Biomass responses of widely and less-widely naturalized alien plants to artificial light at night

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Abstract

1. Artificial light at night has rapidly increased during the last century, and could potentially affect many ecological processes, from individuals via communities to entire ecosystems. Recent research has shown that artificial light at night may not only affect the behaviour of animals but also growth of plants and vegetation composition. However, it is not known yet whether artificial light at night may also affect other global change components such as plant invasions.

2. Here, we tested how naturalized alien plants respond to artificial light at night, and particularly whether widely naturalized species differ from less-widely naturalized species in their response to artificial light at night. We grew nine taxonomically related pairs of widely naturalized and less-widely naturalized species alone and in competition, with native plants with and without artificial light at night.

3. We found that in the competition treatment, artificial light at night significantly increased the total biomass production per pot, but not the biomass ratio between the naturalized alien plants and the native competitors. Interestingly, although the less-widely naturalized species produced overall significantly less biomass than the widely naturalized species, there was a trend that the less-widely naturalized species increased their biomass more strongly in response to artificial light at night than the widely naturalized species did ($p = 0.07$).

4. Synthesis. Our study shows that although widely naturalized plants produce more biomass than less-widely naturalized plants across different environmental conditions, they took less advantage of artificial light at night. This suggests that artificial light at night might lead to increased spread of currently less-widely naturalized species, at least when artificial light at night continues to increase.

KEYWORDS
Anthropocene, biological invasion, exotic, invasiveness, light pollution, naturalization, non-native, plant–environment interactions
1 | INTRODUCTION

Artificial light at night, characterized by both diffuse skylight and direct emissions from artificial light sources, has been recently recognized as a key component of global change (Bennie et al., 2016; Gaston et al., 2014, 2017; Höcker et al., 2010; Irwin, 2018). It was recently estimated that 23% of the World’s terrestrial surfaces between 75°N and 60°S have light polluted nights, and that in Europe, this percentage is even as high as 88% (Falchi et al., 2016). Moreover, artificial light at night is still increasing, both in extent (2.2% per year between 2012 and 2016) and intensity (i.e. irradiance; 1.8% per year between 2012 and 2016) (Kyba et al., 2017). As artificial light at night could potentially affect many ecological processes, from individuals via communities to ecosystems (Bennie et al., 2015; Gaston, 2018; Höcker et al., 2010; Irwin, 2018; Maggi et al., 2019), it has emerged as an important topic in ecological research (Davies & Smyth, 2018).

Although many studies have documented how artificial light at night affects animals, and particularly their behaviour (Dominoni, 2015; Ouyang et al., 2017; Robert et al., 2015), its potential impacts on plants have received less attention so far (Bennie et al., 2016). Since plants use light both as a resource for growth and as a source of sensory information about their environment, artificial light at night is likely to affect their physiology (Briggs, 2006) and ecology directly (Bennie et al., 2016). The few plant studies on this topic found that artificial light at night can influence the growth and flowering of various plant species (Bennie et al., 2015, 2016). Moreover, Bennie et al. (2018) found that artificial light at night can change the cover and productivity of species grown in a community, and that while some species increased, others decreased. In other words, artificial light at night is likely to affect the composition of the vegetation (Bennie, Davies, Cruse, Bell, et al., 2018).

A major source of artificial light at night is street lighting. Therefore, it is likely that particularly the roadside vegetation may be affected by artificial light at night. Roadside vegetation provides important ecological functions, as they serve for example as refuges and corridors for wildlife in built-up areas (Lázaro-Lobo & Ervin, 2019). However, roadsides may also be an important invasion corridor for alien plants (Brisson et al., 2010; Christen & Mooney, 1999; Liu et al., 2017; Sorte et al., 2013). Nevertheless, to the best of our knowledge, no study has yet tested how artificial light at night could affect plant invasion.

Alien plants vary widely in their invasion success (Pyšek et al., 2017), and frequently, the species that are adapted to high-resource levels are successful as invaders (e.g. Dostál et al., 2013). Artificial light at night can be considered as an increase in the resource light, on which photosynthesis and thus plant growth ultimately depend. Moreover, the photosynthetic system itself is also sensitive to light at night, making it even more likely that carbon fixation of plants might be influenced by artificial light at night (Bennie et al., 2016). It is generally expected that alien species capable of taking advantage of increased amounts of resources should have a higher invasion success (Baker, 1974; Davidson et al., 2011; Richards et al., 2006). Indeed, successful alien species were shown to have a higher plasticity of biomass allocation and leaf area (Feng & van Kleunen, 2014; Feng et al., 2007), and consequently, successful alien species may benefit more from increasing light intensities than less-successful alien species (Hou et al., 2015). Similarly, it was shown that invasive alien species are more plastic in responding to various environmental conditions than native ones (Davidson et al., 2011). Therefore, we expect that widely naturalized species take more advantage of artificial light at night than less-widely naturalized plants, particularly when grown in competition with native plants.

To test the effects of artificial light at night on performance of alien species, we conducted a multispecies experiment using nine taxonomical related pairs of widely naturalized and less-widely naturalized alien species. We grew all alien species alone or in competition with native plants with and without artificial light at night to address the following specific questions: (a) How does light at night affect the absolute and relative biomass production of alien species? (b) Do the widely naturalized and less-widely naturalized alien species respond differently to light at night, and how does this depend on the presence of native competitors?

2 | MATERIALS AND METHODS

2.1 | Study species

To test the effects of artificial light at night on performance of alien herbaceous plants, we selected nine taxonomical related pairs of alien species, of which one is widely and the other one is less widely naturalized in Germany. We used taxonomic pairs of species to avoid confounding of naturalization success with taxonomy (Felsenstein, 1985). To cover a wide taxonomic range, we selected the species from eight families, and, for the large Asteraceae family, we selected two congeneric pairs (Table S1). To test whether effects of artificial light at night on the alien plants were affected by the presence of native competitors, we additionally selected six native species, including three grasses and three forbs, as competitors. We classified the species as alien and native to Germany based on information in the BioFlor database (www.ufz.de/bioflor). We assigned the alien species to the categories ‘widely naturalized’ and ‘less-widely naturalized’ based on the number of 10° longitude × 6° latitude (~130 km²) grid cells in which the species has been recorded in Germany (maximum 3,000), extracted from the FloraWeb database (www.floraweb.de). The widely naturalized species are...
recorded in more than 900 grid cells (median = 1,766, range = 977–2,660), and the less-widely naturalized species are recorded in fewer than 500 grid cells (median = 76, range = 7–437; Table S1). All native species that have been recorded in more than 1,300 grid cells (median = 2,766, range = 1,334–2,986; Table S1), which indicates that all six native competitors are very common in Germany. All seed materials were acquired from commercial seed companies or from botanical gardens across Europe (Table S1).

2.2 | Pre-cultivation and experimental setup

Pre-cultivation of the seedlings was done in a greenhouse, and the experiment was conducted outside in the Botanical Garden of the University of Konstanz, Germany (N: 47°69′19.56″, E: 9°17′78.42″). We started to sow seeds on 18 April 2017. As previous experiments showed that the speed of germination varied among the study species (Liu et al., 2018), we sowed the species on different dates (Table S1) to ensure that all transplanted seedlings would be in a similar developmental stage. We sowed each of the alien species into a small plastic tray (13.4 cm × 12.2 cm × 4.9 cm), and each of the native competitors, for which we needed more seedlings, into a large plastic tray (48 cm × 33 cm × 6.5 cm) filled with potting soil (Topferde®, Einheitserde Co., Sinntal-Altengronau, Germany; pH 5.8; 2.0 g/L KCl; 340 mg/L N; 380 mg/L P2O5; 420 mg/L K2O; 200 mg/L S; 700 mg/L Mg). All trays were placed into a greenhouse compartment with a temperature between 18 and 24°C, and a day:night cycle of 16:8 hr.

On 15 May 2017, we selected 20 similarly sized seedlings of each alien species, and transplanted them in the centres of 2.5-L circular plastic pots (i.e. 20 seedlings × 18 species = 360 pots) filled with the same type of potting soil as used for germination. In 10 pots per alien species, we planted a community of native competitors, and the other 10 pots per alien species were used as competitor-free controls. To create the community of native competitors, we transplanted one individual of each of the six native species at equal distances in a circle (diameter = 10 cm) around the alien plant. We planted forbs and grasses to alternating positions in the pots, starting with Prunella vulgaris, clockwise followed by Dactylis glomerata, Leucanthemum ircutianum, Anthoxanthum odoratum, Plantago lanceolata and Poa pratensis. To habituate the greenhouse-grown seedlings to the conditions outside, we first put all pots in an outdoor area covered with a shading cloth for 10 days. Seedlings that died during this period were replaced with new seedlings.

On 24 May 2017, we transferred the pots to an area without shading, and we started the ambient and artificial-light-at-night treatments. We distributed the 360 pots over five plots with ambient light conditions (i.e. control plots) and five plots with artificial light at night (Figure 1). Each plot (2 m × 2 m) had two pots per alien species, one without competition and one with competition. In total, there were 36 pots per plot, and they were randomly allocated to fixed positions in a 6 × 6 grid. For the artificial-light-at-night treatment, we illuminated the plot with a cool white fluorescent tube (OSRAM LUMILUX L 58W/840, OSRAM GmbH, München, Germany) each day from 9 p.m. to 5 a.m. the next day (i.e. from sunset to sunrise). The fluorescent tubes, which emit photosynthetically active radiation (Figure S1), were 1.55 m long and positioned at a height of 1.45 m above the soil surface using metal frames (Figure 1). The light intensity at ground level was reduced to 28.05 ± 1.25 lx, which is within the range of light intensities at ground level under street lights (Bennie et al., 2016), with the help of black shading net (Figure S1). The five control plots also had metal frames but no fluorescent tubes, and the light intensity at night in these control plots was 0 lx.

As we conducted the experiment in an idle climate-warming facility (Haeuser et al., 2017), the positions of the plots were fixed. To minimize possible light scattering from the artificial-light-at-night
plots to the control plots, the positions of the five control plots and five treatment plots were chosen in such a way that there would be minimal interference (Figure 1). As this area of the botanical garden is flat and not shaded by trees, the environmental conditions are very homogeneous, and the effects of the non-random plot allocation should be minimal. To ensure that plants were not water limited, we watered the plants regularly for the whole duration of the experiment. To reduce biomass loss due to herbivores, we distributed snail and slug bait across the plots, at the beginning and middle of the experimental period.

2.3 Measurements

To be able to account for variation in initial size of the plants in the analyses, we measured initial plant height, the length and width of the largest leaf, and counted the number of leaves for each alien plant on 16–17 May 2017. From these measurements, we calculated a proxy of initial leaf area as the length × width of the largest leaf × the number of leaves. On 17 July 2017 (i.e. 63 days after transplanting), we harvested for each pot the above-ground parts of the alien plants and native competitors separately. All plant materials were dried at 70°C for at least 72 hr, and then weighed. As some plants had died during the experiment, we only harvested 340 pots (164 without competition and 176 with competition) instead of 360 pots. Mortality was higher for the plants grown without competition (164 without competition and 176 with competition) instead of 360 plants had died during the experiment, we only harvested 340 pots.

For the competition treatment pots, we calculated the total biomass of each pot (biomass of alien plant + biomass of native competitors) and the biomass proportion of the alien plant (biomass of alien plant/total biomass).

2.4 Statistical analysis

To test whether responses to artificial light at night differed between the widely and less-widely naturalized species grown with and without competition, we ran linear mixed effect models using the lme function in the package nlme (Pinheiro et al., 2016) in R 3.3.2 (R Core Team, 2016). We first ran a model for the whole dataset, in which the above-ground biomass of the alien species was the response variable. To meet the assumption of normality, above-ground biomass of the alien species was natural-log transformed. We included status of the alien species (widely naturalized versus less-widely naturalized), light treatment (ambient versus artificial light at night), competition treatment (with versus without native competitors), and their interactions as fixed effects in the model. To account for initial variation in plant size, we also added initial plant leaf area and initial plant height as centred and scaled natural-log-transformed covariates in the model. We tested whether the light treatment could affect the cumulative biomass of the alien species and native competitors, and the relative dominance of alien plants in community, we also ran another two models for the subset of data for pots in the competition treatment. In these models, total biomass per pot and the biomass proportion of the alien species in each pot were the response variables respectively. To meet the assumption of normality, biomass proportion of the alien species in each pot (with competition) was natural-log-transformed. In these models, we included status of the alien species (widely naturalized versus less-widely naturalized), light treatment (ambient versus artificial light at night) and their interactions as fixed effects.

To account for non-independence of replicates from the same light treatment plot and the same species, we included plot and identity of the alien species as random effects in all models. In addition, to account for phylogenetic non-independence of species, we also included family as random effects in all models. To meet the homogeneity assumption of the models analysing the above-ground biomass and the biomass proportion of the alien species, we also added variance structures to model different variances per species using the ‘varIdent’ function of nlme package (Pinheiro et al., 2016). As species within each naturalized status might respond differently to artificial light at night, we also ran models with random slopes for family and species with respect to the light treatment. However, because this increased the AIC values (i.e. decreased model fit) for all models, we only present results of the models without random slopes. For all models described above, the significance of fixed effects and their interactions was assessed with likelihood-ratio tests (Zuur et al., 2009).

3 RESULTS

Averaged across all competition and light treatments, the widely naturalized alien species produced significantly more above-ground biomass (mean: 3.07 g) than the less-widely naturalized species (2.08 g; Table 1; Figure 2). The alien plants produced significantly less above-ground biomass when grown with native competitors (mean: 1.32 g) than without native competitors (3.84 g; Table 1; Figure 2). Although the main effect of the light treatment was not significant, averaged across all competition treatments, the less-widely naturalized species tended to increase their above-ground biomass production more strongly in response to artificial light at night (+48.2%) than the widely naturalized species did (+6.0%; Figure 2 and Figure S3; marginally significant S × L interaction in Table 1; p = 0.07).

For the subset of pots with competition, the total above-ground biomass production was significantly increased by artificial light at night (+15.9%; Table 1; Figure 3). The total above-ground biomass per pot also tended to be higher when the alien species was widely naturalized (mean: 8.37 g) instead of less-widely naturalized (6.87 g; Figure 3; marginally significant status effect in Table 1; p = 0.06). Furthermore, the above-ground biomass proportion
of the widely naturalized species (mean: 21.1%) was significantly higher than that of the less-widely naturalized species (11.6%; Table 1; Figure 3).

**TABLE 1** Results of linear mixed-effect models testing the effects of alien species status (widely versus less widely naturalized), competition, artificial light at night and all interactions thereof, on above-ground biomass production of the alien plants, above-ground biomass proportion of alien plants in the competition treatment and total above-ground biomass per pot in the competition treatment. Significant effects ($p < 0.05$) are in bold and marginally significant effects ($p < 0.1$) are underlined.

| Fixed effects                           | Above-ground biomass of alien species (ln-transformed) | Total above-ground biomass per pot | Above-ground biomass proportion of alien species (ln-transformed) |
|-----------------------------------------|-------------------------------------------------------|-----------------------------------|------------------------------------------------------------------|
|                                        | $df$ | $\chi^2$ | $p$ | $df$ | $\chi^2$ | $p$ | $df$ | $\chi^2$ | $p$ |
| Initial leaf area                      | 1    | 1.367    | 0.242 | –    | –    | –    | –    | –    | –    |
| Initial height                         | 1    | 3.989    | 0.0458 | –    | –    | –    | –    | –    | –    |
| Status (S)                             | 1    | 4.698    | 0.030 | 1    | 3.640 | 0.056 | 1    | 3.741 | 0.053 |
| Competition (C)                        | 1    | 122.866  | $<0.0001$ | –    | –    | –    | –    | –    | –    |
| Light (L)                              | 1    | 0.728    | 0.394 | 1    | 4.878 | 0.027 | 1    | 0.711 | 0.399 |
| $S \times C$                           | 1    | 0.295    | 0.587 | –    | –    | –    | –    | –    | –    |
| $S \times L$                           | 1    | 3.350    | 0.067 | 1    | 1.121 | 0.290 | 1    | 0.851 | 0.356 |
| $L \times C$                           | 1    | 0.965    | 0.326 | –    | –    | –    | –    | –    | –    |
| $S \times C \times L$                  | 1    | $<0.0001$| 0.984 | –    | –    | –    | –    | –    | –    |

Random effects

| SD | SD | SD |
|----|----|----|
| Family | 0.664 | 0.609 | 0.523 |
| Species | 0.607 | 1.024 | 0.864 |
| Plot | 0.207 | 0.524 | 0.197 |
| Residual | 1.036 | 2.945 | 1.349 |

Marginal | Conditional | Marginal | Conditional | Marginal | Conditional

$R^2$ of the model | 0.261 | 0.588 | 0.086 | 0.36 | 0.064 | 0.408

$^{a}$Standard deviations for individual alien species random effects for the saturated model are found in Table S3.

**FIGURE 2** Mean values of above-ground biomass averaged across the nine widely naturalized and the nine less-widely naturalized alien species grown with or without competition (alone), and under ambient light or with additional artificial light at night. Error bars represent standard errors.

**FIGURE 3** Mean values of total above-ground biomass in pots with competition (a) and above-ground biomass proportion of alien plants (b) averaged across the nine widely naturalized and the nine less-widely naturalized alien species grown under ambient light or with additional artificial light at night. Error bars represent standard errors [Colour figure can be viewed at wileyonlinelibrary.com]

4 | **DISCUSSION**

Our study tested for the first time how the global change factor artificial light at night affects biomass production of naturalized alien plants grown alone or in competition with native plants. We found that the total above-ground biomass of the pots with competitors
was significantly increased by artificial light at night, suggesting that the plant community in the pots capitalized on the additional light. Although the widely naturalized species overall produced significantly more biomass than the less-widely naturalized species, there was a marginally significant trend that the less-widely naturalized species responded more strongly to artificial light at night than the widely naturalized species. This suggests that with increasing artificial light at night, many currently non-widely naturalized species might become more widespread.

It has frequently been suggested that large plants are likely to be more competitive, and therefore more likely to become invasive (Baker, 1974; Blossey & Notzold, 1995). In line with this, we found that the widely naturalized species produced significantly more above-ground biomass, across the different experimental treatments, than the less-widely naturalized species. As a consequence, the proportional biomass of the alien plants in the pots with native competitors was also significantly higher when the species are widely naturalized, suggesting that they can more easily dominate in plant communities. The maintenance of a high biomass production by the widely naturalized species in the different experimental treatments is consistent with the theory that a ‘Jack-of-all-trades’ strategy could facilitate invasion (sensu Richards et al., 2006). Similarly, a recent multispecies experiment found that native Central European species that are globally widely naturalized grew faster than less widely naturalized ones, both under low and high nitrogen availabilities (Liu & van Kleunen, 2019). Similarly, previous studies on native Central European species found that those that are globally widely naturalized grew faster and produced more biomass than less widely naturalized species under different light conditions (van Kleunen et al., 2011) and nutrient conditions (Schlaepfer et al., 2010).

Together with those studies, our current study thus suggests that fast growth and high biomass production across different environments increases the chance that alien species become more widespread.

Interestingly, although the less-widely naturalized species had a lower overall performance than the widely naturalized species, we found that they tended to take more advantage of artificial light at night (marginal significant $S \times L$ interaction in Table 1, $p = 0.07$). This suggests that artificial light at night may result in an increased spread of currently less-widely naturalized species. Why these species are able to take more advantage of artificial light at night is not clear. Therefore, more studies are needed to test whether this is a general phenomenon. Furthermore, it should be tested whether this also applies when instead of fluorescent tubes, which are not frequently used outdoors, other more commonly used outdoor lamps are used.

Overall, the increased biomass production of the communities suggests that plants can use the additional light to do photosynthesis or reduce night respiration. Indeed, photosynthesis measurements at night on a small subset of the plants showed that the net photosynthetic rate was higher with artificial light at night (Figure S4). It could be that the less-widely naturalized species are due to their smaller biomass (Figure 2) and smaller maximum height (the highest value reported for the species in Rothmaler Excursion Flora of Germany; Jäger et al., 2017; Table S1)—as also frequently found among other naturalized species (e.g. Divišek et al., 2018)—better used to being shaded by taller species than the widely naturalized species, and therefore have evolved a lower light compensation point, that is, a higher sensitivity of their photosynthetic machinery to low light conditions (Falster et al., 2018; Givnish, 1988). This would then allow them to take advantage of the low light intensity at night provided by the fluorescent lamps. In line with this, it has been found that widely naturalized species have higher light compensation points and higher dark respiration than less-widely naturalized species (Ugoletti et al., 2011). In our study, however, a comparison of the photosynthetic rates at night between the widely and less-widely naturalized species was not significant (Figure S4). This, however, might be due to the small sample size, and thus low statistical power. Clearly, more physiological research is needed to assess why some species can take more advantage of artificial light at night than others.

Although artificial light at night affected the less-widely naturalized species more strongly than the widely naturalized species, it did not affect the proportional biomass of the widely and less-widely naturalized species in the pots with native competitors. This suggests that if an alien plant benefited from artificial light at night, the native competitors did so too (Figure S5). In other words, the competitive balance between the naturalized species and native communities appears to be unaffected in our study. However, a post hoc analysis for the proportional biomass of each native competitor species showed that artificial light at night increased the proportional biomass of the native species $D. glomerata$ (Table S4; Figure S6a). Moreover, the biomass proportion of $P. lanceolata$ decreased with artificial light at night when competing with the widely naturalized alien species, whereas the reverse was true when it was competing with the less-widely naturalized alien species (Table S4; Figure S6b). This is in line with the results of Bennie, Davies, Cruse, Bell, et al. (2018), who found that artificial light at night changed the competitive balance between native plant species. Our study thus provides further evidence that artificial light at night can change the competitive balance between species, even after a relatively short period (i.e. 63 days in our study), and thus affect community dynamics. Nevertheless, longer lasting experiments are needed to test whether competition between native and alien plants could be changed by artificial light at night in the long term.

While changes in absolute biomass and biomass proportion are indicative of changes in competitive dynamics, the consequences of artificial light at night on alien-native competitions might also act through other trophic levels such as herbivores (Bennet et al., 2015, 2018) and pollinators (Knop et al., 2017; Macgregor et al., 2019). Native species and successful and less successful alien species may attract different numbers and types of herbivores (Cappuccino & Carpenter, 2005; Jogesh et al., 2008; Keane & Crawley, 2002) and pollinators (Razanajatovo et al., 2015; Razanajatovo & van Kleunen, 2016; Richardson et al., 2000). Therefore, future studies should focus more
on how artificial light at night can indirectly affect invasion success of alien species through changes in trophic interactions.

In conclusion, our study showed that widely naturalized species performed better than less-widely naturalized species. This was true both without and with artificial light at night, but with artificial light at night the difference in performance between both groups of species tended to decrease. Still, more studies are needed to test the potential effects, and particularly the indirect effects, of artificial light at night on plant invasion. Nevertheless, the slightly positive effect of artificial light at night on the less-widely naturalized species indicates that increased artificial light at night might lead to a further invasion risk of those species.

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AUTHORS’ CONTRIBUTIONS
Y.L. conceived the idea; Y.L. and M.v.K. designed the experiment; B.S. and Y.L. performed the experiment and analysed the data; B.S. wrote the first draft of the manuscript; Y.L. and M.v.K. revised the manuscript.

DATA AVAILABILITY STATEMENT
Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.0p2ngf20j (Speißer et al., 2021).

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REFERENCES
Baker, H. G. (1974). The evolution of weeds. Annual Review of Ecology and Systematics, 5, 1–24. https://doi.org/10.1146/annurev.es.05.110174.000245
Bennie, J., Davies, T. W., Cruse, D., Bell, F., & Gaston, K. J. (2018). Artificial light at night alters grassland vegetation species composition and phenology. Journal of Applied Ecology, 55, 442–450. https://doi.org/10.1111/1365-2664.12927
Bennie, J., Davies, T. W., Cruse, D., & Gaston, K. J. (2016). Ecological effects of artificial light at night on wild plants. Journal of Ecology, 104, 611–620. https://doi.org/10.1111/1365-2745.12551
Bennie, J., Davies, T. W., Cruse, D., Inger, R., & Gaston, K. J. (2015). Cascading effects of artificial light at night: Resource-mediated control of herbivores in a grassland ecosystem. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 370(1667), 20140131. https://doi.org/10.1098/rstb.2014.0131
Bennie, J., Davies, T. W., Cruse, D., Inger, R., & Gaston, K. J. (2018). Artificial light at night causes top-down and bottom-up trophic effects on invertebrate populations. Journal of Applied Ecology, 55, 2698–2706. https://doi.org/10.1111/1365-2664.13240
Blossey, B., & Notzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. Journal of Ecology, 83, 887–889. https://doi.org/10.2307/2261425
Bradley, B. A., Blumenthal, D. M., Wilcove, D. S., & Ziska, L. H. (2010). Predicting plant invasions in an era of global change. Trends in Ecology & Evolution, 25, 310–318. https://doi.org/10.1016/j.tree.2009.12.003
Briggs, W. R. (2006). Physiology of plant responses to artificial lighting. In C. Rich & T. Longcore (Eds.), Ecological consequences of artificial night lighting (pp. 389–411). Island Press.
Brisson, J., de Blois, S., & Lavoie, C. (2010). Roadside as invasion pathway for common reed (Phragmites australis). Invasive Plant Science and Management, 3, 506–514.
Cappuccino, N., & Carpenter, D. (2005). Invasive exotic plants suffer less herbivory than non-invasive exotic plants. Biology Letters, 1, 435–438. https://doi.org/10.1098/rsbl.2005.0341
Christen, D., & Matlack, G. (2006). The role of roadsides in plant invasions: A demographic approach. Conservation Biology, 20, 385–391. https://doi.org/10.1111/j.1523-1739.2006.00315.x
Davidson, A. M., Jennions, M., & Nicotra, A. B. (2011). Do invasive species show higher phenotypic plasticity than native species and if so, is it adaptive? A meta-analysis. Ecology Letters, 14, 419–431. https://doi.org/10.1111/j.1461-0248.2011.01596.x
Davies, T. W., & Smyth, T. (2018). Why artificial light at night should be a focus for global change research in the 21st century. Global Change Biology, 24, 872–882. https://doi.org/10.1111/gcb.13927
Divíšek, J., Chytrý, M., Beckage, B., Gotelli, N. J., Lososová, Z., Pyšek, P., Richardson, D. M., & Molofsky, J. (2018). Similarity of introduced plant species to native ones facilitates naturalization, but differences enhance invasion success. Nature Communications, 9, 4631.
Dominoni, D. M. (2015). The effects of light pollution on biological rhythms of birds: An integrated, mechanistic perspective. Journal of Ornithology, 156, 409–418. https://doi.org/10.1007/s10336-015-1196-3
Dostál, P., Dawson, W., van Kleunen, M., Keser, L. H., & Fischer, M. (2013). Central European plant species from more productive habitats are more invasive at a global scale. Global Ecology and Biogeography, 22, 64–72. https://doi.org/10.1111/j.1466-8238.2011.00754.x
Dukes, J. S., & Mooney, H. A. (1999). Does global change increase the success of biological invaders? Trends in Ecology & Evolution, 14, 135–139. https://doi.org/10.1016/S0169-5347(98)01554-7
Falchi, F., Cinzano, P., Duriscoe, D., Kyba, C. C. M., Elvidge, C. D., Baugh, K., Portnov, B. A., Rybnikova, N. A., & Furgoni, R. (2016). The new world atlas of artificial night sky brightness. Science Advances, 2, e1600377.– https://doi.org/10.1126/sciadv.1600377
Falster, D. S., Duursma, R. A., & FitzJohn, R. G. (2018). How functional traits influence plant growth and shade tolerance across the life cycle. Proceedings of the National Academy of Sciences of the United States of America, 115, E6789. https://doi.org/10.1073/pnas.1714044115
Felsenstein, J. (1985). Phylogenies and the comparative method. The American Naturalist, 125, 1–15. https://doi.org/10.1086/284325
Feng, Y., & van Kleunen, M. (2014). Responses to shading of naturalized and non-naturalized exotic woody species. Annals of Botany, 114, 981–989. https://doi.org/10.1093/aob/mcu163
Feng, Y., Wang, J., & Sang, W. (2007). Biomass allocation, morphology and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels. Acta Oecologica, 31, 40–47. https://doi.org/10.1016/j.actao.2006.03.009
Gaston, K. J. (2018). Lighting up the nighttime. Science, 362, 744–746. https://doi.org/10.1126/science.aau8226
Gaston, K. J., Davies, T. W., Nedelec, S. L., & Holt, L. A. (2017). Impacts of artificial light at night on biological timings. Annual Review of Ecology,
Ugoletti, P., Stout, J. C., & Jones, M. B. (2011). Ecophysiological traits of invasive and non-invasive introduced impatiens species. *Biology and Environment. Proceedings of the Royal Irish Academy, 111B,* 143–156.

van Kleunen, M., Schlaepfer, D. R., Glaettli, M., & Fischer, M. (2011). Preadapted for invasiveness: Do species traits or their plastic response to shading differ between invasive and non-invasive plant species in their native range? *Journal of Biogeography, 38,* 1294–1304. https://doi.org/10.1111/j.1365-2699.2011.02495.x

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R.* Springer.

**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

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