

RESEARCH ARTICLE

The Matthew effect: Common species become more common and rare ones become more rare in response to artificial light at night

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Abstract

Artificial light at night (ALAN) has been and still is rapidly spreading and has become an important component of global change. Although numerous studies have tested its potential biological and ecological impacts on animals, very few studies have tested whether it affects alien and native plants differently. Furthermore, common plant species, and particularly common alien species, are often found to benefit more from additional resources than rare native and rare alien species. Whether this is also the case with regard to increasing light due to ALAN is still unknown. Here, we tested how ALAN affected the performance of common and rare alien and native plant species in Germany directly, and indirectly via flying insects. We grew five common alien, six rare alien, five common native, and four rare native plant species under four combinations of two ALAN (no ALAN vs. ALAN) and two insect-exclusion (no exclusion vs. exclusion) treatments, and compared their biomass production. We found that common plant species, irrespective of their origin, produced significantly more biomass than rare species and that this was particularly true under ALAN. Furthermore, alien species tended to show a slightly stronger positive response to ALAN than native species did ($p = .079$). Our study shows that common plant species benefited more from ALAN than rare ones. This might lead to competitive exclusion of rare species, which could have cascading impacts on other trophic levels and thus have important community-wide consequences when ALAN becomes more widespread. In addition, the slightly more positive response of alien species indicates that ALAN might increase the risk of alien plant invasions.

KEYWORDS

anthropocene, exotic, invasiveness, light pollution, non-native, plant-insect interaction, trophic level

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1 | INTRODUCTION

Light pollution due to artificial light at night (ALAN) has increased dramatically in the last century and has altered the natural nighttime environment in large areas of the Earth (Falchi et al., 2016; Kyba et al., 2017). As a consequence, the ecological impacts of ALAN have become an important focus for global change research in recent years (Bennie et al., 2016; Davies & Smyth, 2018; Gaston et al., 2014; Giavi et al., 2021; Holker et al., 2010; Irwin, 2018; Knop et al., 2017). To date, most research on the impacts of ALAN has focused on the behavior, physiology, and life history of animals (Ditmer et al., 2021; Dominoni, 2015; Ouyang et al., 2017; Sanders et al., 2021).

In a few cases, ALAN (e.g., street lighting) has been shown to induce a photosynthetic response (Speißeier et al., 2021), and to influence the growth and resource allocation of vascular plants (Bennie et al., 2016; Speißeier et al., 2021), as well as algae (Diamantopoulou et al., 2021). Given that such direct impacts usually vary among plant species (Bennie et al., 2018a; Sanders et al., 2021; Speißeier et al., 2021), ALAN is likely to affect the plant community structure (Bennie et al., 2018a). As invasive alien plants frequently respond more strongly to environmental change than natives do (Davidson et al., 2011), it is not unlikely that ALAN may also influence alien and native plants differently, and consequently affect the process of alien plant invasion. For example, Murphy et al. (2021a) did field surveys in urban areas and found that the presence of the invasive plant *Bromus tectorum* was positively associated with the presence of streetlights. Speißeier et al. (2021), however, found a trend that widely distributed alien plants took less advantage of ALAN than less-widely alien plants, suggesting that the latter might become more invasive. Although these studies indicate ALAN might affect community dynamics, it remains largely unexplored when and how ALAN affects plant invasions.

A key challenge to understanding how ALAN affects the plant invasion process is to correctly identify variations in the strength of alien and native plants in response to ALAN (Speißeier et al., 2021). To the best of our knowledge, only two recent experimental studies have tested how ALAN affects the performance of alien and native plants. In a previous study, we found that ALAN did not affect the relative biomass production of alien species when grown in mesocosms with native competitors (Speißeier et al., 2021). Murphy et al. (2021b), on the contrary, showed that ALAN significantly increased biomass production of the invasive alien species *Bromus tectorum*, but had no significant effects on the invasive alien species *Bromus inermis* and four native grass species. These inconsistent findings may partly reflect that the studies did not consider how successful or common the native species are. While Speißeier et al. (2021) differentiated between rare and common aliens, this was solely based on how widespread they are and not on whether the species are also known to dominate local communities. The latter might be more informative about the competitive strength of the species. Indeed, when distinguishing rare and common species based on both occurrence frequency and local abundance, common alien plants were shown to be more competitive than rare native

plants but not than common native plants (Zhang & van Kleunen, 2019). Therefore, rigorous tests of whether ALAN might affect future plant invasions should also consider how common or rare the alien and native species are. Given that common species are often considered to have high resource-capture abilities (Thompson & Davis, 2011; van Kleunen et al., 2011; Zhang & van Kleunen, 2019), it is plausible that common species might benefit more from ALAN than rare species.

ALAN is known to affect the behavior of many animals such as insects (Boyes et al., 2021a; Gaston et al., 2013; Giavi et al., 2021; Macgregor et al., 2019), and consequently, ALAN could indirectly affect plants by modifying plant-insect interactions (Bennie et al., 2015, 2018b; Giavi et al., 2020, 2021; Knop et al., 2017; Macgregor et al., 2019). For example, some empirical studies have shown that ALAN could significantly decrease the abundance and richness of moths (i.e., serving as pollinators; Knop et al., 2017; Macgregor et al., 2017), as well as the associated moth *caterpillars* (i.e., serving as herbivores; Boyes et al., 2021b). In contrast, a field study by McMunn et al. (2019) found increasing levels of herbivory damage in plants under ALAN compared to unlit controls. So, depending on the context, ALAN might increase or decrease herbivory. Furthermore, as alien plants might be released from their natural herbivores (Keane & Crawley, 2002; Liu & Stiling, 2006; Meijer et al., 2016), indirect effects of ALAN, mediated by herbivores, might be weaker for aliens than for natives. On the contrary, if the herbivores that are present are mainly generalists, alien plants might be more naïve and thus vulnerable to the herbivores than the native plants that co-evolved with the herbivores (Parker et al., 2006; Verhoeven et al., 2009). In that case, the indirect effects of ALAN, mediated by herbivores, might be stronger for aliens than for natives. Which of those possible scenarios predominates remains unknown.

To test the direct and indirect effects of ALAN on the performance of common and rare aliens and natives, we conducted a multispecies, common-garden experiment. We compare the biomass production in response to ALAN with and without insect-exclusion treatments among five common alien, six rare alien, five common native, and four rare native plant species. We address the following specific questions: (1) Does ALAN promote biomass production of plants? (2) If so, do alien and common plant species benefit more from ALAN than native and rare plant species? (3) Does ALAN affect biomass production of plants indirectly via effects on insects, and does such an effect depend on the origin and commonness of plant species?

2 | MATERIAL AND METHODS

2.1 | Study species

To investigate the effects of ALAN on a common alien, rare alien, common native, and rare native species, we selected a total of 20 terrestrial grasses and forbs co-occurring in grasslands in Germany. To cover a wide taxonomic breadth, these species were chosen from

six different families. To prevent possible taxonomic bias regarding origin and commonness, we tried to include for each family at least one species for each of the four categories. However, due to poor germination and limited seed availability for some species, our final species set was not fully balanced with regard to taxonomy; we used five common alien, six rare alien, five common native, and four rare native species (Table S1). We classified the species as naturalized alien or native to Germany based on the BioFlor database (www.ufz.de/bioflor). As species commonness has multiple dimensions (Fristoe et al., 2021; Rabinowitz, 1981), a species had to fulfill two criteria in order to be classified as common (the same approach to see Zhang & van Kleunen, 2019). First, the species must be known to be able to dominate local plant communities in Germany (i.e., if it can form large groups in the field according to the expert knowledge in the FloraWeb database of the German flora; <https://www.floraweb.de/>). Second, the species must occur in more than 900 out of all 3000 grid cells in Germany (median = 2057.5, range = 977–2928; Table S1). A species was thus categorized as rare if it is not known to be able to dominate local plant communities in Germany and if it occurs in relatively few grid cells. As the number of grid cells is a continuous measure, we made only categorized a species as rare if it occurs in fewer than 400 grid cells (median = 180.5, range = 76–355; Table S1), so that there is at least a difference of 500 grid cells between rare and common species. Seeds of the species used in

the experiment originated from botanical gardens, commercial seed companies, or wild populations (Table S1).

2.2 | Experimental ALAN and insect-exclusion facility

To impose the ALAN and insect-exclusion treatments, we arranged 20 metal cages (2 m × 2 m × 2 m) on a 21 m × 8 m area (Figure 1) outdoors in the Botanical Garden of the University of Konstanz, Germany (N: 47°69'19.56", E: 9°17'78.42"). We assigned each of the 20 cages to one of the four combinations of two ALAN (no ALAN, i.e., ambient vs. ALAN) and two insect-exclusion (no exclusion vs. exclusion) treatments. In other words, each of the four treatment combinations had five replicate cages. To impose ALAN, we randomly selected 10 of the cages, and installed LED spotlights (LED-Strahler Flare 10 W, IP 65, 900 lm, cool white 6500 K; REV Ritter GmbH, Mömbris, Germany), which were switched on each day from sunset to sunrise. The lamps were controlled by a photoelectric switch (DÄ 565 08, Eberle Controls GmbH, Nürnberg, Germany), switching them on at an ambient light intensity below 30 lux, and switching them off if ambient light intensity exceeded 30 lux. To reduce lateral light radiation of the LED spotlights, we used plastic boxes (40 cm × 50 cm × 27 cm) as lampshades so that only the 2 m × 2 m plot (i.e., the ground area of each cage) received direct illumination.

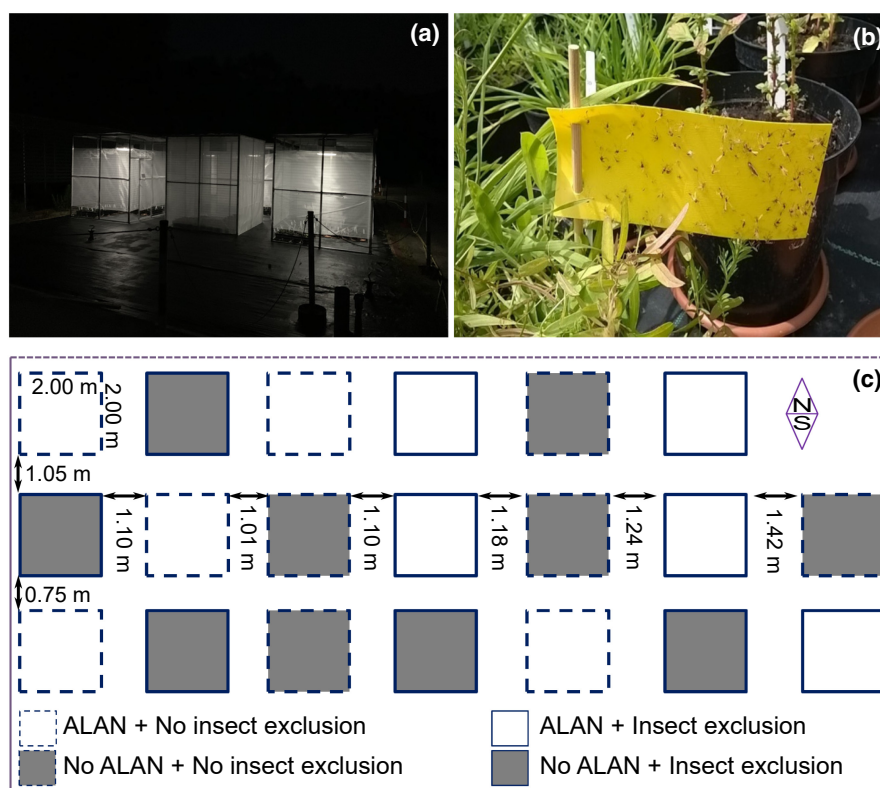


FIGURE 1 Illustration of the experimental setup. (a) Photograph of the experiment at night. (b) Photograph of the insect traps within the cages to monitor insect abundance for the different treatments. (c) The locations of the cages and their assignment to the four combinations of two ALAN and two insect-exclusion treatments outside in the Botanical Garden of the University of Konstanz

The LED spotlights, which emit photosynthetically active radiation (Figure S1), were fixed at 2 m height in the center of each cage (Figure 1). To achieve a realistic light intensity, as can be found under street lights, two layers of white tissue were fixed beneath the spotlights. This way, the final light intensity was 23.8 ± 1.2 lux, which is within the range of light intensities at ground level under street lights (Bennie et al., 2016). The remaining ten cages, serving as ambient light treatments, also had the lampshades installed, but without LED spotlights, to control for shading effects during the day. The light intensity at ground level for nine of these ten cages was lower than the detection limit of the LI-250A Light Meter with a LI-190SA Quantum Sensor (LI-COR, Lincoln, NE, USA). In other words, the equipment showed values of zero when measuring light intensity for these cages. The only exception cage had a light intensity of 0.58 lux at night. As this is above the light intensity that might affect plant growth (Crump et al., 2021), we also analyzed the data after excluding this case (Table S2). However, as it did not affect the results, we present the analysis based on all cages.

We randomly assigned 5 of the 10 cages with and 5 of the 10 cages without ALAN to the insect-exclusion treatment. The sides and roofs of all 20 cages were covered with a metal grid with a mesh width of 3 cm \times 5 cm, allowing insects to enter, with the exception of some large butterflies. The 10 insect-exclusion cages, we completely covered (sides and roof) with insect netting (mesh width: 0.4 mm \times 0.77 mm, 115 g/m²; FVG Folien-Vertiebs GmbH, Dernbach, Germany). To minimize differences in light intensity and rain shelter effects between the treatments with and without insect exclusion, we also partly covered the cages that were not part of the insect-exclusion treatment with insect netting. The roofs of these cages were completely covered, while at each side a 1.5 m high strip was attached. This way 25-cm wide strips at the bottom and top of each side were not covered with netting and allowed insects to enter the cages. To test the effectiveness of the insect-exclusion treatment, we placed two sticky, yellow insect traps for three days in each cage (see Figure 1b). Counts of the caught insects showed that the number of flying insects was 70.6% lower in the insect-exclusion cages (mean \pm SE: 4.1 ± 4.6) than in the control cages (mean \pm SE: 15.2 ± 15.0), and that it was 717.4% higher in the cages with ALAN (mean \pm SE: 15.2 ± 15.0) than in the cages without ALAN (mean \pm SE: 1.4 ± 0.45 ; Table S3; Figure S2).

2.3 | Pre-cultivation and experimental setup

On May 13, 2019, we started to sow the study species separately into trays (13.4 cm \times 12.2 cm \times 4.9 cm) filled with potting soil (Einheitserde, Pikiererde CLP). To obtain seedlings of a similar developmental stage at the start of the experiment, we sowed the species on different dates (Table S1), based on prior germination experience with those species. After sowing, we kept all trays in a greenhouse with a temperature between 18 and 21°C, and a day:night cycle of approximately 16:8 h. On June 3 and 4, 2019, we transplanted similar-sized seedlings into 2-L circular plastic pots filled with the

same type of potting soil as used for germination. In each pot, we planted three individuals of the same species. To maximize the use of germinated seedlings and to increase the statistical power of the study, we transplanted 33 pots for each species, resulting in a total of 660 pots (i.e., 99 seedlings per species and 2079 seedlings in total). It should be noted that because the species *Galega officinalis* was one seedling short, we only had 32 pots for this species. To keep the total number of pots at 660, we had one additional pot for the species *Lepidium heterophyllum*.

After transplanting the seedlings, we distributed the 660 pots over the 20 cages with the four combinations of ALAN \times insect-exclusion treatments (i.e., five cages for each treatment combination). We replaced dead seedlings on June 9 and 10, 2019. For each species, we first distributed 20 of the 33 pots over the 20 cages, and then randomly assigned the remaining 13 pots to 13 of the 20 cages. In other words, each cage had one to two pots for each of the 20 species. Therefore, we had six to ten replicates of each species in each combination of the ALAN \times insect-exclusion treatments (Table S1). To distribute the pots as evenly as possible over the cages, we had 35 pots for each of 13 cages, and 34 pots for each of the remaining seven cages. Within each cage, the pots were randomly assigned to fixed positions and were re-randomized every 14 days. To prevent nutrient limitation during the experiment, we fertilized all pots weekly (with 1‰ [w/v] Universol[®] blue oxide, ICL SF Germany & Austria, Nordhorn, Germany) from 4 June 2019 (i.e., four weeks after the start of the experiment) onward. We also watered the plants regularly to keep the substrate moist throughout the entire experiment.

From August 13 to 15, 2019, 10 weeks after transplanting, we harvested the plants. As the roots could not be extracted from the potting soil, we only harvested the aboveground biomass of each pot. All aboveground biomass per pot was dried at 70°C for at least 72 h and then weighed. We focused on biomass because it is a parameter that can easily be compared among species, is related to survival and reproduction (Mulder & Ruess, 1998; Younginger et al., 2017), is a good indicator of plant growth rate and competitive ability (Zhang & van Kleunen, 2019), and is frequently affected by herbivory (Oduor et al., 2011).

2.4 | Statistical analysis

To analyze the effects of ALAN, insect exclusion, and their interaction on the performance of common alien, rare alien, common native, and rare native species, we fitted a linear mixed-effects model using the lme function of the “nlme” package (Pinheiro et al., 2020) in R 4.0.3 (R Core Team, 2020). The aboveground biomass production of each pot was the response variable. To meet the assumption of normality, aboveground biomass production was square-root-transformed. We included ALAN treatment (no ALAN vs. ALAN), insect-exclusion treatment (no exclusion vs. exclusion), species origin (alien vs. native), species commonness (common vs. rare), and all their interactions as fixed effects in the model. To account for

the non-independence of individuals of the same species and the phylogenetic non-independence of the species, we included species identity nested within the family as random effects in the model. In addition, to account for the non-independence of plants that were in the same cage, we also included cage as a random effect in the model. As the homoscedasticity assumption of the model was violated, we included variance structures to model different variances per species using the “*varIdent*” function in the R package “nlme” (Pinheiro et al., 2020). We used log-likelihood ratio tests to assess the significance of the fixed effects of ALAN treatment, insect-exclusion treatment, species origin, species commonness, and their interactions (Zuur et al., 2009). In brief, we compared the log-likelihood of the full model with one of the models from which the respective interaction term was removed to determine the significance of each interaction term. Then, we compared the log-likelihood of the model with all main effects (i.e., without any interactions) with one of the models from which the respective main effect was removed to determine the significance of each main effect (i.e., origin, commonness, ALAN, and insect).

3 | RESULTS

Averaged across all treatments and origins, the common species produced significantly more aboveground biomass (mean: 6.6 g) than the rare species (3.9 g; Table 1; Figures 2 and 3). Whereas common species responded positively to ALAN (+9.2%), the reverse was true for rare species (−2.0%; significant C × L interaction in Table 1; Figure 3). We also found a trend that alien species responded more positively (+7.7%) to ALAN than native species (+2.3%; Figure 3), although the interactive effect between species origin and ALAN treatment was not statistically significant ($p = .079$; Table 1). We found no significant main effect of the insect-exclusion treatment, and no significant interactions of insect exclusion with ALAN, commonness, or origin (Table 1).

4 | DISCUSSION

Our study tested how ALAN interacts with the presence of insects to affect the performance of common alien, rare alien, common native, and rare native species. We found that common species, irrespective of whether they are alien or native, had a significantly higher performance than rare ones and that this difference was amplified by ALAN. Furthermore, we also found a trend ($p = .079$) that alien species tended to show a slightly more positive response to ALAN than native species. Overall, these results indicate that ALAN might benefit species that are already common, and that ALAN might promote alien plant invasion.

It has been suggested that common alien species and common native species are both successful and thus should share similar attributes (Dawson et al., 2012a; Thompson & Davis, 2011; van Kleunen et al., 2011; Zhang & van Kleunen, 2019). Furthermore,

many common native species have successfully established self-sustaining wild populations (i.e., have become naturalized) outside their native region (e.g., Pyšek et al., 2009). Indeed, our multispecies experiment showed that common plant species generally produced more aboveground biomass than rare species, regardless of whether they are alien or native. It is also worth noting that the aboveground biomass production of common plant species increased to a greater degree with ALAN than it did for rare species. This most likely reflects that common species often have a greater ability than rare ones to capitalize on additional resources, such as light (Dawson et al., 2012b; Hou et al., 2015). Moreover, urban skyglow (<0.5 lux) may already be sufficient to induce a small photosynthetic response (Bennie et al., 2016; Raven & Cockell, 2006), and thus the light emitted by streetlamps we used (c. 24 lux in the present study) should indeed be bright enough for plants to do photosynthesis, partly or entirely compensating dark respiration (Speißen et al., 2021). So, our results corroborate those of Dawson et al. (2012a), who found that common species benefit more from additional resources (i.e., nutrients in the case of Dawson et al., 2012a) than rare species do.

Our present findings, however, contrast with the results of Speißen et al. (2021), who found that the less widely naturalized species tended to increase their biomass more strongly in response to ALAN than the widely naturalized species did. A possible explanation for this could be that the two studies differed in the number of dimensions of commonness that they used to categorize species as common and rare (Catford et al., 2016; van Kleunen et al., 2018). While Speißen et al. (2021) classified species as common or rare based on their grid-cell occurrence frequency (in Germany) only, we here used local abundance as an additional, more restrictive, criterion. Consequently, although the results of Speißen et al. (2021) indicate that currently less widely naturalized species might increase their distributions when ALAN continues to increase, our present study implies that the invasion risk of alien species under ALAN is particularly high if they also have the ability to be locally dominant. The latter would be typical for strong competitors. To gain more insights into how ALAN affects the performance of common and rare plants, future studies should test how ALAN affects the different dimensions of commonness. Irrespective of the exact mechanism, our present study highlights that the ongoing increase in ALAN caused by urbanization may trigger the so-called “Matthew Effect” (Merton, 1968), i.e., that common species become even more common.

ALAN is particularly common along roadsides (Bennie et al., 2016; Irwin, 2018), which are also important invasion corridors for alien plants (Brisson et al., 2010; Lázaro-Lobo & Ervin, 2019). Indeed, it was recently shown that the presence of an invasive grass species was positively associated with the presence of streetlights (Murphy et al., 2021a). Our experimental study provides further evidence that alien plant invasion might be facilitated by ALAN, as the alien plants tended to respond more positively to ALAN than native plants. The trend of greater biomass response to ALAN for alien plants may have been due to their higher resource-use efficiency (Chen et al., 2019; Funk & Vitousek, 2007) and greater phenotypic plasticity (Davidson

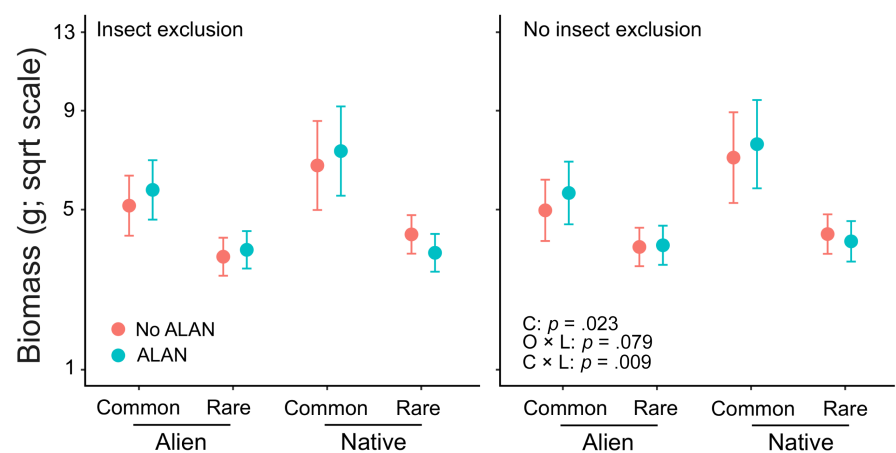
TABLE 1 Results of a linear mixed-effect model testing the effects of species origin (native vs. alien), commonness (common vs. rare), ALAN treatment (no ALAN vs. ALAN), insect-exclusion treatment (no exclusion vs. exclusion), and their interactions on aboveground biomass production

Fixed effects	Biomass (sqrt-transformed)		
	Df	χ^2	<i>p</i>
Origin (O)	1	1.323	.250
Commonness (C)	1	5.155	.023
ALAN (L)	1	0.191	.662
Insect (I)	1	1.207	.272
O × C	1	1.215	.271
O × L	1	3.095	.079
O × I	1	0.210	.647
C × L	1	6.779	.009
C × I	1	0.297	.586
L × I	1	0.009	.927
C × L × I	1	0.054	.817
O × L × I	1	0.428	.513
O × C × I	1	0.609	.435
O × C × L	1	0.811	.368
O × C × L × I	1	0.352	.553
Random effects			SD
Family			0.251
Species ^a			0.469
Cage			0.097
Residual			0.437
	Marginal	Conditional	
R ² of the model	0.163	0.670	

Note: The bold *p* values indicate $p < .05$, while the italicized one indicates $.05 < p < .1$.

^aStandard deviations for individual species random effects for the full model are provided in Table S4.

FIGURE 2 Modeled mean values of aboveground biomass per pot for different ALAN treatments (no ALAN vs. ALAN), species commonness (common vs. rare), and species origin (native vs. alien) in the cages with insect exclusion and the cages without insect exclusion. Error bars represent standard errors. The *p*-values of the model terms (O: origin, C: commonness, L: ALAN) are from log-likelihood ratio tests (see Table 1)



et al., 2011; Funk, 2008; Richards et al., 2006). Although plants in our study did not grow under interspecific competition, our results suggest that the slight increase in biomass of alien plants in response to ALAN might help them when they compete with native plants.

In addition to direct effects, we expected that ALAN might also have indirect effects on alien plant invasion via other trophic levels, herbivorous insects in particular. Our study, however, found no evidence that insect exclusion mediated the effects of

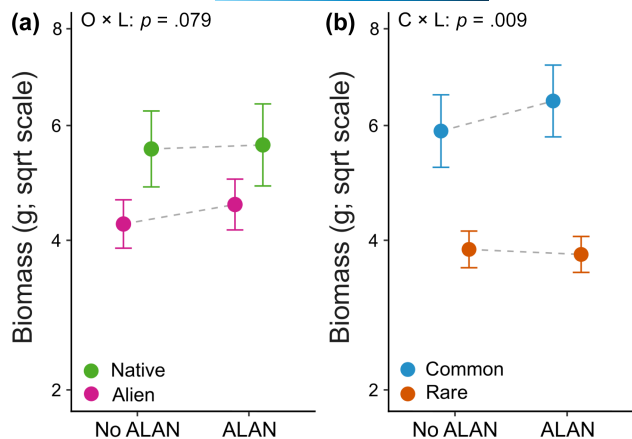


FIGURE 3 Modeled mean values of aboveground biomass per pot for different ALAN treatments (no ALAN vs. ALAN) and species origin (native vs. alien) (a) and different ALAN treatments (no ALAN vs. ALAN) and species commonness (common vs. rare) (b). Error bars represent standard errors. The p values of the model terms (O: origin, C: commonness, L: ALAN) are from log-likelihood ratio tests (see Table 1)

ALAN on the biomass of alien and native plants. Actually, also irrespective of ALAN, insect exclusion had no significant effect on plant growth, although we caught many more flying insects in the open cages than in the closed cages. Most of the insects, however, were Chironomidae (Table S3), and, although some of them might feed on nectar, they do not damage plant tissue and their role in pollination is not clear (Kevan, 2001; Tiusanen et al., 2016; Toledo-Hernández et al., 2017). Thus, the absence of large numbers of herbivores in our study location most likely explains why we did not find an effect of insect exclusion on biomass production. It could also be that the metal wire mesh of all cages, despite its large mesh width of 3 cm × 5 cm, excluded some of the larger herbivores from all plants. Another reason for the unproven indirect effects of ALAN on alien and native plants could be that besides the regulation by herbivores, the indirect effect of ALAN can occur via regulations by pollinators (Giavi et al., 2021; Knop et al., 2017). However, due to the relatively short duration of the experiment (10 weeks) and as many plants did not flower during that period, we did not measure reproductive traits such as the numbers of flowers and seeds. Therefore, long-term studies testing the indirect effects of ALAN on alien plant invasion are needed.

In conclusion, our study showed that common plant species benefit more from ALAN than rare plant species, irrespective of whether they are alien or native. Such differences might lead to competitive exclusion of rare species in grasslands, and their potential extinction, with further increases of ALAN. Given that losses of rare species could disproportionately impact higher trophic levels (Bracken & Low, 2012), our result also implicates that ALAN may further mediate the diversity and abundance of organisms at higher trophic levels, and thus shape community structure and affect ecological processes from the bottom-up. In addition, the slightly more

positive effect of ALAN on the alien plant species compared to the native ones indicates that increased ALAN might also further increase the invasion risk of alien species.

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AUTHOR CONTRIBUTION

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

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository. <https://doi.org/10.5061/dryad.547d7wmb0>.

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