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Artificial light at night as a new threat to pollination

Eva Knop¹, Leana Zoller¹, Remo Ryser¹, Christopher Gerpe¹, Maurin Hörler¹ & Colin Fontaine²

Pollinators are declining worldwide¹ and this has raised concerns for a parallel decline in the essential pollination service they provide to both crops and wild plants^{2,3}. Anthropogenic drivers linked to this decline include habitat changes, intensive agriculture, pesticides, invasive alien species, spread of pathogens and climate change¹. Recently, the rapid global increase in artificial light at night⁴ has been proposed to be a new threat to terrestrial ecosystems; the consequences of this increase for ecosystem function are mostly unknown^{5,6}. Here we show that artificial light at night disrupts nocturnal pollination networks and has negative consequences for plant reproductive success. In artificially illuminated plant–pollinator communities, nocturnal visits to plants were reduced by 62% compared to dark areas. Notably, this resulted in an overall 13% reduction in fruit set of a focal plant even though the plant also received numerous visits by diurnal pollinators. Furthermore, by merging diurnal and nocturnal pollination sub-networks, we show that the structure of these combined networks tends to facilitate the spread of the negative consequences of disrupted nocturnal pollination to daytime pollinator communities. Our findings demonstrate that artificial light at night is a threat to pollination and that the negative effects of artificial light at night on nocturnal pollination are predicted to propagate to the diurnal community, thereby aggravating the decline of the diurnal community. We provide perspectives on the functioning of plant–pollinator communities, showing that nocturnal pollinators are not redundant to diurnal communities and increasing our understanding of the human-induced decline in pollinators and their ecosystem service.

Animal-assisted pollination is a key ecosystem function for wild plant communities and 88% of all angiosperms depend on it to some extent⁷. Pollination by animals is also a crucial ecosystem service for global food supply^{1,8}; the estimated economic value of pollination was US\$361 × 10⁹ in 2009 (ref. 9). Thus, pollination by animals is fundamental to both the functioning of natural ecosystems and food security. Concerns have been raised that the pollination provided by insects may be at risk^{2,3} due to a worldwide decline in wild and managed pollinators as a consequence of human activity¹. The main factors causing this decline are considered to be habitat loss and degradation, conventional intensive agriculture including pesticide use, invasive alien species, pests and pathogens, and climate change¹.

Recently, artificial light at night (ALAN) has been proposed as a factor that increasingly affects nocturnal pollinators^{10,11}. ALAN is rapidly spreading globally at an estimated rate of 6% per year¹². It has been shown to affect the physiology and behaviour of various organisms¹³, with consequences for species communities^{14–16} and population dynamics¹⁷. Changes in species communities because of ALAN may in turn affect associated ecosystem functions and processes, as has recently been demonstrated for aquatic microbial communities¹⁴. For terrestrial systems, the effect(s) of ALAN on the functioning of communities, such as for pollinators and pollination, has yet to be demonstrated⁵.

The negative impact of ALAN might not be restricted to nocturnal pollinators and the plants they pollinate, but could propagate to

the diurnal pollinator community (Fig. 1), thereby increasing the overall environmental pressure on this community. Indeed, we know that plants and their pollinators are embedded in complex interaction networks¹⁸, where perturbations can cascade from species to species depending on network architecture¹⁹. These cascading effects have recently been shown for the effects of grazer presence on flower-visitation networks²⁰. However, to our knowledge, the separate and combined responses of nocturnal and diurnal pollinator networks to environmental change have not been investigated (but see an example of a moth–pollen transport network²¹). It is therefore unknown whether the architecture of pollination networks facilitates or impedes plant-mediated indirect interactions between the diurnal and nocturnal pollinator communities. Hence, we do not know whether the negative effects of ALAN potentially spread from the nocturnal to the diurnal pollinator community, with potential knock-on effects on pollination rates.

Here we show how the negative effects of ALAN on nocturnal pollinator communities translate into negative consequences for plant reproductive success, and we demonstrate that these effects have the potential to cascade from the nocturnal to the diurnal pollinator community (Fig. 1). On 7 out of 14 independent ruderal meadows, which had never been exposed to artificial lighting previously, we set up mobile street lamps, while leaving the other 7 as controls. On these meadows we sampled nocturnal interactions between plants and flower

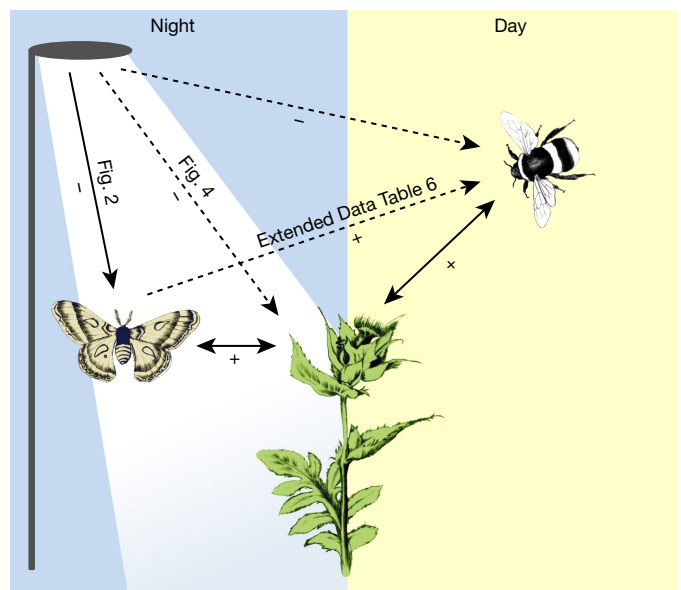


Figure 1 | Interaction web showing the pathway by which artificial light at night affects plant reproduction and diurnal pollinator communities. Solid arrows indicate direct interactions; dashed arrows denote indirect interactions. The sign (+ or –) refers to the expected direction of the direct or indirect effect (see text). The figures and table that present data supporting each of the predicted effects are indicated.

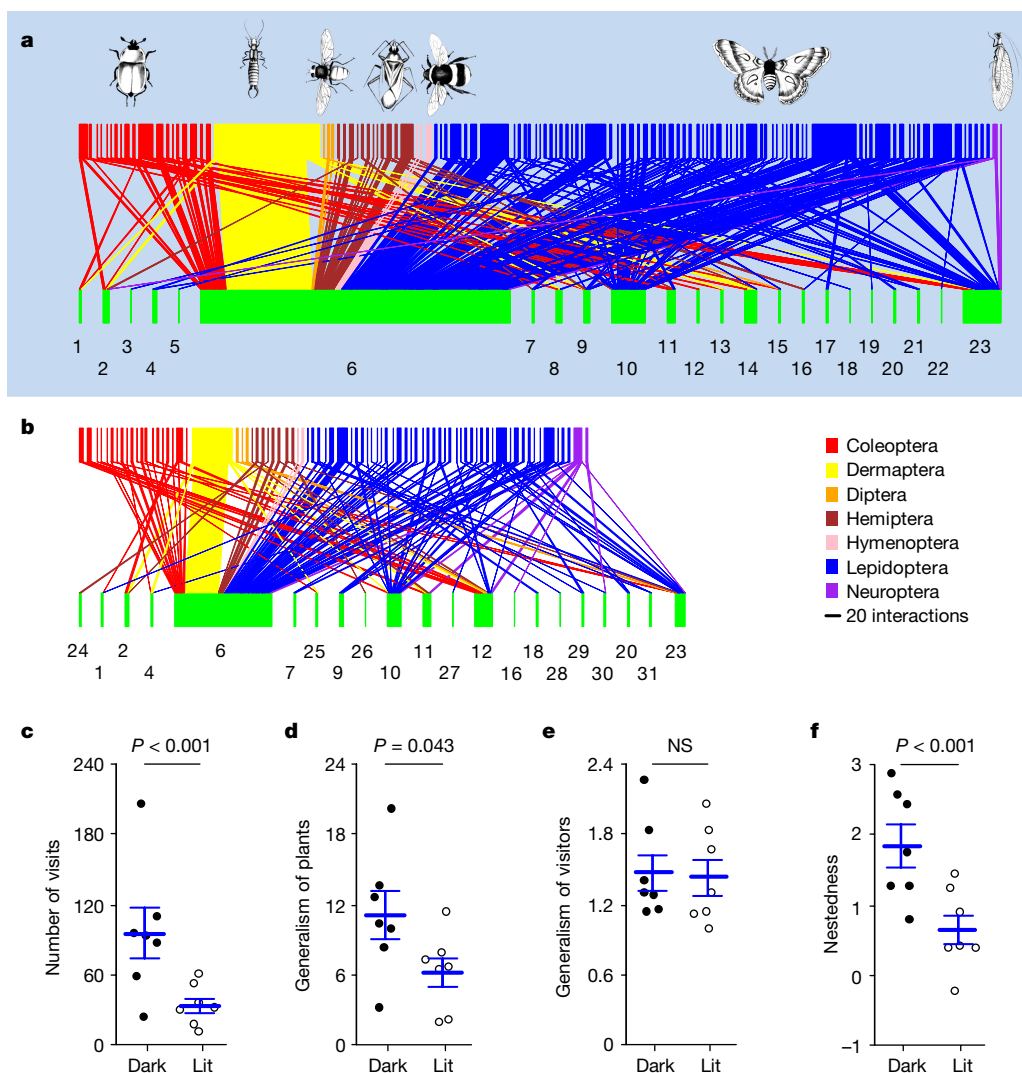


Figure 2 | Effects of artificial lighting on parameters of nocturnal plant-flower visitor networks. **a, b**, Overall quantified plant-flower visitor network of seven dark sites (**a**) and seven experimentally illuminated sites (**b**). The rectangles represent insect species (top) and plant species (bottom), and the connecting lines represent interactions among species. Species codes for the plants and a list of insect species are given in

Supplementary Tables 2, 3. **c–f**, The number of visits (**c**), generalism of plants (**d**), generalism of flower visitors (**e**), and nestedness (z score of NODF) (**f**) for dark sites (dark, $n = 7$) and illuminated sites (lit, $n = 7$). Data are mean \pm s.e.m. (**c–f**). Results from statistical models are given in Extended Data Table 1. NS, not significant.

visitors and analysed how ALAN affects the structure of the interaction networks. In particular, we analysed the number of interactions and species, and two network metrics known to affect the stability of plant–pollinator communities: species generalism²² and network nestedness^{18,19}. We found a significantly lower number of flower visits ($z = -4.7$, degrees of freedom (d.f.) = 10, $P < 0.001$, 62% fewer visitations on illuminated sites; Fig. 2a–c) and species of flower visitors ($z = -4.4$, d.f. = 11, $P < 0.001$; 29% fewer species on illuminated sites; Extended Data Table 1) on illuminated sites. The lower insect richness under the light treatment was mainly explained by the lower number of interactions sampled, suggesting that artificial light affects species equally (Extended Data Fig. 1). This negative effect of ALAN on insect visitation is most likely because of altered behaviour of nocturnal flower visitors, such as attraction to an artificial light source at night, as is known for many moth species²³, and/or to a physiological reaction of flower visitors, although these have rarely been studied²⁴. Alternatively, changes in plant physiology might have altered their attractiveness for flower visitors, but such mechanisms remain largely unexplored²⁵. The number of plant species visited was similar between illuminated sites and dark control sites (subsequently referred to as dark sites) ($z = -1.1$,

d.f. = 11, $P = 0.271$; Extended Data Table 1). However, the generalism of plant species, calculated as the weighted mean effective number of pollinator species per plant species²⁶, was significantly lower for illuminated sites ($t = -2.6$, d.f. = 6, $P = 0.043$; Fig. 2d). As for flower-visitor richness, this reduction in plant generalism was explained by the lower number of interactions under the light treatment and did not reflect an actual change in plant generalism (Extended Data Fig. 2). Notably, flower-visitor generalism (that is, the weighted mean effective number of plant species per pollinator species²⁶) was unaffected by the light treatment ($t = -0.2$, d.f. = 6, $P = 0.836$; Fig. 2e and Extended Data Fig. 3), suggesting that the species visiting flowers with the light treatment were not more selective than those visiting flowers in the dark sites. Given the large differences in network size between control and illuminated sites, nestedness was standardized (z score of NODF (nestedness metric based on overlap and decreasing fill), see Methods). Nestedness was significantly higher in dark sites ($t = -3.3$, d.f. = 12, $P < 0.001$; Fig. 2f) compared to illuminated sites, suggesting that ALAN might have a destabilizing effect on nocturnal plant–pollinator communities. Because not all flower visitors are necessarily functional pollinators and not all specimens within the dataset were identified

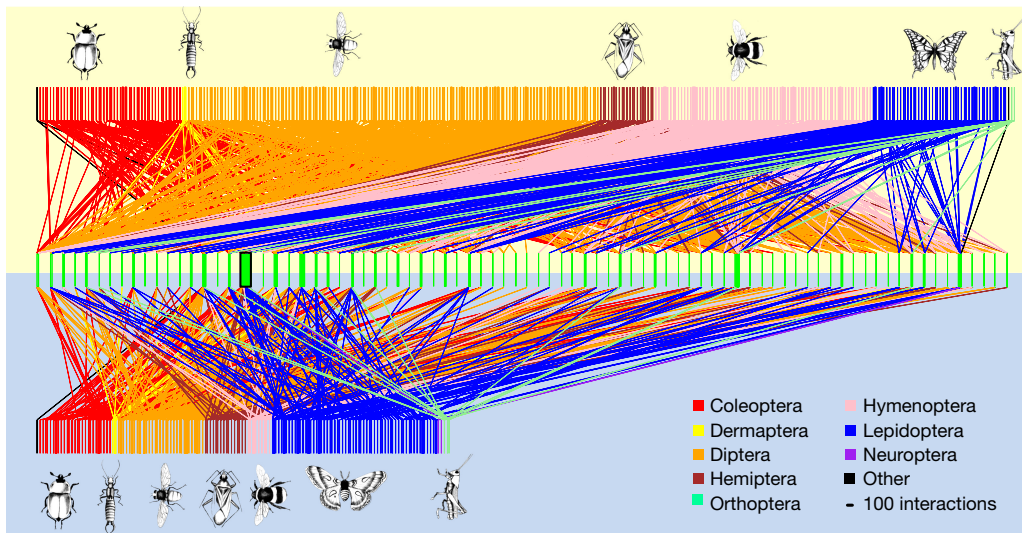


Figure 3 | Merged overall quantified diurnal and nocturnal plant-flower visitor network. The top rectangles represent species of diurnal visitors, the bottom rectangles are species of nocturnal visitors, and the middle rectangles show plant species, respectively. The abundance of all

to a high taxonomic resolution, all analyses were repeated with two different subsets in which specimens were identified to a high taxonomic resolution and more strictly assigned to pollinators on the basis of expert knowledge and whether they carried pollen (see Methods). These analyses gave consistent results (Extended Data Table 1).

To test whether the negative impact of ALAN on night-time pollinators translates into a lower pollination function, we conducted a fruit set experiment using the model plant *Cirsium oleraceum*. This plant was common to all our sites and was one of the most frequently visited species. In the year before the light treatment, this plant species received the highest number of flower visits during the day and during the night (11% of all diurnal visits, 56% of all nocturnal visits; Fig. 3), and the mean number of visits was similar during day and night (Extended Data Table 2). This was consistent for the two subsets of the flower visitors (Extended Data Table 2).

The impact of ALAN on pollination function was assessed by analysing the reproductive output of a total of 100 experimental plants of *C. oleraceum*, distributed equally across 5 illuminated and 5 dark sites. On each site the 10 plants were paired and one plant within a pair was bagged to exclude flower visitors. The number of developed fruits of plants exposed to flower visitors was significantly reduced on the illuminated sites compared to the dark sites ($z = -2.5$, d.f. = 140, $P = 0.014$; Fig. 4a). This effect was most likely not driven by potential bottom-up effects of altered plant growth²⁵, as plant biomass did not differ between illuminated and dark sites ($t = -1$, d.f. = 8.1, $P = 0.261$, mean \pm s.e.m. = 17.5 ± 1.0 for dark sites, mean \pm s.e.m. = 15.0 ± 0.8 for illuminated sites), and the number of developed fruits of self-pollinated plants (that is, bagged plants) was similar between the two treatments ($z = 1.47$, d.f. = 140, $P = 0.140$, Fig. 4a). Similar results were found for the percentage of developed fruits per flower head (Fig. 4b and Extended Data Table 3). A small number of flower heads (4%) were infested with herbivores, which negatively affected the number of developed fruits (Extended Data Table 3). The effect of herbivores on the number of developed fruits did not differ between illuminated and dark sites. No difference was found in the percentage of developed fruits per flower head between flower heads infested by herbivores and herbivore-free flower heads (Extended Data Table 3). Our network data show that the number of flower visits to *C. oleraceum* was significantly reduced for illuminated sites, and this was consistent for the two subsets of flower visitors analysed (Extended Data Table 4). There was no relationship between light intensity measured on the flower head of the plants and number and percentage of developed fruits (Extended

species and the frequency of visitations (day and night) are reflected by the width of the rectangles. *Cirsium oleraceum* was the most frequently visited plant species during day and night (framed in black). A list of all plant and insect species is given in Supplementary Tables 2, 3.

Data Table 5), suggesting that the disruption of the pollination function already occurs at low light intensities. Our results show that the pollination service provided by nocturnal flower visitors is disrupted in the vicinity of streetlamps, and that this leads to a reduced reproductive output of the plant, which cannot be compensated for by pollinators during the day. This further indicates that nocturnal and diurnal pollinators generate complementarity effects, which have previously been demonstrated for different functional groups of diurnal pollinators²⁷.

Because ALAN affects nocturnal pollinators such that this causes a lower fruit set of the plants they pollinate, this negative impact could further affect diurnal pollinators, given that these plants represent an important food source for them. Even in the case of *C. oleraceum*, which can also reproduce clonally, reduced sexual reproductive output is still likely to have negative effects on fitness over the long term²⁸ and hence on the food resource of the pollinators using that plant. To investigate whether the structure of intertwined nocturnal and diurnal networks tend to propagate or buffer such effects, we quantified the potential for indirect effects from nocturnal to diurnal flower visitors (Fig. 4). We then compared the observed potential for indirect effects to the effect of networks in which plants connect the nocturnal and diurnal sub-networks in a randomized manner (see Methods). The observed potential for indirect effects was significantly higher than the effect of randomly inter-connected

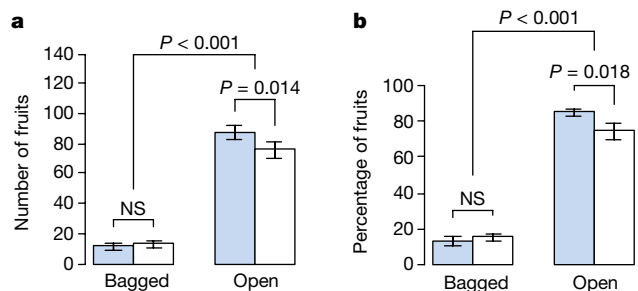


Figure 4 | Effects of artificial lighting on fruit set. a, b, Number of developed fruits (a) and percentage of developed fruits (b) for flower heads with insect pollination (open) and without insect pollination (bagged) on dark sites (light blue bars) and experimentally illuminated sites (white bars). Fifty flower heads were observed per treatment group ($n = 50$ per treatment group), and mean \pm s.e.m. are shown. Results from statistical models are given in Extended Data Table 3.

networks ($P = 0.008$; Extended Data Table 6), indicating that plants connect nocturnal and diurnal flower visitors in a way that favours the spread of indirect interactions between them. This might arise from correlated plant generalism in both sub-networks, a pattern that favours the spread of indirect interactions²⁹. Similar results were obtained for analyses of the two subsets of flower visitors (Extended Data Table 6).

The worldwide decline in pollinators has received much attention in recent years, due to the essential pollination service they provide to both crops and wild plants¹. Here, we demonstrate for the first time that ALAN is a threat to pollination that is rapidly spreading globally¹². Because nocturnal and diurnal pollinators act as complementary functional groups and are linked by plant-mediated indirect interactions, ALAN has the potential to further aggravate the decline of diurnal pollinators through plant-mediated indirect effects from the nocturnal pollinator community, with further knock-on effects on plant pollination. We provide novel perspectives for the understanding of the functional complementarities among pollinators, and show how plant–pollinator interactions are threatened by a hitherto little acknowledged driver of global change.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions E.K. and C.F. conceived the study and analysed the data. E.K., R.R., C.G. and L.Z. developed the set-up of the field sites and protocols. E.K., C.G., R.R., M.H. and L.Z. obtained the samples. E.K. wrote the first manuscript draft and all authors reviewed the manuscript.

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METHODS

Data reporting. No statistical methods were used to predetermine sample size. Where possible experiments were randomized, for example, plants were selected randomly for treatment out of all plants on the study site. Insect sampling on the site was not done in a blinded manner, but the experts who identified the insect species were blinded to which site the insects were obtained from.

Experimental set-up. In 2014, a total of eight independent ruderal meadows were selected in the Prealps of Switzerland (nearest ground distance between two adjacent sites (dist): mean \pm s.e.m. = 0.9 ± 0.3 km, median = 0.6 km). In 2015, nine additional meadows were selected and five of the sites of 2014 were used, resulting in a total of 14 sites (dist: mean \pm s.e.m. = 1.0 ± 0.2 km, median = 0.6 km; see Supplementary Table 1). This region still has low levels of light emission with a radiance of less than $0.25 \times 10^{-9} \text{ W sr}^{-1} \text{ cm}^{-2}$ (data from <http://www.lightpollutionmap.info>). All sites were comparable in vegetation, *C. oleraceum* was present on all sites and a varying subset of the following plant species was common to all sites: *Eupatorium cannabinum*, *Valeriana officinalis*, *Epilobium angustifolium* and *Silene vulgaris*. In 2015, on 7 out of the 14 sites LED street lamps (Schröder GmbH, type: AMPERA MIDI 48 LED, colour temperature: neutral white (4,000 K), nominal LED flux: 6,800 lm) were installed (subsequently referred to as illuminated sites). The lamps were installed on poles at a height of 4 m and were equipped with a twilight switch, which turned the lamps on when the surrounding brightness fell below 5 lx. Varying with the topography of the meadow, this resulted in a mean \pm s.e.m. = 52.0 ± 4.2 lx within a 5-m radius circle around the streetlamp, 25.7 ± 1.1 lx 5–10 m away and $<3.9 \pm 0.4$ lx more than 10 m away. Each of the seven illuminated sites was paired with a dark site (Supplementary Table 1). All dark sites were situated at least 100 m from any permanent light source (that is, street lamp) and had no major light source, such as an illuminated sports ground, in the surrounding 500 m. Pairing was done based on spatial proximity. In addition, due to high nightly variance in nocturnal insect activity, the sites within one pair were sampled at the same time during the same night.

Assessment of interactions between plants and flower visitors. Two datasets were collected, one in 2014 comprising paired diurnal and nocturnal interactions between plants and flower visitors (subsequently referred to as the day–night dataset), and one in 2015, comprising nocturnal observations only, but on illuminated and dark sites (subsequently referred to as the ALAN dataset). The two datasets were collected according to the same method, but with a slightly different sampling effort. Subsequently, the sampling procedure for the day–night dataset is described, and deviations from it in the ALAN dataset are given in brackets. The plant–flower visitor interactions were sampled by collecting all flower visitors actively touching the reproductive organs of the flowers within the area of 1 m on both sides of a transect using a hand net and walking at a steady speed³⁰. Each flower visitor was individually caught and immediately transferred to a separate vial to avoid contamination by contact with other collected insects. For each collected visitor, the plant species was recorded. The flower visitors were frozen, pinned and if possible determined to species level (day–night dataset: 77%, ALAN dataset: 82%) otherwise to morphospecies (day–night dataset: 6%, ALAN dataset: 8%), genus (day–night dataset: 12%, ALAN dataset: 7%) or family level (day–night dataset: 4%, ALAN dataset: 3%). For simplicity, subsequently, they are all referred to as species. However, to ensure that the specimens identified to a low taxonomic resolution and flower visitors that were not functional pollinators did not influence the results, all analyses were repeated using two subsets of the two datasets. The first two subsets (further referred to as day–night_p and ALAN_p) included only specimens that were identified to the level of genus, species, or morphospecies. Furthermore, all specimens of insect orders generally regarded as pollinators, namely Hymenoptera (except specimens of the family Formicidae) and Diptera^{31,32}, were included, whereas specimens of taxa groups generally not regarded as pollinators were excluded, namely specimens of Carabidae, Neuroptera, Araneae and Blattodea. Finally, all specimens that were found to carry more than 5 pollen grains at least once were assigned as pollinators (assignment of specimens identified at the genus level only, if for all the specimens this was the highest taxonomic resolution). The second two subsets (further referred to as day–night_p.strict and ALAN_p.strict) were obtained following the same approach as for the first two subsets, but with a more strict exclusion of taxa generally not regarded as pollinators: all orders were excluded except for Lepidoptera and Coleoptera (except for Carabidae, which were also excluded), Diptera and Hymenoptera. For more details regarding the datasets see Supplementary Table 3.

Observations during the night started 30 min after astronomical sunset. A 50-m transect (ALAN dataset: 100-m transect) was sampled every 30 min for a period of 3 h (ALAN dataset: 4 h), resulting in six sampling rounds per night and site (ALAN dataset: eight sampling rounds). Between May and September 2014 (ALAN dataset: June and September 2015) sampling was repeated six times (ALAN dataset: five times, except for one illuminated and one dark site, which were only sampled four times). As visual aids, night-vision goggles (BIG25-CV, Vectronix) and LED head

torches (873155 Intertronic, Interdiscount) were used in a randomized, alternating pattern (that is, for each hour, either LED head torches or night-vision goggles were randomly used first). Observations during the day started at 13:00 and they were paired with the night sampling, that is, on the same day or the day before or after, except for two times, when there were 3 and 10 days in between two sampling events owing to bad weather conditions. Sampling was only conducted without strong wind and rain, and during the day only in sunny conditions.

Estimation of pollination service. In 2015, on each of 5 dark and 5 illuminated sites (Supplementary Table 1), 5 pairs of 2 individuals of *C. oleraceum* were selected, resulting in 10 plants per site. The plants within a pair were similar in size and were at maximum 1 m apart from each other. Before the onset of flowering, one plant within each pair was randomly selected and its flower heads were bagged with a white nylon mesh (mesh size: 0.5 mm) in order to exclude flower visitors. This resulted in a total of 100 observed plants subjected to four treatments (the 25 plants for each treatment were distributed equally among the sites). Between the end of July and the beginning of September, flower heads were collected as soon as they started to wither and to produce a feathery pappus. All fruits of two flower heads per plant were counted, and a visual distinction between the developed white fruits and the aborted brown ovules was made (Extended Data Fig. 4). Two measurements of reproductive output were calculated: the number of developed fruits and the percentage of developed fruits per flower head. Lux intensities for each position of a plant pair were determined by a Photocurrent Amplifier (Ph-Amp MB7 Version 2.0, Czibula and Grundmann GmbH). The withered plants were harvested (above ground) and dried for three consecutive days in a drying cabinet (70 °C) to assess the dry biomass using a Mettler Toledo scale (NewClassic MF; ML203E). A few flower heads were infested with small herbivores and thus categorized according to whether they were infested or not (herbivores: yes versus no).

Pollen analysis. Pollen grains on insects were assessed using a $1 \times 1\text{-mm}^3$ cube of glycerin gel (1.04094.1000, Merck KGaA) stained with Fuchsin (3256.1, Roth). The insects were swabbed on the entire body, except for wings and parts that are specialized for pollen-carrying, that is, the corbiculum and scopa of bees, as the pollen there is not available for pollination. The gel was then placed on a microscope slide and gently melted. Each microscope slide (that is, one per insect specimen caught) was then scanned for pollen grains using a light microscope, and up to five grains were counted.

Indirect effects from nocturnal to diurnal pollinators. The potential for indirect effects from nocturnal to diurnal pollinators via shared plant species was calculated following the approach developed by Müller *et al.*³³, hereafter referred to as Müller's index. Müller's index is well-suited for assessing the potential for any indirect influence between species (that is, apparent competition or facilitation) and is coded in the PAC function of the R package bipartite. For each pair of nocturnal and diurnal flower visitors within each of the eight networks, we computed the potential for plant-mediated indirect effects from the nocturnal to the diurnal flower visitor. For each of the eight sites, we then computed the mean potential for indirect effects from nocturnal to diurnal flower visitors, hereafter referred to as the observed mean. The observed means were then compared to means derived from a null model similar to the one that was used previously³⁴. This null model keeps the structure of the diurnal and nocturnal plant–pollinator sub-networks identical to the observed ones, but randomizes how plants connect these two sub-networks. In other words, while the network structure of the plant–flower visitor sub-network remained identical, plant names were randomly assigned before merging networks, resulting in a random interconnection of the two sub-networks. For each of the eight sites, we performed 1,000 randomizations and computed for each randomization the mean potential for indirect interactions, hereafter referred to as randomized means. For each site we then calculated the percentage of randomized means that were below the observed mean. A quantile test (sign test) using the quantile function in R was performed to test whether the observed means were above the median of the randomized means across the eight sites.

Network parameters. For the ALAN dataset, six network parameters were calculated: the number of species visiting the flower heads; the number of flower visits; the number of plant species visited; the generalism of plants, that is, the weighted mean effective number of species of flower visitors per plant species²⁶; the generalism of flower visitors, that is, the weighted mean effective number of plant species per pollinator species²⁶; and nestedness (NODF), which reflects the tendency for specialist species to interact with generalists. The last three parameters are known to affect the stability of plant–pollinator communities^{19,22} and were calculated using the function networklevel of the R package bipartite.

Data analysis. *Nocturnal plant–flower visitor networks.* The network parameters were taken as a response variable and analysed using either linear mixed-effects (LME) models with the lmer function in the lme4 package or generalized linear mixed-effects (GLMM) models with a Poisson distribution (see Extended Data Table 1). Treatment (two levels, dark versus illuminated) was included as a fixed factor, and site (seven paired sites of which one was the dark and the other the

illuminated site) as a random factor. All GLMM models were checked for overdispersion by including an observation-level random factor (as many levels as observations) into the model and comparing it to a model without this additional variance parameter. When the observation-level random factor significantly improved the model, it was retained in the model. All LME models were visually checked for a normal distribution of residuals and homoscedasticity, and, if necessary, the dependent variable was transformed to fulfil model assumptions (see Extended Data Table 1). To account for different numbers of interactions sampled between dark and illuminated sites, we generated accumulation curves for species richness and generalism of insects and plants. For each site and treatment, 500 accumulation curves were performed by re-sampling the observed interactions, see for example ref. 20. To account for differences in network size between dark and illuminated sites when estimating nestedness, we calculated z scores by comparing the observed NODF values to 1,000 NODF values generated using a null model that keeps network size, connectance and heterogeneity in generalism constant³⁵.

Flower visitations to *C. oleraceum*. The effect of artificial lighting on nocturnal flower visitations to *C. oleraceum* was analysed with GLMM models that use the number of species of flower visitors and the number of visits of the ALAN dataset as response variables and include the same model structure as described for the network parameters. Similarly, the models were checked for overdispersion and, if necessary, an observation-level random factor was included (see Extended Data Table 4 for specifications). The difference between the flower visitations to *C. oleraceum* between day and night was analysed using the day–night dataset. A GLMM model was run, with the number of flower visitors as the response variable, time of sampling (two levels, day versus night) as a fixed factor, site (eight sites, that is, eight levels) as a random factor, and, if necessary, including an additional observation-level random factor.

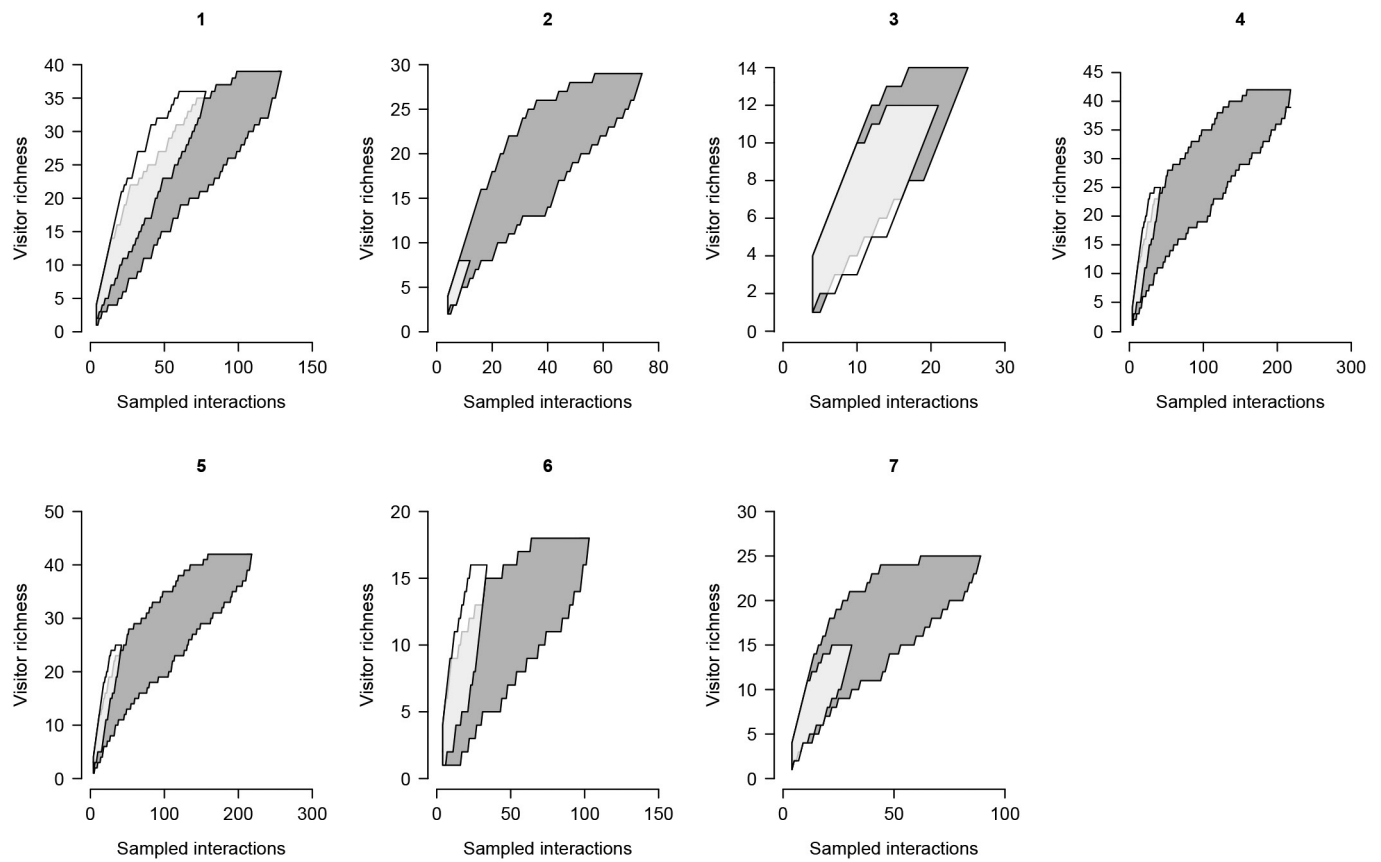
Fruit set of *C. oleraceum*. The effect of artificial lighting on the number of developed fruits was analysed with a GLMM model assuming a Poisson distribution and including plant pair (5 pairs per site, 5 levels) nested within sites (10 sites, 10 levels) nested within site pair (5 pairs, 5 levels) as a random factor. Treatment (two levels, dark versus illuminated), bagging of the flower head (two levels, bagged versus open) and herbivores (two levels, yes versus no) were

included as fixed factors, the dry biomass as a co-variable, and treatment–bagging, treatment–biomass and treatment–herbivores as interactions. If necessary, an additional observation-level random factor was included to correct for overdispersion. The minimal adequate model was determined by Akaike information criterion (AIC)-based stepwise deletion of the interactions first and then single predictors of the full model using likelihood ratio tests. Similarly, the percentage of developed fruits was analysed with a GLMM model and the same model structure was used, except for the assumption of a binomial distribution instead of a Poisson distribution. To test whether the reduction of fruit set varies according to the lux intensity on the flower head, GLMM models were run for the number of developed fruits assuming a Poisson distribution and the percentage of developed fruits assuming a binomial distribution. For these models only data from the unbagged flower heads and illuminated sites were used. In all models plant biomass and lux intensity were included as explanatory variables, and sites (5 sites, 5 levels) as a random factor. The fixed factor, herbivores (yes versus no), was not included as no herbivores were found in the subset. If necessary, the GLMM models were corrected for overdispersion (see Extended Data Table 5 for specifications).

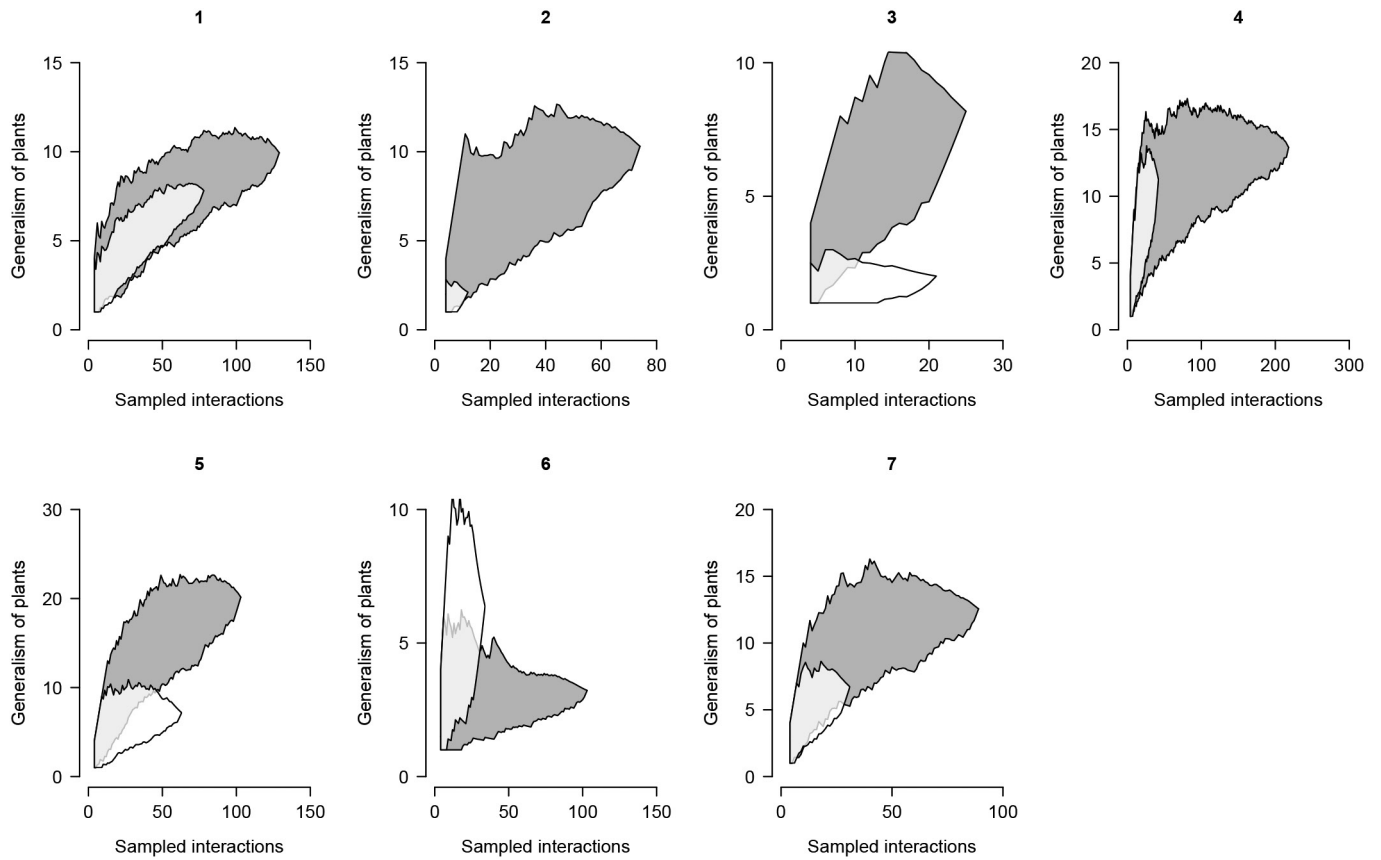
Code availability. The computer code used for this study is available from the corresponding author upon request.

Data availability. The datasets analysed during the study are available from the corresponding author upon request.

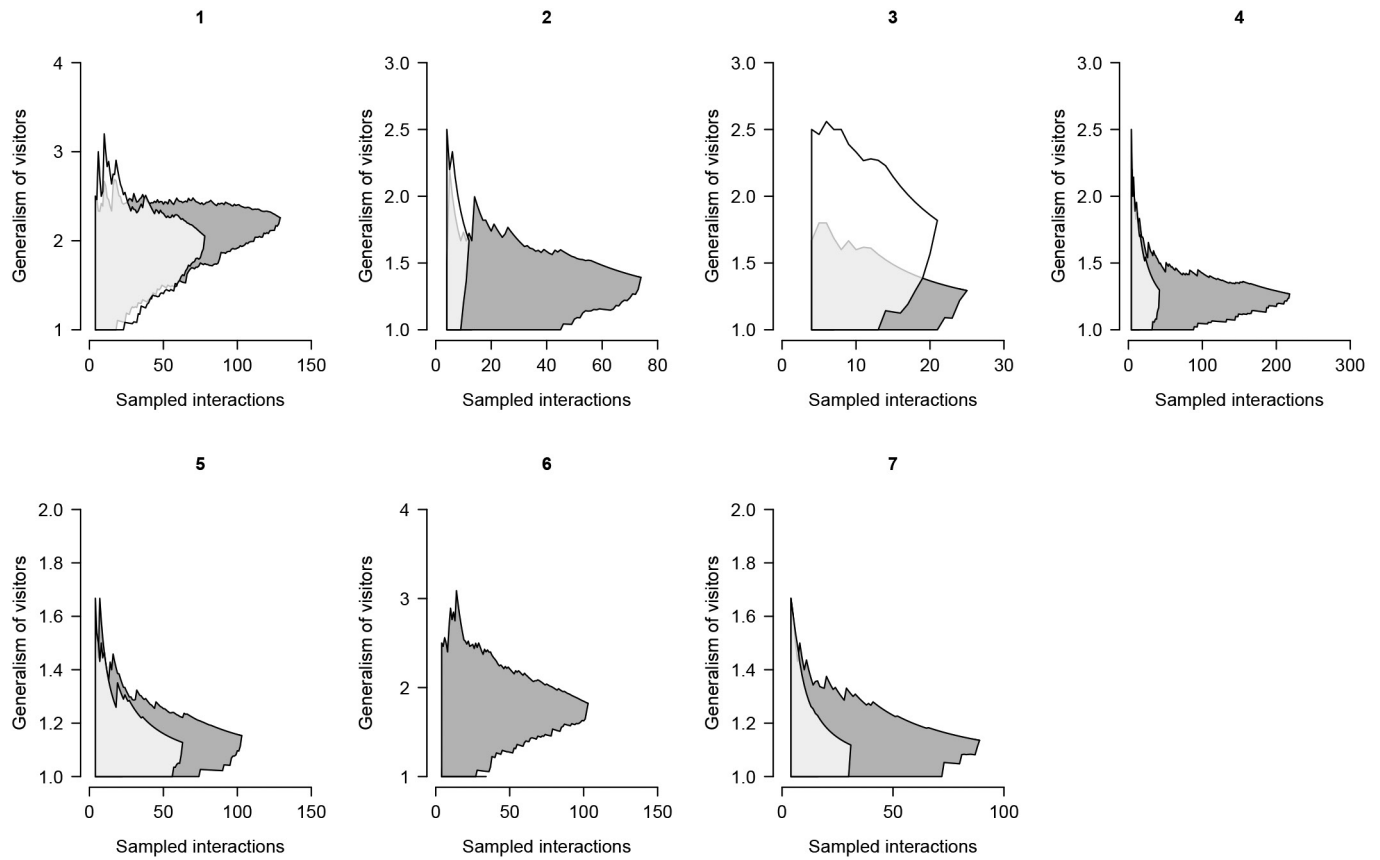
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Extended Data Figure 1 | Accumulation curves for the species richness of flower visitors on illuminated and dark sites. For each site 500 randomizations were performed and 95% confidence intervals are given (illuminated sites in white, dark sites in grey). Numbers above the plots correspond to the number of the pair of sites (see Supplementary Table 1).



Extended Data Figure 2 | Accumulation curves for generalism of plant species on illuminated and dark sites. For each site 500 randomizations were performed and 95% confidence intervals are given (illuminated sites in white, dark sites in grey). Numbers above the plots correspond to the number of the pair of sites (see Supplementary Table 1).



Extended Data Figure 3 | Accumulation curves for generalism of flower visitors on illuminated and dark sites. For each site 500 randomizations were performed and 95% confidence intervals are given (illuminated sites in white, dark sites in grey). Numbers above the plots correspond to the number of the pair of sites (see Supplementary Table 1).



Extended Data Figure 4 | Fruits and aborted ovules of *C. oleraceum*.

Extended Data Table 1 | Comparison of network parameters of dark and illuminated sites

Dataset	Mean ± s.e.m.		Output models				
	dark	illuminated	test stat.	d.f.	P		
Visitor richness							
ALAN	30.1 ± 4.5	18.6 ± 3.5	-4.4	11	<0.001	n	glmer
ALAN_p	23.9 ± 3.7	14.6 ± 2.5	-3.9	11	<0.001	n	
ALAN_p.strict	20.6 ± 3.3	11.9 ± 2.3	-4.0	11	<0.001	n	
Number of visits							
ALAN	105.9 ± 22.3	40.1 ± 8.8	-4.7	10	<0.001	o	glmer
ALAN_p	96.0 ± 21.2	33.7 ± 6.6	-5.4	10	<0.001	o	
ALAN_p.strict	65.1 ± 14.1	21.3 ± 5.4	-11.9	11	<0.001	n	
Plant richness							
ALAN	6.6 ± 1.0	5.1 ± 1.2	-1.1	11	0.271	n	glmer
ALAN_p	5.7 ± 1.0	4.6 ± 1.0	-0.9	11	0.347	n	
ALAN_p.strict	5.3 ± 1.0	4.0 ± 1.0	-1.1	11	0.265	n	
Generalism of plants							
ALAN	11.1 ± 2.0	6.2 ± 1.2	-2.6	6	0.043	n	lmer
ALAN_p	9.6 ± 1.9	5.3 ± 1.1	-2.3	6	0.061	n	
ALAN_p.strict	9.6 ± 1.7	4.9 ± 1.5	-3.7	4.3	0.018	n	
Generalism of visitors							
ALAN	1.5 ± 0.2	1.4 ± 0.2	-0.2	6	0.836	n	lmer
ALAN_p	1.5 ± 0.2	1.4 ± 0.1	-0.3	12	0.789	n	
ALAN_p.strict	1.4 ± 0.2	1.4 ± 0.1	0.1	5.2	0.891	s	
Nestedness							
ALAN	1.8 ± 0.3	0.6 ± 0.2	-3.3	12	<0.001	n	lmer
ALAN_p	1.7 ± 0.3	0.6 ± 0.2	-3.2	12	0.008	n	
ALAN_p.strict	0.9 ± 0.4	-0.1 ± 0.3	-1.8	11	0.100	n	

Results of linear mixed-effects (LME) models comparing the number of pollinator species (visitor richness), number of visits, number of plant species visited (plant richness), generalism of plants, generalism of flower visitors and z score of NODF (nestedness) of dark sites (dark, $n = 7$) and sites that were experimentally illuminated (illuminated, $n = 7$). Test statistics (test stat.): t value for lmer, z value for glmer. n, models without overdispersion or transformation of response variable; o, models that included an observation-level random factor; s, square-root transformation of the response variable.

Extended Data Table 2 | The number of flower visits to *C. oleraceum* during day and night

	Mean \pm s.e.m.		Output glmer		
	day	night	z	d.f.	P
Number of visits					
day-night	27.8 \pm 9.7	34.9 \pm 8.8	1.4	12	0.163
day-night_p	26.9 \pm 9.4	31.1 \pm 8.1	1.0	12	0.320
day-night_p.strict	26.5 \pm 9.1	26.6 \pm 7.2	0.3	12	0.742

Results of generalized linear mixed effects (GLMM) models analysing the difference between the number of flower visits to *C. oleraceum* during the day ($n=8$) compared to during the night ($n=8$). Analyses were run with the full dataset of all flower visitors (day-night) and two subsets (day-night_p and day-night_p.strict; for specifications regarding subsets, see Methods). All models were overdispersed and therefore included an observation-level random factor.

Extended Data Table 3 | Effects of artificial lighting on fruit set

	Output models					
	EST	SE	z	d.f.	P	
Number of developed fruits						
Intercept	2.10	0.186	11.23	140	<0.001	glimmer, poisson
treatLamp	0.38	0.26	1.47	140	0.140	
baggingOpen	2.31	0.219	10.53	140	<0.001	
herbivoresYes	-1.22	0.430	-2.83	140	0.005	
treatLamp:baggingOpen	-0.76	0.309	-2.46	140	0.014	
Percentage of developed fruits						
Intercept	-2.56	0.384	-6.66	141	<0.001	glimmer, binomial
treatLamp	-0.50	0.543	0.91	141	0.361	
baggingOpen	4.92	0.420	11.74	141	<0.001	
treatLamp:baggingOpen	-1.40	0.592	-2.36	141	0.018	

Results of the minimal adequate models showing the effect of artificial lighting on the number and percentage of developed fruits per flower head of *C. oleraceum*. treat, light treatment (Lamp (illuminated sites) versus Dark (dark sites)); bagging, exclusion treatment of flower visitors (Bagged (bagged flowers) versus Open (open flowers)); presence of herbivores (Yes versus No). EST, estimate; SE, standard error. Both models were overdispersed and therefore included an observation-level random factor.

Extended Data Table 4 | Effects of artificial lighting on the diversity of insects visiting *C. oleraceum*

Dataset	Mean \pm s.e.m.		Output glmer		
	dark	illuminated	z	d.f.	P
Number of species of visitors					
ALAN	20.9 \pm 4.5	12.3 \pm 2.4	-4.2	10	<0.001 n
ALAN_p	17.1 \pm 4.0	10.5 \pm 1.9	-3.6	10	<0.001 n
ALAN_p.strict	14.4 \pm 3.4	8.5 \pm 1.6	-3.5	10	<0.001 n
Number of visits					
ALAN	74.6 \pm 23.3	27.2 \pm 7.5	-4.8	9	<0.001 o
ALAN_p	69.7 \pm 22.6	25.0 \pm 7.1	-4.7	9	<0.001 o
ALAN_p.strict	43.7 \pm 13.3	13.7 \pm 3.3	-6.3	9	<0.001 n

Results of GLMM models comparing the diversity of species visiting *C. oleraceum* on dark sites (dark, $n = 7$) and experimentally illuminated sites (illuminated, $n = 7$). Analyses were run with the full dataset of all flower visitors (ALAN) and two subsets (ALAN_p and ALAN_p.strict; for specifications regarding subsets see Methods. n, models without overdispersion; o, models which included an observation-level random factor.

Extended Data Table 5 | Effect of lux intensities on fruit set

	EST	SE	z	d.f.	P
Number of developed fruits					
Intercept	4.24	0.633	6.7	45	<0.001
plant biomass	-0.02	0.036	-0.4	45	0.663
lux	-0.002	0.007	-0.3	45	0.765
Percentage of developed fruits					
Intercept	1.65	1.014	1.6	68	0.103
plant biomass	-0.07	0.052	-1.3	68	0.197
lux	-0.011	0.013	-0.8	68	0.405

Results of GLMM models analysing the effect of different lux intensities and plant dry biomass on the number and percentage of developed fruits of *C. oleraceum*. EST, estimate; SE, standard error. Both models were overdispersed and therefore included an observation-level random factor.

Extended Data Table 6 | Potential for indirect plant-mediated effects from nocturnal to diurnal flower visitors

Site	Percentage of random matrix presenting less potential for indirect interactions than the observed value								Quantile test
	1	2	3	4	5	6	7	8	<i>P</i>
day-night	0.917	0.911	0.947	0.814	0.728	0.943	0.953	0.464	0.008
day-night_p	0.863	0.937	0.964	0.923	0.751	0.919	0.954	0.345	0.008
day-night_p.strict	0.873	0.933	0.940	0.798	0.756	0.817	0.940	0.306	0.008

Results of the analyses quantifying the potential for indirect plant-mediated effects from nocturnal to diurnal flower visitors. The observed mean potential for such effects was compared to the effect for networks in which plants connect the nocturnal and diurnal sub-networks in a randomized manner. A quantile test was performed to test whether the observed value across sites was significantly higher than for randomly inter-connected networks. Analyses were run with the full dataset of all flower visitors (day-night) and the two subsets (day-night_p and day-night_p.strict).