

1 **Interactive effects of herbivory and the level and fluctuations of nutrient**
2 **availability on dominance of alien plants in synthetic native communities**

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17 Running title: Herbivory mediates nutrient-change effects on plant invasion

18

19 **Abstract**

20 Numerous studies have highlighted the role of nutrient availability and
 21 fluctuations therein for invasion success of alien plants. Others also highlighted the
 22 role of herbivores in invasion success. However, how herbivory and the level and
 23 fluctuations in nutrient availability interact in driving alien plant invasion into resident
 24 communities remains largely unexplored.

25 We grew eight invasive alien species as target species in pot mesocosms with
 26 five different synthetic native communities in a three-factorial design with two levels
 27 of nutrient availability (low vs high), two levels of nutrient fluctuations (constant vs
 28 pulsed) and two levels of herbivory (with vs without).

29 The relative biomass production of the alien target plants decreased in response
 30 to an increase in nutrient availability, and increased in response to the presence of
 31 herbivores. Furthermore, herbivory could interact with changes in nutrient availability
 32 and nutrient fluctuations to affect the dominance of the alien target species (a
 33 marginally significant interaction; 90% CIs: [0.125, 2.712]).

34 Our multispecies experiment indicates that herbivory could mediate the
 35 interactive effect of nutrient enrichment and variability in nutrient supply on invasion
 36 of alien plants into native communities. Therefore, we recommend that studies testing
 37 the fluctuating resources hypothesis should also consider interactive effect of other
 38 trophic levels.

39

40 **Keywords:** biological invasions, exotic plants, global change, plant-herbivore
 41 interactions, resource variability, trophic level

42

43 **Introduction**

44 Invasion by alien plants could reduce native biodiversity, influence ecosystem
45 functions, and degrade ecosystem services [1]. Due to the rapid globalization, the
46 increase in the number of naturalized alien plant species does not show any sign of
47 saturation, and it was recently predicted that their numbers may increase on average
48 by 18% from 2005 to 2050 [2-4]. Therefore, a major research objective in the field of
49 ecology is to identify the mechanisms that underlie alien plant invasion [5-9].

50 It has frequently been suggested that an increase in soil-nutrient availability is
51 one of the most important drivers of alien plant invasion [8, 10, 11]. As successful
52 alien plant species are often introduced from anthropogenic and more nutrient-rich
53 environments, they might be more likely to be adapted to high-nutrient environments
54 [12, 13]. Indeed, both a recent meta-analysis [14] and a globally replicated study of 64
55 grasslands [15] showed that successful alien plants respond more strongly to nitrogen
56 enrichment than native plants do. So far, empirical studies that tested how
57 soil-nutrient changes affect alien plant invasion mainly focused on changes in the
58 mean nutrient level [16-22]. However, due to increasing occurrences of extreme
59 events (i.e., droughts, floodings, heat waves, fires), soil-nutrient changes also entail
60 changes in their variability, and this may affect plant invasions [20, 23]. Therefore, it
61 is important to test how changes in soil-nutrient levels, as well as fluctuations in
62 nutrient availability over time, drive alien plant invasion in resident communities.

63 The fluctuating resource hypothesis proposes that temporal fluctuations in
64 nutrient supply could promote alien plant invasion in resident communities [10].
65 However, empirical studies testing the hypothesis found mixed results. For example,
66 Parepa et al. found that a pulsed nutrient supply, compared to a constant nutrient
67 supply, increased the dominance of the invasive plants *Fallopia japonica* and *F. ×*

68 *bohemica* in experimental plant communities [23]. In contrast, Liu et al. showed that a
 69 pulsed nutrient supply decreased the dominance of invasive alien plants [24]. Thus,
 70 more studies are needed to test the hypothesis, and why the results might vary. The
 71 studies that tested the effect of temporal changes in nutrient availability did so under
 72 overall nutrient-rich conditions. Under more nutrient-limiting conditions, however,
 73 the effect of temporal fluctuations may be even stronger. In other words, mean
 74 nutrient availability may interact with temporal fluctuations in nutrient availability to
 75 affect alien plant invasion into resident communities. However, very few studies have
 76 tested whether this expectation holds [25].

77 Although the fluctuating resource hypothesis has become a key theory in
 78 invasion ecology, previous tests only used study systems consisting of a single trophic
 79 level (i.e., only considered plant-plant interactions). Plant growth, however, can be
 80 strongly regulated by other trophic levels, such as herbivores. This might be relevant
 81 for the fluctuating resource hypothesis as alien species are likely to be released from
 82 most of their native enemies, and thus should suffer less herbivory than native species
 83 in their introduced regions [26-28]. Following this logic, the presence of herbivores,
 84 just like increases in resource availability and fluctuations therein [20, 23, 29, 30],
 85 could promote alien plant invasion in resident communities. Moreover, as herbivore
 86 effects on plants are often regulated by soil-nutrient availability, because plants
 87 growing in relatively high-nutrient conditions might be better able to compensate or
 88 tolerate herbivory [31-34], the effects of herbivores might interact with the effects of
 89 nutrients. Therefore, it is reasonable to assume that the presence of herbivores might
 90 amplify the positive effect of increases in resource availability and fluctuations on
 91 alien plant invasion.

92 To test the individual effects of nutrient availability, nutrient fluctuations,

herbivory, and their interactions on alien plant invasion into resident communities, we grew eight invasive alien species as target species in pot mesocosms with five different synthetic native communities, each consisting of three grassland species. 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) 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) Do nutrient availability, nutrient fluctuations and the presence of herbivores promote the absolute and relative biomass of alien plants?
- 2) Does the effect of nutrient fluctuations on absolute and relative biomass of alien plants depend on the overall nutrient availability level?
- 3) Does the presence of herbivores interact with increases in nutrient availability and fluctuations therein to affect the absolute and relative biomass of alien plants?

108 **Material and methods**

109 *Study species*

110 To investigate the individual and interactive effects of nutrient availability,
 111 nutrient fluctuations and the presence of herbivores on alien plant invasion into
 112 resident communities, we chose eight invasive alien species as targets, and 15 native
 113 species as native community members from the herbaceous flora of China (Table S1).
 114 We classified these species as invasive alien or native to China based on information
 115 in the book “The Checklist of the Alien Invasive Plants in China” [35] and the Flora
 116 of China database (www.efloras.org). To cover a wide taxonomic breadth, we
 117 selected the eight alien target species from seven genera of three families. As plants
 118 with different life histories (i.e., annuals or perennials) may respond differently to
 119 nutrient availability and fluctuations [20, 36], we assured that both the alien targets
 120 and native community members included annuals and perennials (Table S1). Seeds of
 121 these species were collected in natural populations in grasslands in China or ordered
 122 from a commercial seed company (see Table S1).

123 To impose a herbivory treatment, we selected two aboveground insect herbivores.
 124 As natural systems usually include both generalist and specialist insect herbivores, we
 125 chose the generalist grasshopper *Stenocatantops splendens* and the specialist
 126 grasshopper *Locusta migratoria* (i.e., grass-feeder) as the shoot herbivores. The
 127 grasshoppers were acquired from a commercial insect company (Cangzhou
 128 Grasshoppers Breeding Center, China). As both grasshoppers and all plant species
 129 occur mainly in grasslands, and according to the GBIF database (www.gbif.org),
 130 overlap in their distributions, they are very likely to co-occur in nature.

131 *Pre-cultivation and experimental setup*

We conducted the experiment 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 potting soil (Pindstrup Plus, Pindstrup Mosebrug A/S, 103 Denmark; pH 6; 120 mg/L N; 12 mg/L P; 400 mg/L K; 28 mg/L Mg; 0.4 mg/L B; 2 mg/L Mo; 1042 mg/L Cu; 3 mg/L Mn; 0.9 mg/L Zn; 8 mg/L Fe). 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 a 1:1 mixture of sand and fine vermiculite. We transplanted one seedling of an alien target species in the center 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 equally distributed the 40 pots of each alien target over five different native communities (i.e., eight pots 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

(Fig. 1a). After transplanting, we randomly assigned all pots to two cages ($3.5 \times 4.5 \times 2.5$ m) located outside of the pre-cultivation greenhouse. The cages were covered with transparent plastic roofs and white nylon net (mesh size: 0.25×0.25 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 (Fig. 1a). In other words, each cage included 160 pots in total (8 alien target species \times 5 native communities \times 4 nutrient-supply treatments [2 nutrient availability \times 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 in each cage after five weeks.

On 14 July 2020 (i.e., one week after transplanting), we started to apply the nutrient treatments at weekly intervals for a total of 10 weeks (Fig. 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 (Methods S1). During the experiment, we added a total of 50 and 400 ml of the Hoagland solution to the low 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. previously showed that both the low- and high-nutrient availabilities are limiting plant growth, as is usually the case in nature [24]. Within each nutrient-availability treatment, we created two different nutrient-supply patterns, a constant nutrient supply and a pulsed nutrient supply (Fig. 1b). We supplied 5 ml of the nutrient solution for the constant low-nutrient supply each week, and 40 ml of the same nutrient solution for the constant high-nutrient supply. The pulsed treatment at low-nutrient availability consisted of three weeks of 2 ml per week, followed by four weeks of 9.5 ml per week, and again three weeks of 2 ml per week (Fig. 1b). The

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

190 The herbivory treatment started on 14 August 2020, and ended six weeks later on
191 20 September 2020. We added the grasshoppers in one of the two cages, and treated
192 the other cage as control (Fig. 1a). As the commercial company hatched these two
193 species of grasshoppers at different times, we added *Locusta migratoria* from 14
194 August to 6 September 2020, and *Stenocatantops splendens* from 31 August to 6
195 September 2020. We checked the herbivory pressure every day to determine whether
196 we would add more grasshoppers. During the experiment, we added *Locusta*
197 *migratoria* seven times (three times for 3–4th instars and four times for adults), and
198 *Stenocatantops splendens* two times (one time for 3–4th instars and the other time for
199 adults). In total, we added 354 individuals of *Locusta migratoria*, and 450 individuals
200 of *Stenocatantops splendens* in the herbivory-treatment cage.

201 *Measurements*

202 On 25 September 2020 (i.e., eleven weeks after transplanting), we harvested the
203 aboveground biomass of all pots. For each pot, we first harvested the alien target
204 species and then the three native competitor species. As some alien target and native
205 plants died and three pots had accidentally been treated with the wrong nutrient
206 solution, we only harvested 274 instead of 320 pots (see the raw data on

207 <https://doi.org/10.5061/dryad.fj6q573vn>) [37]. We did not harvest the roots of the
208 alien and native species, because the roots of the species were intertwined, and it was
209 impossible to separate them. All aboveground biomass samples were dried at 65°C for
210 72 hours and then weighed. We calculated total aboveground biomass per pot by
211 summing the biomass of the alien target species and the three native competitors. We
212 also calculated the biomass proportion of the alien target species in each pot as the
213 ratio between the biomass of the alien target species and the total aboveground
214 biomass per pot.

215 *Statistical analysis*

216 To test the effects of nutrient availability (low vs high), nutrient fluctuations
217 (constant vs pulsed), herbivory treatments (with vs without) and their interactions on
218 aboveground biomass production of the alien target species, biomass production of
219 the native communities and biomass proportion of the alien target species in each pot,
220 we fitted Bayesian multilevel models using the function `brm` of the R package `brms`
221 [38] in R 4.0.2 [39]. In all models, we included the following explanatory variables
222 nutrient availability (low vs high), nutrient fluctuations (constant vs pulsed) and
223 herbivory treatment (with vs without) as fixed factors. To account for phylogenetic
224 non-independence of species belonging to the same family and for non-independence
225 of replicates of the same species, we included identity of the alien target species
226 nested in their family as random factors in all models. To account for variation among
227 the five different native communities, we also included identity of the native
228 community as random factor in all models. To relax the homogeneity of variance
229 assumption in all models, we allowed the residual standard deviation σ to vary by
230 the identity of alien target species [40].

231 For all models, we used the default priors set by the brms package, and ran four
 232 independent chains. The number of total iterations per chain was 5000, and the
 233 number of warm-up samples was 2500. To directly test hypotheses about the main
 234 effects and interactive effects based on each coefficient's posterior distribution, we
 235 used the sum coding, which effectively 'centers' the effects to the grand mean (i.e.,
 236 the mean value of all data observations) [41]. To implement this in brms, we used the
 237 functions contrasts and contr.sum of the stats package in R. We considered the fixed
 238 effects nutrient availability, nutrient fluctuation and herbivory treatments, and their
 239 interactions as significant when their 95% credible interval of the posterior
 240 distribution did not overlap zero, and as marginally significant when the 90% credible
 241 interval did not overlap zero. As we had only two cages available, one with herbivores
 242 and one without herbivores, our herbivory treatment is obviously pseudoreplicated
 243 [42]. This means that the main effect of herbivory should be interpreted with care
 244 [43]. However, it still allows us to test whether the effects of the nutrient availability
 245 and nutrient fluctuation treatments differ between the cage with and without
 246 herbivores.
 247

Results

Averaged across the nutrient fluctuation and herbivory treatments, an increase in nutrient availability significantly increased the biomass production of alien target species (+600.7%; Table 1; Fig. 2 and Fig. S1) and the biomass production of native communities (+601.0%; Table 1; Fig. 2 and Fig. S1). The presence of herbivores, however, significantly decreased the biomass production of native communities (-39.4%; Table 1; Fig. 2 and Fig. S2). The similar pattern was found for the biomass production of alien target species (-44.3%; Table 1; Fig. 2 and Fig. S2), although it was only marginally significant (90% CIs: [-0.170, -0.010]). The negative effect of herbivory on the biomass production of both 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 \times H interactions in Table 1; Fig. 2 and Fig. S3).

We found that an increase in nutrient availability significantly decreased (-6.5%; Table 1; Fig. 2 and Fig. S1), whereas the presence of herbivores significantly increased the relative biomass production of the alien target species in the native communities (+3.6%; Table 1; Fig. 2 and Fig. S2). Additionally, under low-nutrient availability, the pulsed nutrient supply tended to increase the relative biomass production of the alien target plants in the absence of herbivores (+7.9%), whereas the reverse was true for plants in the presence of herbivores (-18.8%; Fig. 2). Under low-nutrient availability, however, pulsed nutrient supply and the presence of herbivores did not affect the relative biomass production of the alien target species (Fig. 2). The dependency of the effect of the nutrient fluctuation treatment on the levels of the other treatments was indicated by a marginally significant interaction between herbivory, nutrient availability and fluctuation therein (90% CIs: [0.125, 2.712]) in Table 1.

274 **Discussion**

275 Our multispecies experiment showed that an increase of nutrient availability
276 promoted the biomass production for both the alien target species and native
277 communities. However, herbivory suppressed the biomass production of plants, in
278 particular under high-nutrient availability. We found that increases in nutrient
279 availability suppressed, whereas herbivory promoted the dominance of the alien target
280 species in native resident communities. Interestingly, we also found tentative evidence
281 that herbivory could interact with changes in nutrient availability and nutrient
282 fluctuations to affect the dominance of the alien target species. In other words,
283 herbivory could mediate the interactive effect of nutrient enrichment and fluctuations
284 in nutrient supply on alien plant invasion into native communities.

285 Although each pot had one invasive alien and six native plants, the invasive plant
286 accounted for about one quarter of the aboveground biomass in each pot (Fig. 2c).
287 This suggests that the invasive alien species were more dominant than the native
288 species. We also found that this dominance decreased with an increase of the average
289 nutrient availability. This finding does not support the idea that increased nutrient
290 availability could promote alien plant invasion in resident communities, although
291 many theoretical [10, 44] and empirical studies [14, 15, 20, 23, 25] found evidence for
292 this. A potential reason could be that in our study the native species themselves are
293 also quite common, and it are usually the rare species that take less advantage of
294 increased nutrient availability [45].

295 Previous empirical studies testing the nutrient-fluctuation effect on alien plant
296 invasion found mixed results [20, 23-25, 46, 47]. We hypothesized that this might be
297 because the effect of temporal fluctuations may be even stronger under more
298 nutrient-limiting conditions than under less nutrient-limiting conditions. However, we

found no significant interactive effect of nutrient availability and fluctuations therein on the aboveground biomass and dominance of alien target plants in native communities. This is in line with the results of a recent case study by Gao et al. [25]. It is worth noting though that in the absence of herbivory, the absolute and relative aboveground biomass of the invasive alien plants tended to be higher in the low, pulsed nutrient treatment than in the low, constant treatment, while the reverse was true in the presence of herbivory.

Not surprisingly, herbivory decreased the biomass production of plants (also see the total biomass production per pot in Fig. S4a and Fig. S4b). In particular, the biomass suppression of herbivory was stronger under high-nutrient availability than under low-nutrient availability (Fig. S4c). This seems inconsistent with previous findings that plants compensate or tolerate herbivory more when growing in high nutrient conditions [31, 32, 48-51]. However, it should be noted that in our experiment, the herbivores could choose between the plants. As the plants grown at high-nutrient availabilities might be more nutritious [52-55], and have decreased plant secondary metabolite concentrations such as tannins [56, 57], the herbivores might have preferably fed on the plants with high nutrient availabilities [53, 58-61]. On the other hand, we found that herbivory increased the dominance of the alien target species in the native resident communities. This is also not surprising, because according to the enemy release hypothesis, alien plants often have escaped from many of their herbivorous enemies, and therefore could in their introduced range outcompete resident plants [26].

When growing under low-nutrient availability and also in the absence of herbivores, the nutrient pulse promoted the dominance of alien plants, which supports the fluctuating resource hypothesis [10]. However, when growing under low-nutrient

availability but in the presence of herbivores, the nutrient pulse suppressed the dominance of alien plants in pots. This may because herbivores often reduce the abundance (biomass, cover) of dominant species [62, 63]. On the other hand, under high-nutrient availability, the nutrient pulse and the herbivory treatment hardly affected the dominance of alien plants. One plausibility explanation for this finding is that the overall high-nutrient availability reduces, or even cancels, the nutrient-limitation shifts over time caused by nutrient fluctuations [20, 24, 64], resulting in very weak effects of the nutrient pulse on dominance changes in plant communities [65]. In addition to the weak evidence that herbivory mediated the effects of changes in nutrient availability and fluctuations on alien plant invasion, a recent case study also found that the parasitic plant *Cuscuta australis* could also regulate the effects of nutrient availability and fluctuations on the invasion success of the alien plant *Bidens pilosa* [25](Gao et al. 2021). Therefore, if organisms from other trophic levels frequently mediate the effects of nutrient fluctuations on alien plant invasion, we recommend that studies testing the fluctuating resources hypothesis should more frequently consider the interactive effect of other trophic levels.

340

341 **Conclusions**

342 The fluctuating resource hypothesis has become a key theory for explaining
343 invasion success of alien plants. However, our study is, to the best of our knowledge,
344 the first multi-species experiment that tested how another trophic level influences the
345 effects of nutrient fluctuations on alien plant invasion. Partly in line with the
346 fluctuating resource hypothesis, we found tentative evidence that nutrient variability
347 promotes alien plant invasion only under overall low-nutrient conditions, and only in
348 the absence of herbivores. Therefore, other trophic levels, such as herbivores in our

349 study, might mediate the interactive effect of nutrient enrichment on alien plant
350 invasion into resident communities.

351

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357

358 **Author contributions**

359 Y Liu conceived the idea and designed the experiment. Y Li and Y Gao
360 performed the experiment. Y Li and Y Liu analyzed the data. Y Li and Y Liu wrote
361 the first draft of the manuscript, with further inputs from Y Gao and M van Kleunen.

362

363 **Data availability**

364 All data and code available from the Dryad Digital Repository
365 <https://doi.org/10.5061/dryad.fj6q573vn> (Li et al., 2021).

366

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Table 1 Output of the models testing effects of nutrient availability (low vs high), nutrient fluctuations (constant vs pulsed), herbivory treatments (with vs without), and their interactions on aboveground 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	Intercept	1.105	0.786	-0.506	2.634	-0.105	2.279
	Nutrient availability (NA)	0.416*	0.058	0.303	0.532	0.322	0.515
	Nutrient fluctuation (NF)	0.046	0.047	-0.047	0.139	-0.032	0.124
	Herbivory treatment (H)	-0.090†	0.049	-0.185	0.005	-0.170	-0.010
	NA×H	-0.113*	0.048	-0.208	-0.018	-0.190	-0.035
	NF×H	-0.009	0.048	-0.104	0.086	-0.087	0.071
	NA×NF	0.031	0.049	-0.066	0.127	-0.050	0.111
	NA×NF×H	0.020	0.049	-0.076	0.116	-0.060	0.100
Biomass production of native communities	Intercept	3.529*	1.154	1.114	5.759	1.609	5.321
	Nutrient availability (NA)	3.252*	0.110	3.033	3.467	3.069	3.434
	Nutrient fluctuation (NF)	0.023	0.111	-0.191	0.238	-0.158	0.204
	Herbivory treatment (H)	-1.150*	0.109	-1.361	-0.939	-1.328	-0.973
	NA×H	-0.735*	0.110	-0.951	-0.520	-0.913	-0.554
	NF×H	-0.144	0.109	-0.359	0.071	-0.324	0.035
	NA×NF	-0.044	0.109	-0.254	0.167	-0.224	0.133
	NA×NF×H	-0.086	0.109	-0.302	0.129	-0.267	0.095
Biomass proportion of alien target plants	Intercept	23.129*	11.495	0.112	46.144	4.487	41.768
	Nutrient availability (NA)	-1.890*	0.766	-3.387	-0.380	-3.127	-0.623
	Nutrient fluctuation (NF)	0.649	0.753	-0.820	2.125	-0.592	1.897
	Herbivory treatment (H)	4.229*	0.882	2.470	5.937	2.754	5.647
	NA×H	-1.064	0.766	-2.554	0.435	-2.321	0.182
	NF×H	-0.57	0.765	-2.079	0.921	-1.835	0.665
	NA×NF	0.918	0.770	-0.636	2.419	-0.343	2.188
	NA×NF×H	1.432†	0.786	-0.123	2.959	0.125	2.712

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

Figure legends

Figure 1 Graphical illustration of the experimental design. Overview of the herbivory treatment, the herbivory-treatment cage during the experiment, and the pot design (a); the amount of nutrient solution supplied each week during the ten weeks of the experiment (b). The constant and pulsed nutrient supply under low- or high-nutrient availability received the same total amount of nutrients during the ten weeks.

Figure 2 Mean values (\pm 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. Parameters whose 95% credible intervals do not overlap with zero are indicted with asterisks (*), whose 90% credible intervals do not overlap with zero are indicated with daggers (\dagger), and whose 90% credible intervals do not overlap with zero are indicated with “ns”.

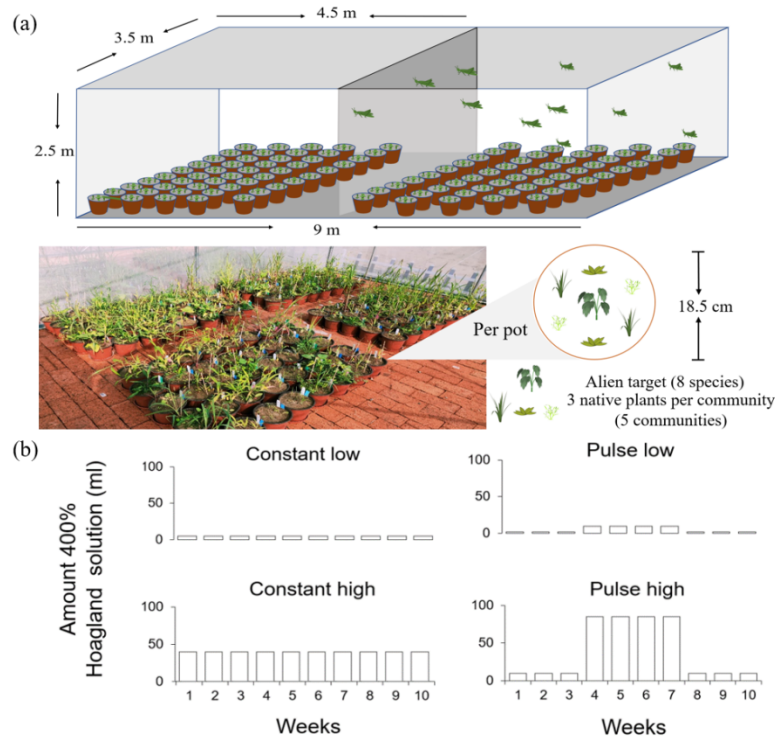


Figure 1 Graphical illustration of the experimental design. Overview of the herbivory treatment, the herbivory-treatment cage during the experiment, and the pot design (a); the amount of nutrient solution supplied each week during the ten weeks of the experiment (b). The constant and pulsed nutrient supply under low- or high-nutrient availability received the same total amount of nutrients during the ten weeks.

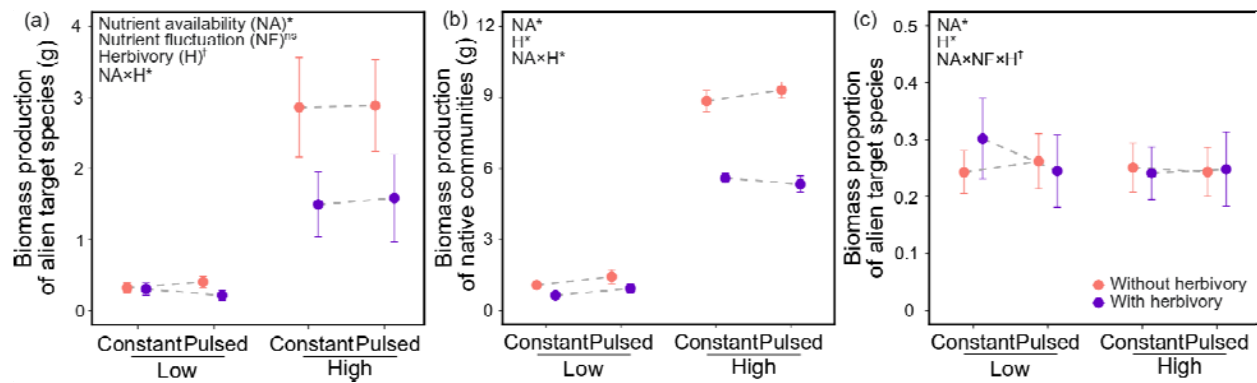


Figure 2 Mean values (\pm SE) of biomass production of alien target species (a) and native communities (b) and biomass proportion of the alien target species (c) under each combination of two nutrient availability (low vs high), two nutrient-fluctuation (constant vs pulsed) and two herbivory (with vs without) treatments. Parameters whose 95% credible intervals do not overlap with zero are indicted with asterisks (*), whose 90% credible intervals do not overlap with zero are indicated with daggers (†), and whose 90% credible intervals do not overlap with zero are indicated with “ns”.

Supporting information

Methods S1

Recipe for 400% strength Hoagland's Complete Nutrient Solution

The preparation of Hoagland nutrient solution essentially followed recommendations by Hoagland and Arnon (1950) and Liu et. al (2017), with the exception of the form in which iron was added (see below). We prepared the stock solutions 1-6 and micronutrient-stock solution given below, and used the amounts indicated to prepare 1 liter of nutrient solution:

(1) 4 mL of 1.00 M/L KH_2PO_4

(2) 20 mL of 1.00 M/L KNO_3

(3) 20 mL of 1.00 M/L $\text{Ca}(\text{NO}_3)_2$

(4) 8 mL of 1.00 M/L MgSO_4

(5) 4 ml of micronutrient stock solution (see recipe below)

(6) 10 ml of 1000 mg/liter iron from iron chelate (Fe-EDTA)

* Micronutrient-stock solution per liter:

2.86 g H_3BO_3

1.81 g $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$

0.22 g $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$

0.08 g $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$

0.018 g H_2MoO_4 (Assaying 94% MoO_3)

* Hoagland's recipe called for 1 ml of 0.5% iron tartrate stock per liter of nutrient solution but we used iron chelate instead.

Reference: Hoagland, D.R. & Arnon, D.I. 1950. The water-culture method of growing plants without soil. California Agricultural Experiment Station, Circular 347.

613 **Table S1** Detailed information on the eight alien target species and 15 native competitor species used in this study

Species	Family	Status	Life history	Seed sources	Sowing date
<i>Bidens frondosa</i> L.	Compositae	Alien	Annual	Zhejiang	26.06.2020
<i>Bidens pilosa</i> L.	Compositae	Alien	Annual	Zhejiang	26.06.2020
<i>Solidago canadensis</i> L.	Compositae	Alien	Perennial	Zhejiang	26.06.2020
<i>Xanthium strumarium</i> L.	Compositae	Alien	Annual	Nei Mongol	26.06.2020
<i>Abutilon theophrasti</i> Medik.	Malvaceae	Alien	Annual	Jilin	26.06.2020
<i>Hibiscus trionum</i> L.	Malvaceae	Alien	Annual	Jilin	05.07.2020
<i>Lolium perenne</i> L.	Poaceae	Alien	Perennial	Greenwood flower seed company	26.06.2020
<i>Paspalum notatum</i> Flügge	Poaceae	Alien	Perennial	Zhejiang	15.05.2020
<i>Catolobus pendulus</i> (L.) Al-Shehbaz ⁵	Brassicaceae	Native	Biennial	Nei Mongol	26.06.2020
<i>Cynanchum chinense</i> R. Br. ²	Apocynaceae	Native	Annual	Nei Mongol	26.06.2020
<i>Lappula myosotis</i> V. Wolf ¹	Boraginaceae	Native	Annual or Biennial	Nei Mongol	26.06.2020
<i>Artemisia rubripes</i> Nakai ⁴	Compositae	Native	Perennial	Nei Mongol	26.06.2020
<i>Achillea asiatica</i> Serg. ²	Compositae	Native	Perennial	Nei Mongol	26.06.2020
<i>Convolvulus arvensis</i> L. ³	Convolvulaceae	Native	Perennial	Jilin	26.06.2020
<i>Gypsophila licentiana</i> Hand.-Mazz. ⁴	Caryophyllaceae	Native	Perennial	Nei Mongol	26.06.2020
<i>Euphorbia humifusa</i> Willd. ⁵	Euphorbiaceae	Native	Annual	Nei Mongol	26.06.2020
<i>Chloris virgata</i> Sw. ²	Poaceae	Native	Annual	Nei Mongol	26.06.2020
<i>Cleistogenes squarrosa</i> (Trin.) Keng ⁵	Poaceae	Native	Perennial	Jilin	26.06.2020
<i>Digitaria sanguinalis</i> (L.) Scop. ¹	Poaceae	Native	Annual	Jilin	26.06.2020
<i>Echinochloa crus-galli</i> (L.) P.Beauv. ⁴	Poaceae	Native	Annual	Jilin	26.06.2020
<i>Setaria pumila</i> (Poir.) Roem. & Schult. ³	Poaceae	Native	Annual	Jilin	27.06.2020
<i>Portulaca oleracea</i> L. ³	Portulacaceae	Native	Annual	Nei Mongol	26.06.2020
<i>Rumex crispus</i> L. ¹	Polygonaceae	Native	Perennial	Nei Mongol	26.06.2020

614 ^{1,2,3,4,5} Allocation of native species to the five native communities; each group included three different native species

615 **Table S2** Output of the models residual standard deviations sigma for individual alien species. Shown are the model estimates and
616 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	<i>Abutilon theophrasti</i> Medik.	-0.785*	0.138	-1.033	-0.499	-1.001	-0.547
	<i>Bidens frondosa</i> L.	1.074*	0.127	0.839	1.341	0.874	1.290
	<i>Bidens pilosa</i> L.	0.327*	0.126	0.092	0.590	0.128	0.544
	<i>Hibiscus trionum</i> L.	-0.730*	0.175	-1.072	-0.388	-1.018	-0.443
	<i>Lolium perenne</i> L.	0.667*	0.138	0.413	0.953	0.452	0.907
	<i>Paspalum notatum</i> Flügge	0.444*	0.123	0.217	0.700	0.249	0.659
	<i>Solidago canadensis</i> L.	-0.488*	0.125	-0.718	-0.232	-0.688	-0.277
	<i>Xanthium strumarium</i> L.	0.681*	0.127	0.445	0.944	0.480	0.900
Biomass production of native communities	<i>Abutilon theophrasti</i> Medik.	0.373*	0.133	0.135	0.652	0.169	0.602
	<i>Bidens frondosa</i> L.	0.591*	0.129	0.354	0.862	0.388	0.810
	<i>Bidens pilosa</i> L.	0.511*	0.125	0.275	0.766	0.310	0.725
	<i>Hibiscus trionum</i> L.	0.603*	0.127	0.370	0.869	0.403	0.822
	<i>Lolium perenne</i> L.	0.484*	0.146	0.216	0.788	0.253	0.737
	<i>Paspalum notatum</i> Flügge	0.960*	0.122	0.731	1.209	0.768	1.168
	<i>Solidago canadensis</i> L.	0.721*	0.113	0.510	0.949	0.539	0.911
	<i>Xanthium strumarium</i> L.	0.563*	0.123	0.335	0.816	0.369	0.773
Biomass proportion of alien target plants	<i>Abutilon theophrasti</i> Medik.	2.471*	0.134	2.219	2.749	2.258	2.700
	<i>Bidens frondosa</i> L.	2.559*	0.133	2.314	2.833	2.353	2.783
	<i>Bidens pilosa</i> L.	2.206*	0.128	1.971	2.470	2.004	2.426
	<i>Hibiscus trionum</i> L.	2.624*	0.141	2.355	2.912	2.398	2.860
	<i>Lolium perenne</i> L.	2.962*	0.144	2.698	3.262	2.737	3.211
	<i>Paspalum notatum</i> Flügge	2.908*	0.123	2.679	3.162	2.712	3.116
	<i>Solidago canadensis</i> L.	2.416*	0.125	2.176	2.669	2.218	2.626
	<i>Xanthium strumarium</i> L.	2.596*	0.127	2.355	2.858	2.394	2.811

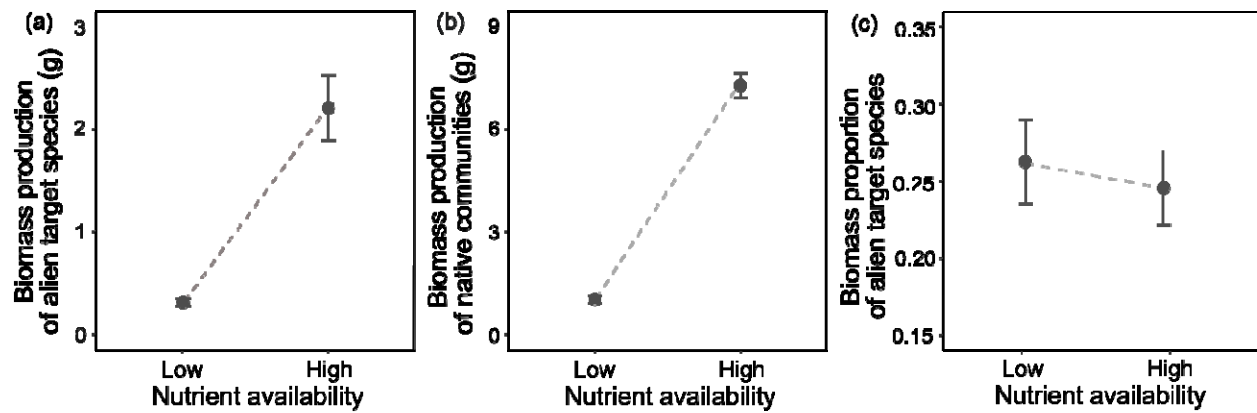


Figure S1 Mean values (\pm SE) of biomass production of the alien target species (a) and the native communities (b) and biomass proportion of the alien target species (c) under different nutrient availability conditions.

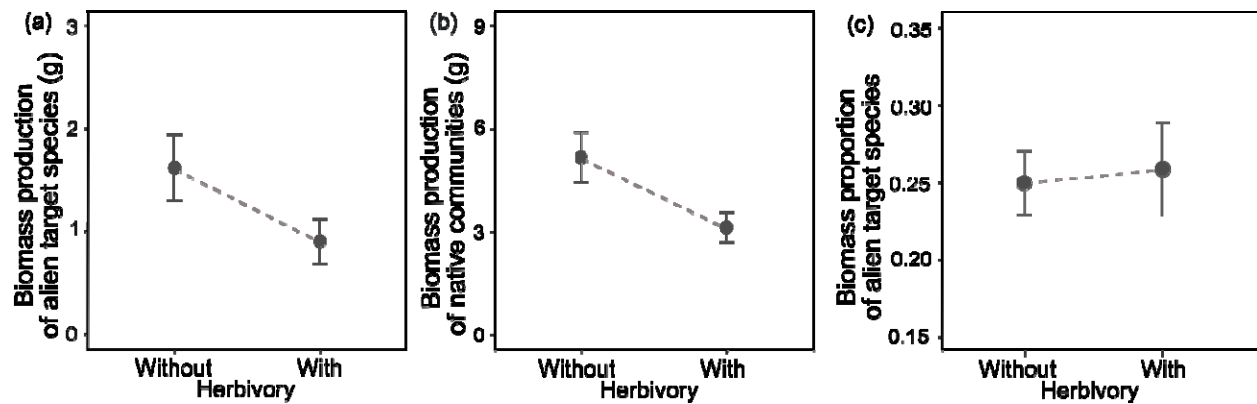


Figure S2 Mean values (\pm SE) of biomass production of the alien target species (a) and the native communities (b) and biomass proportion of the alien target species (c) growing with and without herbivory.

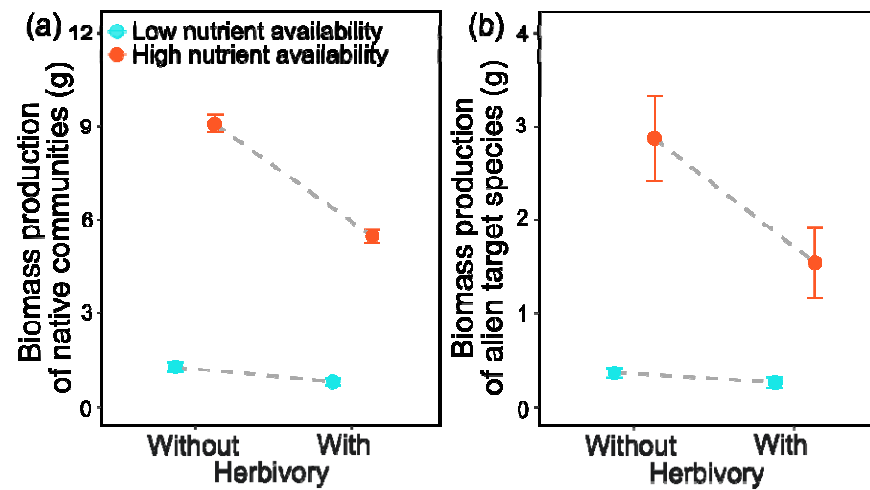


Figure S3 Mean values (\pm SE) of biomass production of native communities (a) and alien target species (b) under each combination of two nutrient availability (low vs high) and two herbivory (with vs without) treatments.

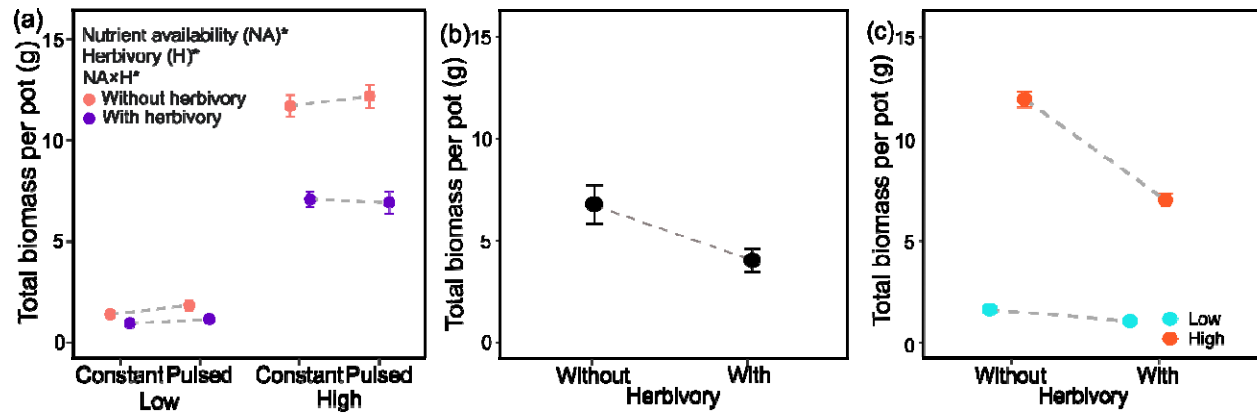


Figure S4 Mean values (\pm SE) of total biomass per pot under each combination of two nutrient availability (low *vs* high), two nutrient fluctuation (constant *vs* pulsed) and two herbivory (with *vs* without) treatments (a), with and without herbivory (b), and under each combination of two nutrient availability (low *vs* high) and two herbivory (with *vs* without) treatments (c). Parameters whose 95% credible intervals do not overlap with zero are indicated with asterisks (*).