen, 2017; Parepa et al., 2013; Pearson et al., 2018), could promote alien plant invasion in resident communities. Moreover, herbivore effects on plants may be regulated by soil-nutrient availability, because plants growing in relatively high-nutrient conditions should be better able to compensate or tolerate herbivory (Gianoli & Salgado-Luarte, 2017; Hawkes & Sullivan, 2001; Hu & Dong, 2019; Meyer, 2000). Therefore, we expect that the presence of herbivores might amplify the positive effect of increases in resource availability and fluctuations on alien plant invasion.

To test the individual effects of nutrient availability, nutrient fluctuations and herbivory, as well as their interactions on alien plant invasion into resident communities, we grew eight invasive alien herbaceous species as target species in pot-mesocosms with five different synthetic native communities, each consisting of three grassland species (forbs and grasses). Then, we exposed the plants to eight combinations of two nutrient availability (low vs. high), two nutrient-fluctuation (constant vs. pulsed) and two herbivory (with vs. without herbivores) treatments. By comparing the absolute aboveground biomass production of the alien target species as well as their biomass production relative to the total biomass production (i.e. by the native competitors and alien target species), we addressed the following specific questions: (a) Do nutrient availability, nutrient fluctuations and the presence of herbivores promote the absolute and relative biomass of alien plants? (b) Does the effect of nutrient fluctuations on absolute and relative biomass of alien plants depend on the overall nutrient availability level? (c) Does the presence of herbivores interact with increases in nutrient availability and fluctuations therein to affect the absolute and relative biomass of alien plants?

2 | MATERIALS AND METHODS

2.1 | Study species

To investigate the individual and interactive effects of nutrient availability, nutrient fluctuations and the presence of herbivores on alien plant invasion into resident communities, we chose eight invasive alien species as targets, and 15 native species as native community members from the herbaceous flora of China (Table S1). According to the iPlant database (www.iplant.cn), all species, except *Xanthium*

strumarium, occupy at least more than seven out of 34 provinces in China (median = 20, range = 2–32; Table S1). In other words, all species are common in China, and could co-occur with each other in nature. We classified these species as invasive alien or native to China based on information in the book 'The Checklist of the Alien Invasive Plants in China' (Ma & Li, 2018) and the Flora of China database (www.efloras.org). To cover a wide taxonomic breadth, we selected the eight alien target species from seven genera of three families. As plants with different life histories (i.e. annuals or perennials) may respond differently to nutrient availability and fluctuations (Liu & van Kleunen, 2017; Roumet et al., 2006), we assured that both the alien targets and native community members included annuals and perennials (Table S1). Although the maximum heights of the alien plants (mean ± *SE*: 150 ± 24.2) tended to be larger than those of the natives (106 ± 24.2), the differences were not statistically significant (Table S1**)**. Seeds of the study species were collected in natural grassland populations in China or ordered from a commercial seed company (Table S1).

To impose a herbivory treatment, we selected two above-ground insect herbivores. As natural systems usually include both generalist and specialist insect herbivores, we chose the generalist grasshopper *Stenocatantops splendens* (Hsiao et al., 2016) and the specialist grasshopper *Locusta migratoria* (i.e. a grass-feeder; Raubenheimer & Simpson, 2003) as the shoot herbivores. The grasshoppers were acquired from a commercial insect company (Cangzhou Grasshoppers Breeding Center, China). As both grasshoppers and all plant species occur mainly in grasslands, and according to the GBIF database (www.gbif.org), overlap in their distributions, they are very likely to co-occur in nature.

## 2.2 | Pre-cultivation and experimental setup

We conducted the experiment, which took 142 days from sowing to harvesting, at the Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences (43°5′49″N, 125°24′40″E). From 7 May to 26 June 2020, we sowed each of the invasive alien and native species separately into plastic circular trays (diameter = 25.5 cm, height = 4 cm) filled with non-sterilized potting soil (Pindstrup Plus, Pindstrup Mosebrug A/S, 103 Denmark). Because the time required for germination varies among the species, we sowed them at different times (Table S1) to ensure that at transplanting the seedlings were in a similar developmental stage. All trays with seeds were kept in a greenhouse (temperature: 18–27°C; natural lighting with an intensity of ~75% of the light outdoors; and ~68% relative humidity).

On 10 July 2020, we selected similar-sized seedlings from each of the eight invasive alien and 15 native species, and transplanted them into 2.5-L circular plastic pots (top diameter: 18.5 cm, bottom diameter: 12.5 cm, height: 15 cm) filled with non-sterilized substrate. As substrate, we used a nutrient-poor 1:1 (v:v) mixture of fine washed sand and fine vermiculite, which was thoroughly mixed to make sure that we had a homogeneous substrate in all pots. We transplanted one seedling of an alien target species in the centre

of each pot. For each of the eight alien target species, we transplanted a total of 40 seedlings into 40 pots (i.e. one individual per pot), resulting in total of 320 pots. Immediately after transplanting the alien target species, we randomly assigned the 40 pots of each alien target to each of five different native communities (i.e. eight pots of each alien species per native community). To create the five different native grassland communities, we randomly assigned the 15 native species into five groups of three species (Table S1). We planted two seedlings of each native community member so that each pot included six individuals of native species, equally spaced in a circle (diameter = 10 cm) around the alien target seedling. The two individuals of the same species were planted at opposite positions of the circle (Figure 1a). Based on a vegetation survey of grasslands we studied, the plant density is 150–300 individuals per 1 m × 1 m area (unpublished data), which would correspond to 4–8 individuals per area of the pots used in our experiment. Therefore, our experimental density of six native individuals and one alien individual per pot is within the range of natural densities.

After transplanting, we randomly assigned all pots to two cages (3.5 m × 4.5 m × 2.5 m) located outside of the pre-cultivation greenhouse. The cages were covered with transparent plastic roofs and white nylon net (mesh size: 0.25 mm × 0.25 mm) all around. Half of the pots of each combination of an alien target species and a specific native community were assigned to one cage, and the remaining ones to the other cage (Figure 1a). In other words, each cage included 160 pots in total (8 alien target species × 5 native communities × 4 nutrient-supply treatments [2 nutrient availability × 2 nutrient fluctuation treatments]). To avoid the loss of water and nutrient solution, we put a plastic tray under each pot. We re-randomized the positions of the pots within each cage after 5 weeks.

On 14 July 2020 (i.e. 1 week after transplanting), we started to apply the nutrient treatments at weekly intervals for a total of 10 weeks (Figure 1b). We applied two nutrient availability treatments (low vs. high) crossed with two nutrient-fluctuation treatments (constant vs. pulsed), using a 400%-strength Hoagland solution (for the recipe, see Liu & van Kleunen, 2017). As we used a 1:1 mixture of fine washed and fine vermiculite as substrate, which both have low nutrient holding capacities, the background nutrient level before the nutrient application was very low. During the experiment, we added a total of 50 and 400 ml of the Hoagland solution to the low nutrient and high nutrient availability pots, respectively. Although it is difficult to compare the absolute nutrient levels in a pot experiment to those found in a natural system, Liu et al. (2018) previously showed that both the low- and high nutrient availabilities are limiting plant growth, as is usually the case in nature. Within each nutrient availability treatment, we created two nutrient-supply patterns: a constant nutrient supply and a pulsed nutrient supply (Figure 1b). For the constant low nutrient and high nutrient treatments, we supplied 5 and 40 ml, respectively, of the nutrient solution each week. The pulsed treatment at low nutrient availability consisted of 3 weeks of 2 ml of the nutrient solution per week, followed by 4 weeks of 9.5 ml per week, and again 3 weeks of 2 ml per week (Figure 1b). The pulsed treatment
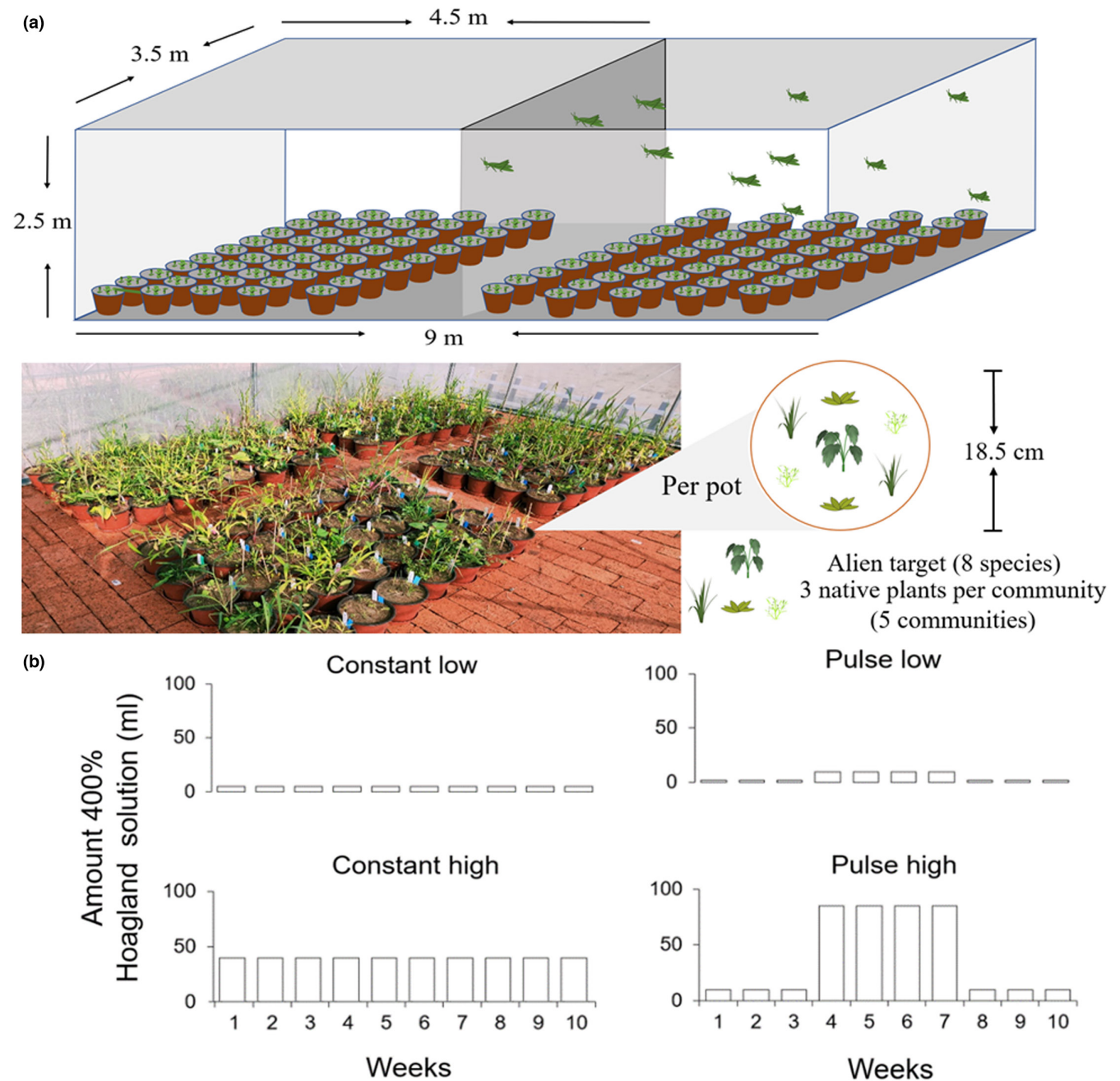
FIGURE 1 Graphical illustration of the experimental design. Overview of the herbivory treatment, the herbivory-treatment cage during the experiment, and the positions of the alien and native plants in the pots (a); the amount of nutrient solution supplied each week during the 10 weeks of the experiment (b). The constant and pulsed nutrient supply within the low or high nutrient availability treatment received the same total amounts of nutrients during the 10 weeks

at high nutrient availability consisted of 3 weeks of 10 ml of nutrient solution per week, followed by 4 weeks of 85 ml, and again 3 weeks of 10 ml (Figure 1b). To avoid differences in water supply among the four treatments, we added extra water to the amount of nutrient solution in each treatment to ensure that each pot received a total of 85 ml of water per nutrient application. In each cage, there were five replicates per alien target species for each of the four nutrient-supply treatments (i.e. one replicate for each of the five native communities). To avoid water limitation, we watered all plants regularly by filling the dish under each pot.

The herbivory treatment started on 14 August 2020, and ended 6 weeks later on 20 September 2020. We added both species of grasshoppers in one of the two cages, and treated the other cage as control (Figure 1a). As the commercial company hatched the two species of grasshoppers at different times, we added *L. migratoria* from 14 August to 26 August 2020, and *S. splendens* from 31 August to 6 September 2020. During the experiment, we added *L. migratoria* eight times (three times for 3rd–4th instars and four times for adults), and *S. splendens* two times (one time for 3rd–4th instars and the other time for adults). We checked the herbivory pressure

every day to determine whether we should add more grasshoppers. However, after we had added 354 individuals of each grasshopper species, the herbivory pressure was still not sufficient. As we had no *L. migratoria* left, we then only added 96 more *S. splendens*.

2.3 | Measurements

On 25 September 2020 (i.e. 11 weeks after transplanting), we harvested the above-ground biomass of all pots. For each pot, we first harvested the alien target species and then the three native competitor species. As some alien target and native plants died and three pots had accidentally been treated with the wrong nutrient solution, we only harvested 274 instead of 320 pots (see the raw data at https://doi.org/10.5061/dryad.fj6q573vn). We could not harvest the roots of the alien and native species, because the roots of the species were intertwined, and it was impossible to separate them. All above-ground biomass samples were dried at 65°C for 72 hr and then weighed. We calculated total above-ground biomass per pot by summing the biomass of the alien target species and the three native competitors. We also calculated the relative biomass of the alien target species in each pot as the alien target species divided by the total biomass (i.e. the biomass of the alien target species + native competitors).

2.4 | Statistical analysis

To test the effects of nutrient availability (low vs. high), nutrient fluctuations (constant vs. pulsed), herbivory treatments (with vs. without herbivores) and their interactions on absolute above-ground biomass production of the alien target species, absolute biomass production of the native communities and relative biomass of the alien target species in each pot, we fitted Bayesian multilevel models using the function brm of the R package BRMS (Bürkner, 2017) in R 4.0.2 (R Core Team, 2020). To improve normality and homoscedasticity of the residuals, above-ground biomass production of the alien target species and biomass production of the native communities were cubic-transformed, and relative biomass of the alien target species in each pot was logit-transformed prior to analyses. In all models, we included nutrient availability (low vs. high), nutrient fluctuations (constant vs. pulsed) and herbivory treatment (with vs. without) as fixed factors. To account for phylogenetic non-independence of species belonging to the same family and for non-independence of replicates of the same species, we included identity of the alien target species nested in their family as random factors in all models. To account for variation among the five different native communities, we also included identity of the native community as random factor in all models. To relax the homogeneity of variance assumption in all models, we allowed the residual standard deviation sigma to vary by the identity of alien target species (Zuur et al., 2009).

For all models, we used the default priors set by the BRMS package, and ran four independent chains. The number of total iterations per chain was 8,000, and the number of warm-up samples was 4,000. To directly test hypotheses about the main and interaction effects based on each coefficient's posterior distribution, we used the sum coding, which effectively 'centres' the effects to the grand mean (i.e. the mean value across all observations; Schad et al., 2020). To implement this in brms, we used the functions contrasts and contr.sum of the STATS package in R. We considered the fixed effects nutrient availability, nutrient fluctuation and herbivory treatments, and their interactions as statistically significant when their 95% credible interval of the posterior distribution did not overlap zero, and as marginally significant when the 90% credible interval did not overlap zero. As we had only two cages available, one with herbivores and one without herbivores, our herbivory treatment is obviously pseudo-replicated (Hurlbert, 1984). This means that the main effect of herbivory should be interpreted with care (Colegrave & Ruxton, 2018). However, it still allows us to test whether the effects of the nutrient availability and nutrient fluctuation treatments differ between the cage with and without herbivores.

3 | RESULTS

In general, an overall increase in nutrient availability (i.e. high vs. low) significantly increased the biomass production of the alien target species (+600.7%; Table 1; Figure 2; Figure S1) and of the native communities (+601.0%; Table 1; Figure 2; Figure S1). The presence of herbivores significantly decreased the biomass production of the alien target species (−44.3%; Table 1; Figure 2; Figure S2) and of the native communities (−39.4%; Table 1; Figure 2; Figure S2). The negative effect of herbivory on the biomass production of the alien target species and native communities was stronger under high nutrient availability (alien: −46.4%; native: −39.7%) than under low-nutrient availability (alien: −28.0%; native: −36.6%; significant NA × H interactions in Table 1; Figure 2; Figure S3). We also found that an increase in nutrient availability significantly decreased (−6.5%; Table 1; Figure 2; Figure S1), whereas the presence of herbivores significantly increased the relative biomass production of the alien target species in the communities (+3.6%; Table 1; Figure 2; Figure S2).

Although we found no significant main effect of nutrient fluctuations, a pulsed nutrient supply tended to decrease the relative biomass production of the alien target species in the communities more strongly under low-nutrient availability (−6.9%) than under high nutrient availability (−0.1%; Figure S4). This pattern was indicated by a marginally significant interaction between nutrient availability and fluctuation therein in Table 1 (90% CIs: [0.007, 0.173]). Furthermore, this effect was most pronounced in the presence of herbivores (−18.8%), whereas even the opposite was true in the absence of herbivores (+7.9%; Figure 2). Under high nutrient availability, however, pulsed nutrient supply and the presence of herbivores did not affect the relative biomass production of the alien target species (Figure 2). The dependency of the effect of the nutrient fluctuation treatment on the levels of the other treatments was indicated by a marginally significant three-way interaction between herbivory,

TABLE 1 Output of the models testing effects of nutrient availability (low vs. high), nutrient fluctuations (constant vs. pulsed), herbivory treatments (with vs. without herbivores) and their interactions on above-ground biomass production of the alien target species, biomass production of the native communities and biomass proportion of the alien target species in each pot. Shown are the model estimates and standard errors as well as the lower (L) and upper (U) values of the 95% and 90% credible intervals (CI)

	Estimate	SE	L95% CI	U95% CI	L90% CI	U90% CI
Biomass production of alien target plants (cubic-transformed)						
Intercept	8.185*	1.854	4.326	11.858	5.131	11.154
Nutrient availability (NA)	2.473*	0.165	2.153	2.795	2.203	2.743
Nutrient fluctuation (NF)	0.101	0.135	−0.165	0.365	−0.120	0.322
Herbivory treatment (H)	−0.545*	0.161	−0.865	−0.240	−0.813	−0.284
NA × H	−0.351*	0.139	−0.625	−0.076	−0.581	−0.122
NF × H	−0.074	0.133	−0.339	0.187	−0.294	0.143
NA × NF	0.133	0.133	−0.129	0.393	−0.086	0.352
NA × NF × H	0.108	0.137	−0.161	0.377	−0.116	0.335
Biomass production of native communities (cubic-transformed)						
Intercept	13.449*	2.087	9.099	17.565	9.989	16.733
Nutrient availability (NA)	4.765*	0.104	4.562	4.967	4.595	4.935
Nutrient fluctuation (NF)	0.087	0.103	−0.113	0.289	−0.079	0.258
Herbivory treatment (H)	−1.552*	0.105	−1.758	−1.345	−1.725	−1.380
NA × H	−0.335*	0.102	−0.530	−0.134	−0.502	−0.167
NF × H	−0.090	0.103	−0.290	0.114	−0.259	0.082
NA × NF	−0.092	0.102	−0.291	0.108	−0.261	0.075
NA × NF × H	−0.092	0.104	−0.294	0.113	−0.261	0.081
Biomass proportion of alien target plants (logit-transformed)						
Intercept	−1.618	1.050	−3.791	0.441	−3.347	0.070
Nutrient availability (NA)	−0.139*	0.053	−0.243	−0.036	−0.226	−0.054
Nutrient fluctuation (NF)	0.034	0.052	−0.068	0.137	−0.051	0.119
Herbivory treatment (H)	0.271*	0.055	0.162	0.378	0.179	0.361
NA × H	−0.053	0.052	−0.156	0.048	−0.139	0.033
NF × H	−0.053	0.051	−0.153	0.048	−0.136	0.033
NA × NF	0.090†	0.051	−0.010	0.188	0.007	0.173
NA × NF × H	0.091†	0.052	−0.011	0.192	0.005	0.176

Note: Parameters whose 95% credible intervals do not overlap with zero are indicated with asterisks (*), and whose 90% credible intervals do not overlap with zero are indicated with daggers (†). Residual standard deviations *sigma* for individual alien species are found in Table S2.

nutrient availability and fluctuation therein (90% CIs: [0.005, 0.176]) in Table 1.

4 | DISCUSSION

Our multi-trophic multi-species experiment showed that the suppressive effect of herbivory on plant biomass was particularly evident under high nutrient availability. Furthermore, although nutrient availability increased the absolute biomass of both the alien target species and native communities, it suppressed the dominance of the alien target species in native resident communities. Herbivory, on the other hand, increased the dominance of the alien target species. However, we also found tentative evidence that herbivory may interact with changes in nutrient availability and nutrient fluctuations to affect the dominance of the alien target species. In particular, the dominance of the alien plants decreased in response to a nutrient

pulse, but only when the overall nutrient availability was low and when herbivores were present. In other words, the results suggest that herbivory might mediate the interactive effect of nutrient enrichment and fluctuations in nutrient supply on alien plant invasion into native communities.

4.1 | Main effects of nutrient availability and herbivory on biomass production

Although each pot had one invasive alien and six native plants, the invasive plant accounted for about one-quarter of the above-ground biomass in each pot (Figure 2c). This suggests that the invasive alien species were more dominant than the native species. This can partly reflect that the alien species tended to have higher maximum heights than the natives, although this difference was not significant (Table S1). Surprisingly, we also found that the dominance of the alien
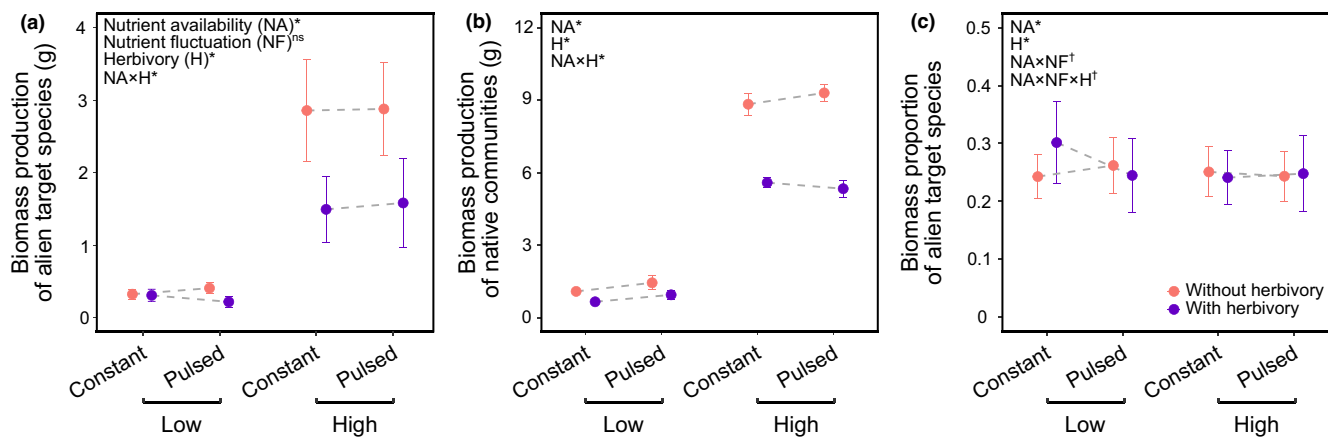
FIGURE 2 Mean values (±SE) of biomass production of alien target species (a) and native communities (b) and biomass proportion of the alien target species (c) under each combination of two nutrient availability (low vs. high), two nutrient-fluctuation (constant vs. pulsed) and two herbivory (with vs. without) treatments. The biomass proportion of alien target species indicates the biomass production of alien target species relative to the combined biomass of the alien target species and the native competitors. Parameters whose 95% credible intervals do not overlap with zero are indicated with asterisks (*), whose 90% credible intervals do not overlap with zero are indicated with daggers (†), and whose 90% credible intervals overlap with zero are indicated with 'ns'

plants decreased with an increase in the average nutrient availability. This finding does not support the idea that increased nutrient availability could promote alien plant invasion in resident communities, although many theoretical (Davis et al., 2000; Sher & Hyatt, 1999) and empirical studies (Gao et al., 2021; Liu & van Kleunen, 2017; Liu et al., 2017; Parepa et al., 2013; Seabloom et al., 2015) found evidence for this. A potential reason could be that in our study the native species themselves are also quite common, and possibly even more common than some of the alien species. Common species frequently take more advantage of increased nutrient availability than rare species do (Dawson, Fischer, et al., 2012). This is also in line with the recent finding that already common, usually nutrient-demanding species have become even more common in recent decades (Staude et al., 2021).

Not surprisingly, herbivory decreased the biomass production of plants (also see the total biomass production per pot in Figure S4a,b). However, the biomass suppression by herbivory was stronger under high nutrient availability than under low nutrient availability (Figure S4c). This seems inconsistent with previous findings that plants compensate or tolerate herbivory more when growing in high nutrient conditions (Alvarenga et al., 2019; Garcia & Eubanks, 2019; Getman-Pickering et al., 2021; Hawkes & Sullivan, 2001; Meyer, 2000; Zhong et al., 2021). However, it should be noted that in our experiment, the herbivores could choose between plants in low nutrient and high nutrient conditions. As the plants grown at high nutrient availabilities might be more nutritious (Deng et al., 2017; Oldroyd & Leyser, 2020; Sardans, Grau, et al., 2017; Scalon et al., 2017), and frequently have decreased plant secondary metabolite concentrations such as tannins (Jamieson et al., 2017; Li et al., 2016), the herbivores might have preferably fed on the plants with high nutrient availabilities (Anderson et al., 2018; Borgström et al., 2017; Hernán et al., 2019; Kudo, 2003; Sardans, Grau, et al., 2017). As we did not quantify herbivory damage, we do

not know whether this was really the case. Therefore, future studies on this topic should explicitly assess herbivory damage on each plant in each of the specific nutrient treatments.

We found that herbivory increased the dominance of the alien target species in the native resident communities. This is in line with expectations based on the enemy release hypothesis, which poses that alien plants often have escaped from many of their herbivorous enemies, and therefore have, in their introduced ranges, more resources to invest in biomass production (Keane & Crawley, 2002). On the other hand, it has also been posed that alien plants might be more naïve towards the generalist herbivores in their introduced range (Verhoeven et al., 2009). This does not appear to be the case in our study. Possibly, the generalist herbivore, as well as the specialist herbivore, in our study were more naïve towards the alien species than the other way around.

4.2 | Interaction effect of nutrient availability and fluctuations therein on biomass

Previous empirical studies testing nutrient-fluctuation effects on alien plant invasion found mixed results (Dener et al., 2016; Gao et al., 2021; Liu & van Kleunen, 2017; Liu et al., 2018; Parepa et al., 2013; Zhao et al., 2020). We hypothesized that this might be because the effect of temporal fluctuations may be even stronger under more nutrient-limiting conditions than under less nutrient-limiting conditions. The only case study that tested this hypothesis so far showed that there was no significant interaction effect of nutrient availability and fluctuations therein on plant invasion (Gao et al., 2021). Here, we found a trend (i.e. a marginally significant effect) that a pulsed nutrient supply actually decreased the dominance of the alien target plants when there was an overall low nutrient availability and that this was not the case under high nutrient

availability (Figure S5). This is in contrast to our initial prediction, but as we discuss below, this interaction effect was most pronounced in the presence of herbivores.

4.3 | Interaction effect of herbivory, nutrient availability and fluctuations therein on biomass

We found evidence, although weak (i.e. a marginally significant effect only), that herbivory may mediate the effects of nutrient availability and fluctuations therein on alien plant invasion. When growing under low nutrient availability and also in the absence of herbivores, the nutrient pulse tended to promote the dominance of alien plants, which supports the fluctuating resource hypothesis (Davis et al., 2000). However, when growing under low nutrient availability but in the presence of herbivores, the nutrient pulse tended to suppress the dominance of alien plants. One possible explanation would be that the generalist herbivore reduced the abundance (biomass, cover) of the most dominant species (Koerner et al., 2018; Olff & Ritchie, 1998). On the other hand, under high nutrient availability, the nutrient pulse and the herbivory treatment hardly affected the dominance of the alien plants. One plausibility explanation for this finding is that the overall high nutrient availability reduced, or even cancelled, the nutrient-limitation shifts over time caused by the nutrient fluctuations (Allington et al., 2013; Liu & van Kleunen, 2017; Liu et al., 2018), resulting in very weak effects of the nutrient pulse on dominance changes in plant communities (Sakavara et al., 2018). In addition, a recent case study found that the parasitic plant *Cuscuta australis* could also regulate the effects of nutrient availability and fluctuation therein on the invasion success of the alien plant *Bidens pilosa* (Gao et al., 2021). Therefore, if organisms at other trophic levels can mediate the effects of nutrient fluctuations on alien plant invasion, we recommend that studies testing the fluctuating resources hypothesis should more frequently consider the effect of other trophic levels.

4.4 | Study limitations

Although our study is the first multi-trophic multi-species experiment that tested how another trophic level influences the effects of nutrient fluctuations on alien plant invasion, our study has several caveats that should be considered in future studies. First, the mediating effects of herbivores on the effects of nutrient fluctuations on plant invasion might depend on the intensity of herbivory and the feeding period, which were not considered in the present study. Second, as it is difficult to separate the roots in mixed culture systems, we only considered above-ground biomass in the present study. To gain more insights into how herbivory interacts with nutrient availability and fluctuations therein on below-ground biomass of the alien and native species, molecular techniques could be used in future to determine how much of the root biomass belongs to which species (see McNickle et al., 2008; Mommer et al., 2011).

5 | CONCLUSIONS

Although the fluctuating resource hypothesis has become a key theory for explaining invasion success of alien plants, empirical tests found mixed results. This indicates that effects of nutrient fluctuations may be context dependent. Partly in line with the fluctuating resource hypothesis, we found tentative evidence that nutrient fluctuations promote alien plant invasion only under overall low-nutrient conditions, and only in the absence of herbivores. Therefore, other trophic levels, such as herbivores in our study, might mediate the interaction effect of nutrient enrichment on alien plant invasion into resident communities.

CONFLICT OF INTEREST
The authors have no conflict of interest.

AUTHORS' CONTRIBUTIONS
Y.Liu conceived the idea and designed the experiment; Y.Li and Y.G. performed the experiment; Y.Li and Y.Liu analysed the data; Y.Li and Y.Liu wrote the first draft of the manuscript, with further inputs from Y.G. and M.v.K.

DATA AVAILABILITY STATEMENT
All data and code available from the Dryad Digital Repository https://doi.org/10.5061/dryad.fj6q573vn (Li et al., 2022).

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