



Artificial light at night (ALAN) disrupts timing of floral resource availability[☆]

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ABSTRACT

Artificial light at night (ALAN) is a rapidly expanding form of pollution that alters natural light regimes and threatens biodiversity. While many studies have documented its effects on animal behaviour, the consequences for plants, and the ecological services they provide, remain underexplored. We investigated how ALAN modifies the timing and availability of floral resources in wild plant communities of central European agricultural landscapes. From 2022 to 2023, we conducted a large-scale field experiment in Swiss wildflower strips, exposing sites to LED streetlights to simulate ALAN ($n = 14$) while paired controls remained dark ($n = 14$). Using phenological monitoring and time-lapse photography, we quantified both daily and seasonal changes across multiple species. At the daily scale, ALAN altered flower opening and closing patterns, delaying petal closure in a night-flowering species and advancing morning opening in a day-flowering species. At the seasonal scale, ALAN advanced seedling emergence in half of the species studied ($n = 6$) and shifted flowering schedules in 75 % ($n = 16$). In some cases, flowering onset, progression, and peak bloom occurred more than 10 days earlier, while other species showed delayed flower disappearance. These shifts change when floral resources are available in the landscape, potentially exposing reproductive stages to suboptimal abiotic conditions and disrupting synchrony with pollinators and herbivores. Such desynchronization may reduce reproductive success, alter interaction networks, and cascade to affect community composition. Our findings demonstrate that ALAN alters the temporal dynamics of plant resources at both daily and seasonal scales, potentially disrupting ecosystem stability.

1. Introduction

Over the past century, the widespread increase in artificial light at night (ALAN) has profoundly disrupted the natural light cycles that organisms have depended on for millions of years to regulate their biological rhythms (Bará and Falchi, 2023; Guarnieri, 2018; Hölker et al., 2010). Today, over three-quarters of the Earth's land area is exposed to direct ALAN emissions or skyglow, which interfere with the timing, intensity, and spectral composition of natural light (Cox and Gaston, 2023; Falchi et al., 2016; Gaston et al., 2013). Evidence of ALAN's far-reaching ecological impacts continues to accumulate, with growing concern over its effects on physiology and behaviour, leading to consequences across all levels of biodiversity, from individuals and populations to communities, species interaction, and entire ecosystems (Boyes et al., 2021; Gaston et al., 2021; Gaston and de Miguel, 2022; Knop and Dominoni,

2024). Plants, being sessile organisms that cannot avoid exposure to ALAN, are expected to be particularly vulnerable (reviewed in Bennie et al., 2016; Briggs, 2006). Yet, our understanding of its effects on plants, and the interactions they mediate, remains limited (Heinen, 2021), especially with respect to phenology. Most existing data are observational and focus on deciduous trees (Ffrench-Constant et al., 2016; Han et al., 2015; Meng et al., 2022; Škvareninová et al., 2017), with relatively few experimental studies available. Even among those, findings are inconsistent (Bennie et al., 2018) or limited to single-species models (Bennie et al., 2015; Wang et al., 2022). This knowledge gap is concerning given the essential ecological roles that plants play in supporting biodiversity and sustaining ecosystem processes (Diaz and Cabido, 1997; Lavorel, 2013).

Our limited understanding of how ALAN influences plant phenology is particularly striking given the central role of light in regulating these

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processes. Seasonal events such as flowering are largely controlled by photoperiodic pathways mediated by light-sensitive photoreceptors, including phytochromes and cryptochromes, which synchronize development with seasonal changes in daylength (Creux and Harmer, 2019; McClung, 2001; Shim et al., 2017; Webb, 2003). Based on their photoperiodic response, flowering plants are typically classified into short-day plants (SDP), which flower when nights are sufficiently long; long-day plants (LDP), which flower when nights are short; and day-neutral plants (DNP), whose flowering is unaffected by daylength and instead responds to other cues (Bennie et al., 2016). Classical flowering induction experiments have shown that these pathways can be triggered by light exposures at specific times of night (Amasino, 2010; Garner and Allard, 1920; Hayama & Coupland, 2003), and that even dim or short-duration illumination can shift or disrupt these rhythms (McClung, 2006). Germination timing, a key determinant of plant life histories (Long et al., 2015), is likewise shaped by photoperiodic cues and light–dark sensitivity. Species vary in their responses: some require light to germinate (positive photoblastism), others are inhibited by it (negative photoblastism), and some are unaffected, but in most cases these responses are mediated through phytochrome pathways (Luna and Moreno, 2010; Milberg et al., 2000; Xia et al., 2016). Beyond seasonal rhythms, short-term phenological events such as floral nyctinasty, the diel opening and closing of petals (Samarakoon and Peiris, 2005; Van Doorn, 2003; Van Doorn & Kamdee, 2014), are also regulated by circadian clocks that respond primarily to light and temperature cues (Ke et al., 2018; Muroya et al., 2021; Shim et al., 2017). These diel movements are ecologically significant because they regulate when and how pollinators access floral resources (Halket, 1931; Kwiatkowska et al., 2019; You et al., 2023), while also shielding flowers from sub-optimal abiotic conditions (e.g., cold or wet nights), and reducing damage from floral herbivores (Prokop and Fedor, 2016; Van Doorn & Kamdee, 2014). Together, these mechanisms highlight the potential for ALAN to alter phenology from daily to seasonal timescales.

Understanding the impact of ALAN on plant phenology is critical given its consequences for plant survival, reproduction, and demographic performance. At the seasonal scale, altered germination timing can influence population dynamics and community composition, as shown in desert annual plant communities (Kimball et al., 2010). In spring, earlier flowering may increase frost damage risk, reducing seed production (Augspurger, 2013; Gezon et al., 2016; Inouye, 2008), whereas delayed flowering can expose reproductive structures to drought and heat stress (Franks et al., 2007). At the diel scale, shifts in petal opening or closing may expose nectar and pollen to suboptimal environmental conditions, with potential negative effects on reproductive output (Delph et al., 1997; Plos et al., 2023; Waser and Price, 2016). Phenological changes also cascade to higher trophic levels: seasonal shifts in flowering can desynchronize interactions between nectar-producing plants and their avian consumers (Wolfe et al., 2017), disrupt co-flowering dynamics within plant communities (CaraDonna et al., 2014), and cause mismatches between migratory birds and critical food resources (McKinney et al., 2012). Insect pollinators, particularly those dependent on ephemeral flowers, are especially sensitive, with most studies reporting adverse effects for both plants and pollinators (Hegland et al., 2009; Iler et al., 2021; Kudo and Cooper, 2019; Memmott et al., 2007). By contrast, the biotic consequences of shifts in diel petal movements remain undocumented, despite plausible effects such as temporal mismatches with their primary pollinators. These knowledge gaps underscore the need for experimental approaches that assess how ALAN alters the timing of floral resource availability in natural plant communities.

In this study, we used a field experiment to test whether ALAN alters floral resource timing at both diel and seasonal scales in wild plants characteristic of central European agricultural landscape. To this end, we exposed both wild and potted individuals to ALAN and tracked key phenological traits over the growing season. Specifically, at the diel scale, we addressed the following questions: Does (1.1) short-term ALAN

exposure (i.e., plants exposed to ALAN for only three consecutive nights), and (1.2) long-term ALAN exposure (i.e., wild plants growing in the vicinity of a lamp), alter the timing of diel movements of petals (floral nyctinasty)? At the seasonal scale, we asked the two following questions: 2) Does ALAN influence the timing of seeds germination in wild plants? And 3) does ALAN affect flowering phenology in wildflower communities? At the diel scale (question 1), we hypothesized that ALAN would disrupt the floral nyctinastic movements that occur following nocturnal illumination, namely morning petal opening in day-flowering plants and petal closing in night-flowering plants. We further hypothesized that the strength and direction of plant responses would differ between short-term (question 1.1) and long-term (question 1.2) exposure: brief light exposure can trigger highly sensitive photoperiodic pathways (Hayama & Coupland, 2003), while prolonged exposure may result in physiological adjustments (Walters, 2004). At the seasonal scale, we hypothesized that ALAN would advance germination time (question 2), as the annual, small-seeded species in our study are typical positively photoblastic plants (i.e. species in which light triggers germination) a trait common among Central European spring-flowering flora (El-Keblawy, 2017; Khurana and Singh, 2001; Woolley and Stoller, 1978). For flowering phenology (question 3), we hypothesized that ALAN would advance flowering onset in wildflower communities, as extended night-time illumination can act as a long-day cue, a signal known to accelerate flowering in many Central European wild species (Hayama & Coupland, 2003; Heide, 1994; Yanovsky and Kay, 2003).

2. Material and methods

2.1. Experimental set up

Our study was conducted in the Seeland region of Switzerland (Fig. S1) in 2022 and 2023. This area is characterized by high agricultural activity, low human population density, and relatively low levels of artificial light at night (ALAN) compared to the rest of the Swiss Lowlands (21 mag/arcsec², according to <https://www.lightpollutionmap.info>). We selected wildflower strips that had never been illuminated directly, were at least 500 m from the nearest artificial light source (e.g., street lamps), and were located more than 1000 m away from major light sources (such as football fields or brightly lit industrial buildings). Study sites were usually bordered on one or two sides by low-traffic agricultural roads, and the distance to the nearest primary road was 598.9 ± 353.2 m (standard deviation, SD). Prior to the light treatment, nocturnal light intensity at these sites was measured on moonless nights using a TESTO 540 luxmeter and found to be consistently below 0.1 lx. Standardized seed mixtures consisting of 34 indigenous plant species (listed in the Swiss federal ordinance for biodiversity subsidies, Table S1) were sown in autumn by local farmers 3–5 years prior to the start of our experiments. The study site areas ranged from 2102 to 33,894 m², with a mean of 12,981 ± 7313 m² and elevations between 435 and 550 m asl (mean ± SD: 467.4 ± 39.8 m). We used a paired design (2022: 6 pairs, 2023: 8 pairs, Fig. S1), with each pair consisting of one site illuminated at night (from 15th of April to 15th of September) and a nearby dark control. This yielded 12 sites in 2022 and 16 in 2023 (tot = 28 sites). Paired sites were matched for age (i.e. paired wildflower strips were sown on the same year, when possible) and located close to each other to ensure conditions as comparable as possible in terms of species communities, climate and forest cover within a 1 km radius of the lamps (distances between paired wildflower strips: 661 to 5272 m, mean = 2333, ± 1505 m). In each ALAN-treated site (i.e. half of the site), a 6-m telescopic mast (CLARK MASTS: CSQT6–4/HP, Fig. S2C & D) was used to mount a commercial LED lamp used for streetlamps (SCHRÖDER: Ampere Midi 48 LED, color temperature: 4000 K, nominal LED flux: 6800 lm), while control sites had dummy lamps (plastic boxes) to ensure comparable conditions. To power the lamps, solar panels (SWISS VICTRON: Monocrystalline Solarpanel 175 W - 12 V) and portable batteries (ECO-FLOW: RIVER 2 Pro 768 Wh) were used. The battery status was monitored

remotely to ensure a consistent light supply, and the batteries were recharged at the research station during extended cloudy periods. Pre-programmed timers ensured that the lamps were switched on and off synchronously with the weekly average civil sunset and sunrise times for the area. Light intensity (measured 70 cm above the ground, using a TESTO 540 luxmeter) followed a negative exponential decay, starting from 48.8 ± 3.3 lx directly beneath the lamp (< 1 m) and decreasing to less than 1 lx at distances of 12 ± 1.0 m in front of the lamp and 16.5 ± 1.0 m on the sides (see Fig. S3 for a detailed map of light intensity and Fig. S4 for information on the spectral range of the lighting system). At each study site, autonomous dataloggers (TOMST: TMS4), installed 3 m in front of the telescopic pole, recorded air (10 cm above ground) and soil (5 cm below ground) temperature every fifteen minutes throughout the field seasons. The light treatment had no significant effect on the minimum, maximum, or average nocturnal air and soil temperatures within the study sites (see Figs. S5 and S6 for more details).

2.2. Movements of petals

2.2.1. Short-term ALAN exposure

To test the effects of short-term ALAN exposure (question 1.1) on timing of diel movements of petals (floral nyctinasty), we sowed seeds from *Silene noctiflora* (night-flowering, petals open at night) and *Malva moschata* (day-flowering, petals open during the day), on the 18th of April 2023 in germination trays with standardized soil in the greenhouses of the Agroscope Research Institute of Reckenholz. The trays were kept in greenhouses and watered at least twice a week. On the 23rd of May, we transferred each seedling into individual pots and moved the pots to a site in our study area without artificial light sources within a radius of 100 m ($46^{\circ} 53' 14.18''$ N $7^{\circ} 01' 07.21''$ E, UTM) and the pots were regularly watered when needed. Each week, from the 12th of July to the 1st of September, we selected an average of 18 ± 7.69 pots (mixing both species) with buds about to bloom and placed them in the study sites for three nights, but only on nights without rain (total = 146 pots, 31.8 % of which were *M. moschata*). On a weekly base, we randomly selected two pairs of study sites (i.e. two lit and two dark sites), and evenly distributed the pots among those four sites. Within each study site, half of the pots were placed together in the middle of a one of the two 'phenology plots' (see the paragraph entitled 'Phenology plot' in the 'Flowering phenology' section of the Methods) located near the lamps (P01 or P04), while the other half were placed in the middle of one of the phenology plots located farther from the lamp (P02 or P03, see Fig. S2 for more details). We mounted a camera trap (RECONYX: Hyperfire 2 professional small mammal) on a metal pole, which was inserted directly into the ground, 1.5 m in front of each group of potted plants (eight camera traps per week). Each camera trap was set to timelapse mode, capturing an image every 5 min and using an infrared flash whenever triggered. The cameras recorded the nyctinastic movements of the potted plants' inflorescences over three days and three nights.

2.2.2. Long-term ALAN exposure

Additionally, we tested the effects of long-term exposure of ALAN (question 1.2) on timing of diel movements of petals in wild plants by deploying the same camera system in front of naturally occurring *M. moschata* at our study sites. From the 25th of June to the 8th of August 2023, during 16 rain-free nights, cameras recorded an average of $6.1 (\pm 2.4)$ wild *M. moschata* per night (total = 91 individuals, growing in 13 different study sites), 55 % of which were in the illuminated sites. Cameras were set up between 3 and 5 pm and retrieved the following day before noon. The selected plants were either growing within the phenology plots or in the immediate vicinity (average distance between plants and the lamps in illuminated sites: 5.13 ± 2.4 m). Unlike the potted plants, where multiple inflorescences were monitored over three nights, only one freshly opened inflorescence per wild individual was observed for a single night using camera traps. A trained project

collaborator visually analysed all image sequences and recorded the following timepoints for each flower: (1) the start and (2) the end of petal opening, as well as (3) the start and (4) the end of the closing process. The start of opening and closing was defined as the first picture where the petals visibly moved and the flower's diameter changed. The end of these processes was marked by the frame in which the flower became motionless and its diameter remained unchanged. Finally, because the lunar cycle affects nocturnal light intensity (Bennie et al., 2016), and several physiological processes in plants appear to respond to moon variations (Sivasankar and Thimmaiah, 2021), we recorded the moon phase for each sampling night (under both short- and long-term ALAN exposure). Moon phase, defined as the proportion of the moon's surface visible during the night when plants were recorded (ranging from 1 for a full moon to 0 for a new moon), was calculated using the SUNCALC (Thieurmel and Elmarhraoui, 2017) package in R (R Core Team, 2021).

2.3. Seed germination

To test whether ALAN influence the seasonal timing of seed germination (question 2), we installed germination trays at each of the 16 sites in 2023, half of them being artificially illuminated at night, positioning their centres two meters in front of the poles supporting the lamps (or dummy lamp in the control sites). Averaged light intensity measured on illuminated germination trays (measured using a TESTO 540 luxmeter, 10 cm above the trays) was 37 ± 1.4 lx and below 0.1 lx in controls (see Fig. S3). Each tray consisted of 45 individual pots (4×5 cm, 5 cm deep), arranged in five rows of nine pots, and filled with standardized commercial soil (CAPITO: Blumenerde). We selected 22 indigenous annual plant species present locally (Table S1), sourcing the seeds from the same supplier that provides seeds for establishing the wildflower strips where experiments were conducted (FENACO Genossenschaft, UFA-Samen: <https://wildblumen.ufasamen.ch>). Seeds were sown in the germination trays on the 10th of May, with 10 seeds per species per tray, split between two pots (five seeds per pot), randomly assigned to 44 of the 45 available spots in each tray, leaving one pot empty in each germination trays. Thus, a total of 160 seeds per species were sown across the 16 germination trays, 8 of them being artificially illuminated at night. From the sowing day until the 20th of June, a camera (BRINNO: TLC200 time-lapse) with water-resistant housing was mounted horizontally 1.5 m on metal poles above each germination tray, capturing one image per hour. We visited the 16 germination trays at least three times a week to water the seedlings and to check the camera batteries. To minimize herbivory on newly emerged seedlings, the pots were placed on a 60×30 cm plastic trays, elevated on bricks inside a 75×50 cm plastic box (10 cm deep) filled with water. The boxes were partially embedded in the soil, ensuring that the pots remained only a few centimetres above ground level. This setup created a 3–4 cm wide water barrier, effectively blocking crawling herbivores, primarily slugs (the dominant herbivores in our study system) from reaching the germination trays. Additionally, the entire setup was enclosed by a 10 cm high, specially designed metal anti-slug barrier (Fig. S7A). All the time-lapse movies were reviewed by a trained project collaborator, who recorded the germination day each time a freshly emerged seedling was first observed in every species and germination tray, specifically, when a seedling appeared in the frame at $t + 60$ min but was not visible at $t + 0$ min (Fig. S7B). Additionally, since we expected that pots on the outer part of the germination tray would be more sensitive to drought due to increased wind exposure, which could slow down the germination, we also recorded whether each germination event occurred in a pot on the inner or outer part of the tray. Finally, and despite our efforts to water the 16 germination trays three times a week, the spring of 2023 was exceptionally hot and dry, resulting in relatively low germination success. To ensure robust analyses, we included only the plant species that had at least five seedlings germinate in both illuminated and non-illuminated sites. Additionally, we retained only the species that

germinated in at least three lit and three unlit sites. As a result, our final analysis was based on seedlings from six species (*Anthemis tinctoria*, *Cichorium intybus*, *Crepis capillaris*, *Hypochaeris radicata*, *Silene pratensis* and *Trifolium incarnatum*, Fig. S7C).

2.4. Flowering phenology

2.4.1. Phenology plots

To assess the effect of ALAN on the seasonal flowering phenology of wildflower communities (question 3), we set up four experimental plots at 11 of the 12 study sites in 2022 (one dark site was excluded for logistical reasons) and at all 16 sites in 2023. Plots were arranged in two rows of two in front of the lamps (hereafter referred to as 'phenology plots'), yielding a total of 108 plots, of which 51.8 % were in ALAN-treated sites. In February and March of both years, we used a rototiller to plough the plots before sowing standardized seed mixtures, which contained 22 annual indigenous plant species (listed in Table S1). All seeds for 2022 were sown on the 26th of April, while those for 2023 were sown on 20th of April. The wildflower seeds were obtained from the same supplier who provided the flower mixes for the germination experiment and for the wildflower strips where we established our plots. As the size and shape of the plots varied between 2022 and 2023, we ensured that the quantity of seeds sown was identical across all phenology plots by standardizing the seed biomass per species and per square meters to the nearest gram. In 2022, the phenology plots ($n = 48$) were one square meter (1×1 m). The centres of the two plots closest to the lamps were aligned 2.5 m in front, while the centres of the two furthest plots were 6.5 m away. The centres of the plots in the same row (either the two in front or the two behind) were spaced 5 m apart (Fig. S2A). The average light intensity measured at the centre of all illuminated plots in front of the lamps was 34.0 ± 1.3 lx, while the plots farther from the lamps had an intensity of 11.8 ± 1.9 lx (Fig. S3). In 2023, the experimental plots ($n = 64$) were larger, measuring 8 square meters (2×4 m). Their relative distance to the lamps remained similar to that in 2022 (Fig. S2B). The light intensity, averaged from measurements taken at each corner of the plots, was 29.0 ± 1.7 lx for the plots in front of the lamps and 9.26 ± 3.0 lx for those farther away (Fig. S3). From the sowing date to the 15th of September 2022 and 2023, all the plots were visited once or twice a week, with the specific weekday of each visit randomly shuffled from week to week. During each visit, project collaborators visually counted the number of floral units for all species observed within each phenology plot. We defined 'floral unit' as the smallest grouping of flowers that a pollinator interacts with; in other words, two inflorescences are considered distinct floral units if a pollinator must fly to move from one to the other.

2.4.2. Phenological parameters

To analyse flowering phenology, we first determined the start of the phenological spring for our study area in each year. This was inspired by the spring index developed by MeteoSwiss (<http://www.meteoswiss.admin.ch/home/climate/climate-change-in-switzerland/vegetation-development/spring-index.html>). This index represents the timing of Swiss spring vegetation development relative to the 1981–2010 average and, based on phenological observations from nearly 80 long-term monitoring stations, it thus serves as a reliable indicator of vegetation trends across Switzerland. To estimate the first day of phenological spring at our study sites in 2022 and 2023, we focused on four plant species from the spring index that are relevant to our study system (wildflower strips in the Seeland region): coltsfoot (*Tussilago farfara*), wood anemone (*Anemone nemorosa*), common dandelion (*Taraxacum officinale*), and cuckooflower (*Cardamine pratensis*). We defined the start of phenological spring (in 2022 and 2023) as the average date when 50 % of individuals across 15 nearby monitored populations of these four species were in bloom (see Table S2). These 15 stations were part of the spring phenology monitoring described above and were located in the same cantons where our study was conducted (Vaud, Bern, and

Fribourg), at elevations between 300 and 600 m asl (see Fig. S8 for details). Accordingly, we identified the first day of the phenological spring in 2022 as the 30th of March, and in 2023 as the 2nd of April. Using this reference date, we calculated four phenological parameters for each plant species and for each plot based on (bi-) weekly counts of floral units: (1) the number of days from the start of phenological spring to the first observation of an open inflorescence (FIRST), (2) the day when one-quarter of the maximum number of inflorescences was reached (QUARTER), (3) the day when the maximum number of inflorescences was observed (PEAK), and (4) the day of the last observed inflorescence (ULTIMATE). Only plant species observed in at least ten different lit and ten different unlit phenology plots were considered for further analysis, resulting in a final list of 16 plant species, 10 of which (62.5 %) were from the list of plants we sowed in April 2022 and 2023.

2.5. Statistical analyses

2.5.1. Movements of petals

To assess the effect of ALAN on the timing of diel movements of petals in *S. noctiflora* and *M. moschata* (question 1.1 & 1.2), we fitted Linear Mixed-effects Models (LMM) using the *lmer* function from the *LME4* package (Bates et al., 2015) in R. As the season progressed, sunset occurred earlier while sunrise was delayed. Therefore, we used the difference between the observed timing of floral movements (petal closure initiation, full closure, reopening initiation, and full opening) and the local times of civil sunset and sunrise as the response variable. This variable was approximately normally distributed, justifying the use of a Gaussian model. Light treatment (two levels: DARK and LIT), exposure duration (two levels: SHORT and LONG; included only for *M. moschata*), and moon phase (ranging from 1 for full moon to 0 for new moon), as well as their interactions, were included as fixed effects. Sampling date and study site were included as random effects. Model fit was assessed using diagnostic plots and residual checks, and this procedure was applied consistently across all subsequent statistical analyses. The model structures were: *S. noctiflora*: $\text{TIME_DIFFERENCE} \sim \text{LIGHT} * \text{MOON_PHASE} + (1|\text{DATE}) + (1|\text{SITE})$; *M. moschata*: $\text{TIME_DIFFERENCE} \sim \text{LIGHT} * \text{EXPOSURE} * \text{MOON_PHASE} + (1|\text{DATE}) + (1|\text{SITE})$.

2.5.2. Seed germination

To investigate the effect of ALAN on the timing of seed germination (question 2), we conducted two complementary analyses. First, we modelled the effects of ALAN on the probability of germination using a Generalized Linear Mixed Model (GLMM), using the *glmer* function from the *LME4* package, with a binomial distribution: $\text{CBIND}(\text{GERMINATED}, \text{UNGERMINATED}) \sim \text{LIGHT} * \text{SPECIES} * \text{DAYS_AFTER_SOWING} + (1|\text{SITE}) + (1|\text{SPECIES}:\text{SITE})$, $\text{FAMILY} = \text{BINOMIAL}$. Daily counts of germinated and ungerminated seedlings per species and germination tray were combined using the *CBIND()* function, with treatment (two levels: DARK and LIT), species (six levels), time after sowing (ranging from 1 to 40 days), and their interactions as predictors. Second, we analysed the effects of ALAN on germination time using a LMM with a Gaussian distribution: $\text{DAYS_TO_GERMINATION} \sim \text{LIGHT} * \text{SPECIES} * \text{LOCATION_WITHIN_TRAY} + (1|\text{SITE}) + (1|\text{SPECIES}:\text{SITE})$, where the response variable was the number of days from sowing to germination. In this second model, we included the location within the germination tray of each germination event (two levels: INNER and OUTER) as a fixed effect, along with its interactions with treatment and species. To account for the hierarchical structure of the data, where responses are nested within study sites and further within species at each site, we included study site and the interaction between plant species and study site as random effects in both models.

2.5.3. Flowering phenology

To examine the effects of ALAN on the flowering phenology of wildflowers (question 3), we analysed four parameters that describe flowering seasonality in our plots: FIRST and LAST, which represent the number of days from phenological spring to the first and last observed

flowering individual of a species in a plot, respectively, and PEAK and QUARTER, which indicate the number of days from phenological spring to the day with the highest recorded number of inflorescences and the day when one quarter of this peak was observed, respectively. Each phenological parameter was analysed separately using a LMM with a Gaussian error distribution: $\text{PHENOLOGY_PARAMETER} \sim (\text{LIGHT} * \text{DISTANCE_TO_LAMP}) + (\text{LIGHT} * \text{SPECIES}) + \text{YEAR} + (1|\text{SITE}) + (1|\text{SPECIES}:\text{SITE})$. Fixed effects included light treatment (two levels: DARK and LIT), distance to the light source (two levels: CLOSE, ~30 lx; FAR, ~10 lx within illuminated sites), their interaction, the plant species (16 levels), as well as interactions among light treatment and species. Sampling year was also included as a fixed effect. As for previous GLMM we used to investigate the effects of ALAN on germination timing, we included study site and the interaction between plant species and study site as random effects.

3. Results

3.1. Movements of petals

3.1.1. Nocturnal-flowering species

In *S. noctiflora* ($n = 152$ recorded petal closings, 125 recorded petal openings, Table S3), ALAN tended to delay the onset of petal closure in the morning ($p = 0.055$, predicted effect (β) = +80 min, 95 % confidence interval (CI) = -2.6 to 162.9). ALAN had no significant effect on the timing of full closure (Fig. 1B), nor did it significantly influence either the onset of floral opening or the timing of full opening in the evening (Fig. 1A). Additionally, we found no effect of lunar cycle, either as a

main effect or in interaction with ALAN, on any aspect of floral nyctinastic movement (Table S4).

3.1.2. Day-flowering species

ALAN significantly advanced the onset of morning floral opening in *M. moschata*, regardless of exposure duration ($n = 176$ recorded petal openings, of which 13 never fully opened; Table S3). On average, illuminated flowers opened 147 min earlier than controls ($p < 0.001$, $\beta = -147$ min, CI: -221.4 to -72.0). ALAN also delayed the timing of full petal closure in the morning, but this effect was limited to short-term exposure ($p = 0.041$, $\beta = +74$ min, CI: 2.7 to 145.0; Fig. 2A). In the evening, ALAN tended to advance the onset of floral closing, although this effect was marginal and detected only under short-term exposure ($n = 176$ recorded petal closings, 4 of which never fully closed; $p = 0.088$, $\beta = -87$ min, CI: -188.3 to 13.8; Fig. 2B). Independently of ALAN, petals of potted plants (short-term treatment) closed significantly later than those of wild plants ($p = 0.002$, $\beta = +122$ min, CI: 44.8 to 199.1). Notably, the ALAN-induced shift in floral opening was modulated by the lunar cycle. We found a positive relationship between the magnitude of ALAN's effect and the proportion of the visible moon ($p = 0.038$). In other words, flowers exposed to ALAN opened earlier during new moon phases compared to controls, but the effect was weaker during full moon phases. This lunar modulation was most pronounced in wild plants under long-term exposure, as indicated by a significant three-way interaction between light treatment, exposure duration, and moon phase ($p = 0.02$; Table S5).

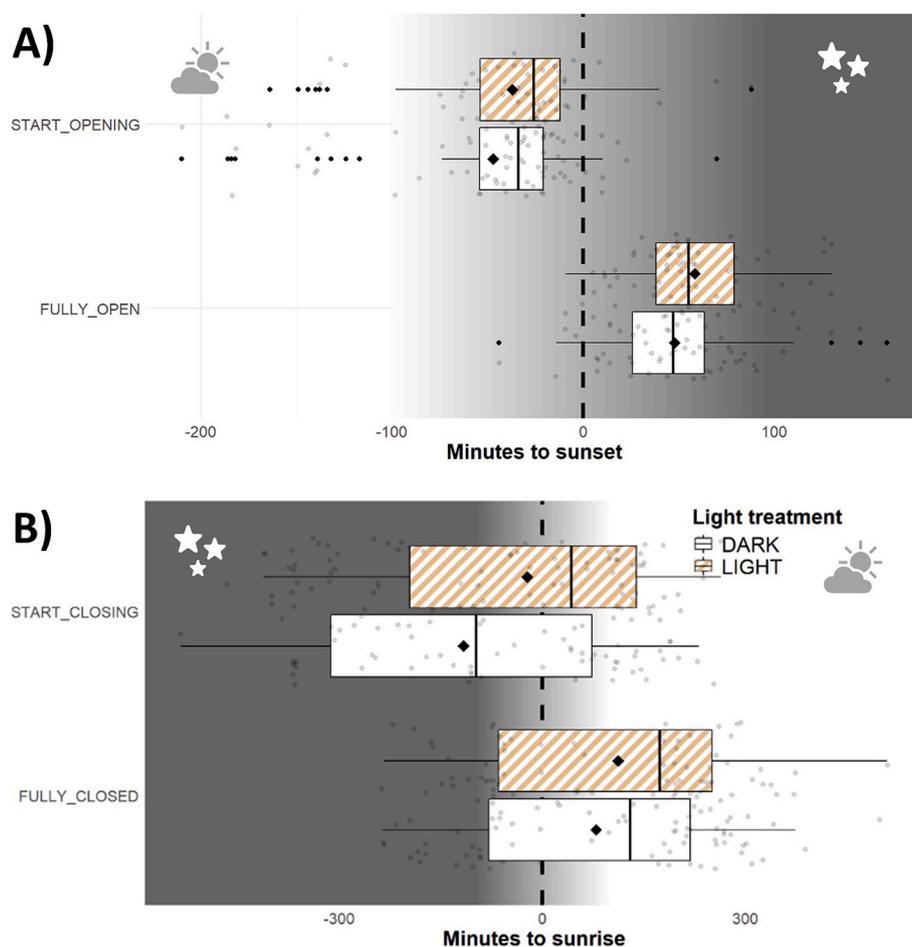


Fig. 1. Effect of ALAN on diel movements of petals in the night-flowering *Silene noctiflora moschata*. (A) Timepoints when flowers began closing and were fully closed in the morning. (B) Timepoints when flowers began opening and were fully open in the evening. For each group, the central line represents the median, diamonds indicate the mean, boxes show the interquartile range, and whiskers extend to 1.5 times the interquartile range.

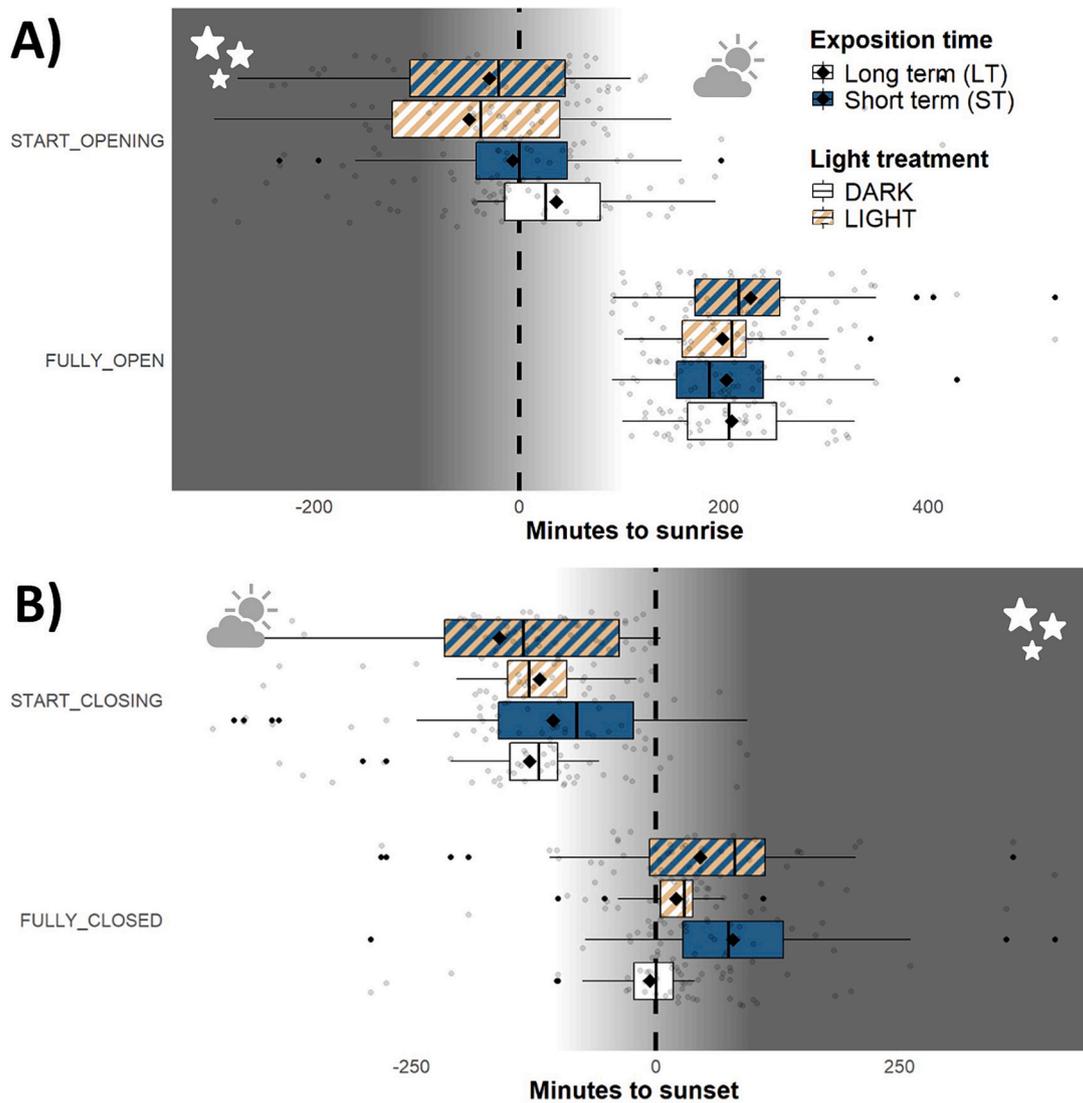


Fig. 2. Effect of ALAN on diel movement of petals in the day-flowering *Malva moschata*. (A) Time when flowers began opening and were fully open in the morning. (B) Time when flowers began closing and were fully closed in the evening. For each group, the central line represents the median, diamonds indicate the mean, boxes show the interquartile range, and whiskers extend to 1.5 times the interquartile range.

3.2. Seeds germination

3.2.1. Probability of germination

Of the 960 sown seeds from six different species, 123 (12.8 %) successfully germinated during the study period (Fig. S7C). ALAN treatment had no significant effect on the probability of germination ($p = 0.30$; Table S6), and none of the interactions involving light treatment reached statistical significance (Fig. S9).

3.2.2. Germination timing

The effect of ALAN on germination timing differed among species ($p = 0.023$), with significant advances detected in *Cichorium intybus* ($\beta = -9.6$ days), *Trifolium incarnatum* (-15 days), and *Silene pratensis* (-18 days), as none of their CI's overlapped with zero (Fig. 2). Seedling location within the trays (inner vs. outer section) had no effect on germination date or its interactions with other variables (Table S7).

3.3. Flowering phenology

ALAN caused significant species-specific shifts in at least one of the four considered flowering stages (FIRST, QUARTER, PEAK, ULTIMATE)

in 12 out of 16 investigated species (75 %). Among them, nine species exhibited advanced phenological stages, two showed delays, and one showed mixed effects, with earlier first flowers but delayed last flowers. Specifically, ALAN significantly advanced the onset of the first inflorescences (FIRST) in three species: *Veronica persica*, *Matricaria chamomilla*, and *Trifolium pratense* (Fig. 4A). It also accelerated the timing at which a quarter of the maximum number of inflorescences was recorded (QUARTER) in five species: *Trifolium pratense*, *Echium vulgare*, *Trifolium incarnatum*, and *Silene pratensis*, as indicated by confidence intervals that did not overlap with zero (Fig. 4B). Peak flowering occurred significantly earlier in the season for five species (*Centaurea cyanus*, *Sinapis arvensis*, *Daucus carota*, *Centaurea jacea*, and *Trifolium incarnatum*) when exposed to ALAN (Fig. 4C). Finally, ALAN influenced the timing of the last observed inflorescences (ULTIMATE) in varying ways. In three species (*Centaurea cyanus*, *Daucus carota*, and *Trifolium incarnatum*), the last flowers disappeared earlier in the season, while in three others (*Sinapis arvensis*, *Centaurea jacea*, and *Veronica persica*), they persisted longer (Fig. 4D). We found an effect of the study year, with both first ($p = 0.002$, $\beta = -8.7$ days, CI = -14 to -2.9) and last ($p < 0.001$, $\beta = -18$ days, CI = -27 to -8) flowers appearing earlier in the season in 2023. Finally, neither the distance from the lamp (CLOSE, ~ 30 lx; FAR, ~ 10 lx

within illuminated sites) nor its interaction with the light treatment (DARK and LIT) affected any of the four phenological stages investigated (Table S8).

4. Discussion

Our study demonstrates that ALAN has the potential to disrupt timing of floral resource availability in wild flower communities across multiple temporal scales. It affected the diel movements of petals (floral nyctinasty) of both focal species, advanced the germination time of half of the investigated species and modified the seasonal flowering time in 75 % of the species. These results demonstrate that ALAN can shift plant phenology in ways that may expose floral resources to suboptimal abiotic conditions, thereby highlighting its capacity to disrupt flower-visitor interactions in complex and previously underappreciated ways.

4.1. Movements of petals

On a diel scale, ALAN significantly altered the timing of opening and closing of petals in both a night-flowering species (*S. noctiflora*) and a day-flowering species (*M. moschata*). As hypothesized, the most pronounced shifts occurred after nighttime ALAN exposure, specifically, a delay in morning petal closure in *S. noctiflora* (Fig. 1A) and an advance in opening in *M. moschata* (Fig. 2A). In species that close their petals at night, nyctinasty is thought to protect flowers from suboptimal abiotic conditions (e.g., cold or wet nights), conserve resources such as energy and floral scent for key pollinators (Prokop et al., 2019; Van Doorn & Kamdee, 2014), and defend against floral herbivores (Prokop and Fedor, 2016). Although the diurnal closing of petals has received less attention, it is reasonable to assume that similar mechanisms underlie both nocturnal and diurnal petal movements. Previous research has shown that exposing floral resources to atypical environmental conditions (Delph et al., 1997; Plos et al., 2023; Waser and Price, 2016) or increased florivory (Cardel and Koptur, 2010; Carper et al., 2016; Haas and Lortie, 2020) can negatively impact plant reproductive success. Thus, the ALAN-induced shifts observed here, i.e. an 80 min delay in petal closure in *S. noctiflora* and an 147 min advance in opening in *M. moschata* (Table S4), may have important consequences for reproductive outcomes, even though pollination and seed set were not directly measured in this study. Interestingly, slugs were the dominant herbivores in our study system and were largely active at night (Grognez et al., 2025). Therefore, it is likely that some illuminated *M. moschata* flowers opened prematurely while dominant herbivores were still active, potentially increasing damage to the inflorescences and ultimately reducing visitation. Alternatively, prolonged access to floral resources due to altered nyctinasty might increase opportunities for non-targeted pollination (such as early diurnal visitors to *S. noctiflora* or late nocturnal visitors to *M. moschata*). Such effects could even be beneficial: in other *Silene* species, diurnal visitors can partly compensate for reduced nocturnal pollination (Prieto-Benítez et al., 2016), and in *Silene latifolia*, nocturnal and diurnal pollinators act complementary, with flowers receiving visits from both achieve the highest pollination success (Macgregor et al., 2019). In summary, ALAN-induced shifts in diel movements of petals may expose floral resources to abiotic conditions they are not adapted to, but also lead to temporal mismatches in interactions with a range of organisms, including pollinators, herbivores, and seed dispersers, which could compromise reproductive success.

4.2. Lunar modulation of ALAN effects on petal movements

Importantly, we found that the effect of ALAN on morning floral opening was modulated by the lunar cycle, with natural moonlight intensity ranging from approximately 0.01 lx during new moons to 1 lx during full moons (Bennie et al., 2016). ALAN-induced advances in petal opening were more pronounced during new moon phases and diminished during full moon phases. This pattern suggests that in the absence

of natural moonlight, such as during new moon phases, plants may be more sensitive to artificial light, potentially because ALAN becomes the dominant nocturnal light cue. In contrast, during full moon phases, the higher background illumination may partially override or mask the effects of ALAN, reducing its relative impact on floral rhythms. Consistent with this, full-moon illumination has been shown to trigger substantial transcriptional changes in core circadian clock genes in *Coffea arabica* (Breitler et al., 2020), demonstrating that plants can physiologically perceive natural variation in moonlight. The fact that this lunar-mediated modulation was most evident in wild plants, and barely detectable in those exposed to ALAN for only three nights, suggest a potential adaptive response to prolonged ALAN exposure, although little is known about how nocturnal lighting affects plant perception of lunar cues. Further research is therefore needed to clarify these mechanisms and how ALAN interacts with natural nocturnal light variability.

4.3. Seed germination

At the seasonal scale, our study shows that ALAN can also influence early life-history stages, notably the timing of seed germination. While ALAN did not affect overall germination probability during the study period, it caused significantly earlier germination in half of the species studied. For instance, *C. intybus*, *T. incarnatum*, and *S. pratensis* germinated 9 to 18 days earlier under ALAN (Fig. 3). These results suggest that ALAN can act as a germination cue, supporting the hypothesis that these three species are positively photoblastic, a trait common among Central European spring-flowering flora (El-Keblawy, 2017; Khurana and Singh, 2001; Woolley and Stoller, 1978). This is especially plausible for *S. pratensis*, as previous research has shown that light plays an important role in triggering germination in related species (Mondoni et al., 2009). Such ALAN-induced advances in germination timing could expose seedlings to unfavourable abiotic conditions, such as late frosts or cold soils, potentially reducing survival rates and altering species' demographic trajectories and competitive interactions (D'Aguillo and Donohue, 2023; Vázquez-Ramírez, 2025). The non-significant effect of ALAN on the other three species may indicate that other factors known to influence germination (e.g. temperature, humidity; Long et al., 2015) played a more dominant role in triggering germination. We conclude that ALAN can advance germination timing in light-sensitive species, while its limited effect on others highlights the importance of species-specific traits and environmental cues in mediating seed germination responses to nocturnal light exposure.

4.4. Flowering phenology

In addition to its effects on seed germination, ALAN significantly influenced the seasonal flowering phenology of wild plant communities, consistent with our hypothesis that night-time illumination can act as a long-day cue to accelerate flowering. Notable shifts, exceeding one week in at least one of the tested phenological parameters, were detected in 75 % of the investigated species. As hypothesized, most changes involved earlier flowering, including advanced first bloom (e.g., *V. persica*, *M. chamomilla*, Fig. 4A), accelerated progression through early bloom stages (e.g., *T. pratense*, *S. pratensis*, Fig. 4B), and earlier peak flowering (e.g., *L. vulgare*, *T. incarnatum*, *Epilobium* sp. Fig. 4C). These species-specific advances may partly reflect underlying advances in germination timing, as developmental trajectories are often tightly linked to initial emergence (Donohue, 2002). However, direct evidence connecting earlier germination to accelerated phenology at the species level remains limited. Due to low germination success, only two species (*T. incarnatum* and *S. pratensis*) were included in both the germination experiment and the wildflower communities. Notably, both exhibited earlier germination (Fig. 3) and advanced flowering phases (Fig. 4C), suggesting a potential link between early emergence and subsequent phenological development under ALAN. However, the effects of ALAN were clearly species-specific and varied across phenological stages:

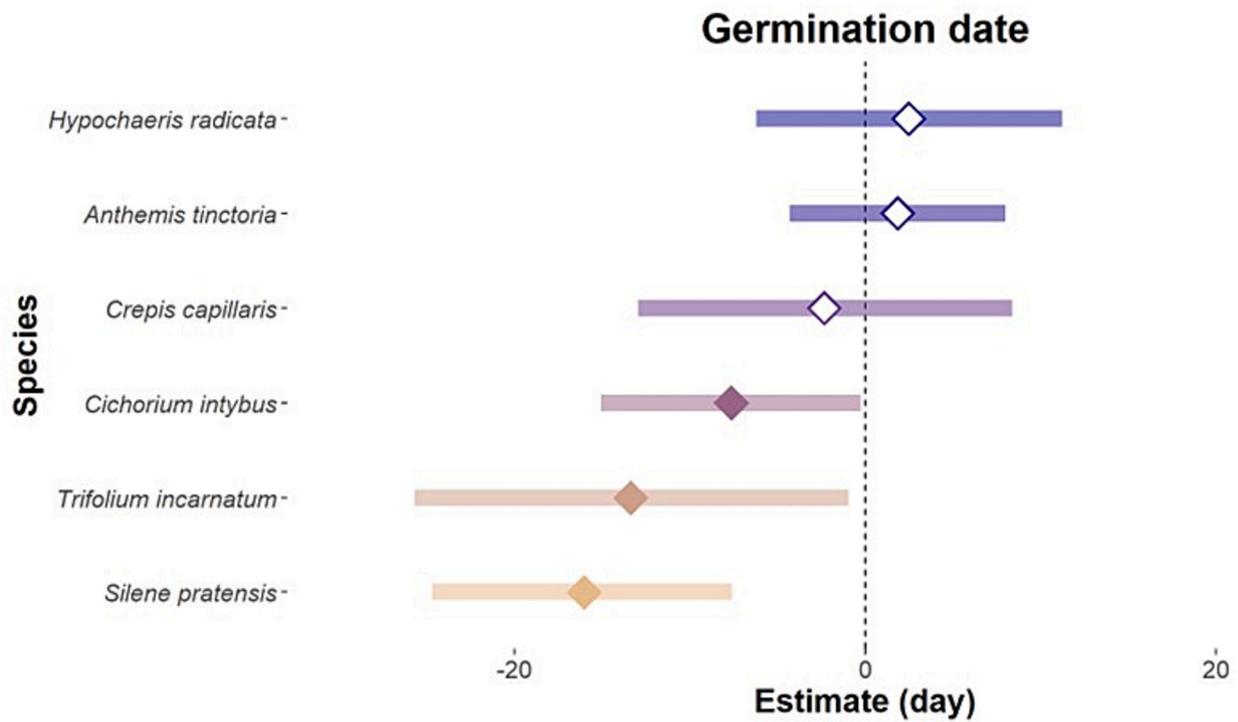


Fig. 3. Effect of ALAN on seed germination in six species. Species-specific estimated effects (median \pm 95 % confidence interval) of the ALAN treatment on the germination timing of emerged seedlings from 6 different species ($n = 248$). Filled diamond (median) indicates that the CI do not overlap with the zeroes. The colour gradient illustrates the strength and direction of the ALAN effect on phenology, ranging from yellow (phenological advancement) to blue (phenological delay). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

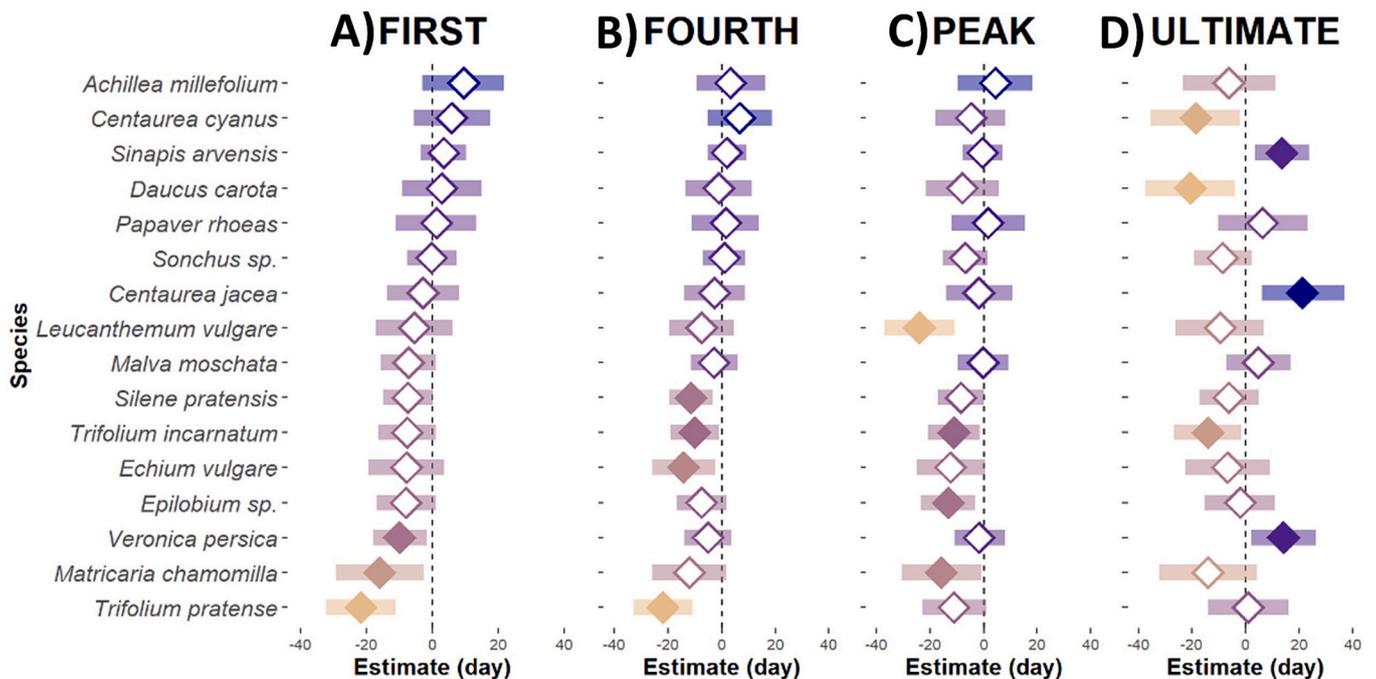


Fig. 4. Effect of ALAN on seasonal flowering phenology in 16 wild plant species. Species-specific estimated effects (median \pm 95 % confidence interval) of the light treatment on (A) when a species was observed for the first time in a plot (FIRST), (B) when one quarter of the maximum number of inflorescences was observed (QUARTER), (C) when the maximum number of inflorescences was observed (PEAK), (D) when the last inflorescence was observed (ULTIMATE). Filled diamond (median) indicates that the CI do not overlap with the zeroes. The colour gradient illustrates the strength and direction of the ALAN effect on phenology, ranging from yellow (phenological advancement) to blue (phenological delay). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

while many species showed advanced timings, others exhibited delayed disappearance of flowers (e.g., *V. persica*, *S. arvensis*, *C. jacea*, Fig. 4D). This pattern is consistent with a review of biological impacts of ALAN, which reported both positive and negative phenological responses across taxa, with no overall directional shift (Sanders, 2021). These asynchronous and heterogeneous shifts suggest that ALAN may disrupt the temporal structure of floral resource availability within communities. Such changes can increase the risk of phenological mismatches, defined as temporal disconnects between flowering plants and their visitors (Maglianesi et al., 2020), potentially impairing mainly mutualistic interactions and reducing plant reproductive success, particularly for early-flowering species or ecological specialists (Gezon et al., 2016; Hegland et al., 2009; Kudo and Cooper, 2019; Memmott et al., 2007; Robbirt et al., 2014). Yet, despite these concerns, ALAN-mediated temporal mismatches between plants and their floral visitors have been rarely documented (Seymour et al., 2023). Moreover, empirical evidence demonstrating whether such shifts under ALAN translate into altered reproductive outcomes in wild plants is still lacking. Beyond mismatches, shifts in flowering duration and overlap could also alter competition for pollinators and exposure to antagonists, with community-level consequences. While some species may adjust by forming new interactions (Burkle et al., 2013; CaraDonna et al., 2017; Forrest, 2015), others could face reduced fitness due to less effective pollination (Rafferty and Ives, 2012) or increased exposure to herbivores (Liu et al., 2011; Wilson and Thomson, 1991) and seed predators active at different times. Taken together, these findings support the idea that ALAN can act as a long-day signal, reshaping seasonal flowering schedules in wild plant species. It underscores the urgent need for studies examining how ALAN-driven shifts in phenology cascade through ecosystems, affecting plant reproductive success, altering population trajectories, and disrupting temporal coordination with pollinators, herbivores, and other mutualists or antagonists.

4.5. Short-term and low-intensity effects of ALAN

Our study demonstrates that the effects of ALAN can manifest even over short timescales and at low light intensities. By altering natural nighttime light environments, ALAN directly disrupts plant circadian rhythms, which are tightly synchronized with light cues (Creux and Harmer, 2019; McClung, 2001; Webb, 2003). These rhythms regulate key processes such as seasonal flowering phenology (Hayama & Coupland, 2003; Johansson and Staiger, 2015; Shim et al., 2017) and diel floral nyctinasty (Ke et al., 2018; Muroya et al., 2021; Shim et al., 2017) both of which play essential roles in shaping the timing and availability of floral resources. Notably, even short-term ALAN exposure (i.e. three nights) induced detectable shifts in petal movements during the morning (Fig. 2A), highlighting the sensitivity of these circadian-regulated behaviours. Moreover, earlier evening petal closure was observed in *M. moschata*, only under short-term ALAN exposure, a response absent in individuals growing under long-term illumination near street lamps (Fig. 2B). This contrast suggests that prolonged exposure may lead to physiological acclimation, consistent with our prediction that long-term ALAN could trigger compensatory adjustments (Walters, 2004), although direct evidence is lacking and further research is needed to clarify the underlying mechanisms. Finally, we found no significant effect of distance from the lamps on phenological shifts (Table S8), indicating that even low light intensities, around 10 lx, in plots located farther from the lamps, were sufficient to alter plant phenology. These changes were comparable to those observed under higher light intensities (~30 lx) in plots closer to the lamps. This highlights the capacity of ALAN to influence plant flowering phenology even at lower intensities (e.g. roadsides or pedestrian pathways; Bennie et al., 2016) and over short timescales, emphasizing the need for further research to better understand the spatial extent and ecological consequences of these effects. These results reinforce the importance of considering both light intensity and duration when evaluating ALAN impacts, particularly

in contexts where conservation efforts seek to maintain resilient plant–pollinator networks, including wildflower strips that provide critical biodiversity support in agricultural landscapes (Feltham et al., 2015; Haaland et al., 2011).

5. Conclusion

ALAN is rapidly reshaping nocturnal environments worldwide (Bará and Falchi, 2023; Guarnieri, 2018; Hölker et al., 2010), with growing recognition of its potential to disrupt ecological processes across multiple levels of biological organization (Boyes et al., 2021; Gaston et al., 2021; Gaston and de Miguel, 2022; Knop and Dominoni, 2024). Our findings reveal that ALAN alters not only flowering phenology on a seasonal scale, but also diel movements of petal in wild plant communities. These changes were species-specific and asynchronous across phenological stages, which could suggest that ALAN might disrupt the temporal architecture of floral resource availability. While the reproductive consequences of such shifts remain to be fully understood, they raise concerns about potential mismatches with pollinators and other floral visitors. Furthermore, ALAN-induced alterations to floral nyctinasty could modify the timing and visibility of floral rewards, potentially exposing flowers to suboptimal abiotic conditions, increasing their vulnerability to herbivores, or shifting the composition of their pollinator assemblages. Wildflowers are keystone components of terrestrial ecosystems, structuring plant–pollinator networks and supporting biodiversity through the provision of floral resources (Grass et al., 2016; Sidhu and Joshi, 2016). The present study demonstrates that ALAN has the capacity to reshape these dynamics in subtle yet consequential ways. As artificial nocturnal lighting continues to alter natural phenologies, understanding the long-term ecological consequences of ALAN-driven changes in floral availability, especially their effects on plant fitness, species interactions, and ecosystem stability, remains a key research frontier and an important consideration for conservation planning in human-modified landscapes.

CRedit authorship contribution statement

Vincent Groguz: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Katja Gisler:** Writing – review & editing, Investigation, Formal analysis. **Eva Knop:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111650>.

Data availability

All data used in this project are available on Mendeley (<https://data>).

mendeley.com/preview/xjmn5jhxyn?a=53038d3f-94ea-4ed6-85d5-2f727aec6f61) with the reserved DOI: 10.17632/xjmn5jhxyn.2

References

- Amasino, R., 2010. Seasonal and developmental timing of flowering. *Plant J.* 61 (6), 1001–1013. <https://doi.org/10.1111/j.1365-313X.2010.04148.x>.
- Augsburger, C.K., 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology* 94 (1), 41–50. <https://doi.org/10.1890/12-0200.1>.
- Bará, S., Falchi, F., 2023. Artificial light at night: a global disruptor of the night-time environment. *Philos. Trans. R. Soc. B Biol. Sci.* 378 (1892), 20220352. <https://doi.org/10.1098/rstb.2022.0352>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- 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. *Philos. Trans. R. Soc. B Biol. Sci.* 370 (1667), 20140131. <https://doi.org/10.1098/rstb.2014.0131>.
- Bennie, J., Davies, T.W., Cruse, D., Gaston, K.J., 2016. Ecological effects of artificial light at night on wild plants. *J. Ecol.* 104 (3), 611–620. <https://doi.org/10.1111/1365-2745.12551>.
- Bennie, J., Davies, T.W., Cruse, D., Bell, F., Gaston, K.J., 2018. Artificial light at night alters grassland vegetation species composition and phenology. *J. Appl. Ecol.* 55 (1), 442–450. <https://doi.org/10.1111/1365-2664.12927>.
- Boyes, D.H., Evans, D.M., Fox, R., Parsons, M.S., Pocock, M.J.O., 2021. Street lighting has detrimental impacts on local insect populations. *Sci. Adv.* 7 (35), eabi8322. <https://doi.org/10.1126/sciadv.abi8322>.
- Breitler, J.-C., Djerrab, D., Leran, S., Toniutti, L., Guittin, C., Severac, D., Pratloug, M., Dereeper, A., Etienne, H., Bertrand, B., 2020. Full moonlight-induced circadian clock entrainment in *Coffea arabica*. *BMC Plant Biol.* 20 (1), 24. <https://doi.org/10.1186/s12870-020-2238-4>.
- Briggs, W.R., 2006. Physiology of plant responses to artificial lighting. In: Rich, C., Longcore, T. (Eds.), *Ecological Consequences of Artificial Night Lighting*. Island Press, pp. 389–412.
- Burkle, L.A., Marlin, J.C., Knight, T.M., 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* 339 (6127), 1611–1615. <https://doi.org/10.1126/science.1232728>.
- CaraDonna, P.J., Iler, A.M., Inouye, D.W., 2014. Shifts in flowering phenology reshape a subalpine plant community. *Proc. Natl. Acad. Sci.* 111 (13), 4916–4921. <https://doi.org/10.1073/pnas.1323073111>.
- CaraDonna, P.J., Petry, W.K., Brennan, R.M., Cunningham, J.L., Bronstein, J.L., Waser, N.M., Sanders, N.J., 2017. Interaction rewiring and the rapid turnover of plant-pollinator networks. *Ecol. Lett.* 20 (3), 385–394. <https://doi.org/10.1111/ele.12740>.
- Cardel, Y.J., Koptur, S., 2010. Effects of florivory on the pollination of flowers: an experimental field study with a perennial plant. *Int. J. Plant Sci.* 171 (3), 283–292. <https://doi.org/10.1086/650154>.
- Carper, A.L., Adler, L.S., Irwin, R.E., 2016. Effects of florivory on plant-pollinator interactions: implications for male and female components of plant reproduction. *Am. J. Bot.* 103 (6), 1061–1070. <https://doi.org/10.3732/ajb.1600144>.
- Cox, D.T.C., Gaston, K.J., 2023. Global erosion of terrestrial environmental space by artificial light at night. *Sci. Total Environ.* 904, 166701. <https://doi.org/10.1016/j.scitotenv.2023.166701>.
- Creux, N., Harmer, S., 2019. Circadian rhythms in plants. *Cold Spring Harb. Perspect. Biol.* 11 (9), a034611. <https://doi.org/10.1101/cshperspect.a034611>.
- D'Aguiulo, M., Donohue, K., 2023. Changes in phenology can alter patterns of natural selection: the joint evolution of germination time and postgermination traits. *New Phytol.* 238 (1), 405–421. <https://doi.org/10.1111/nph.18711>.
- Delph, L.F., Johansson, M.H., Stephenson, A.G., 1997. How environmental factors affect pollen performance: ecological and evolutionary perspectives. *Ecology* 78 (6), 1632–1639. [https://doi.org/10.1890/0012-9658\(1997\)078\[1632:HEFAPP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1997)078[1632:HEFAPP]2.0.CO;2).
- Diaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8 (4), 463–474. <https://doi.org/10.2307/3237198>.
- Donohue, K., 2002. Germination timing influences natural selection on life history characters in *Arabidopsis thaliana*. *Ecology* 83 (4), 1006–1016. [https://doi.org/10.1890/0012-9658\(2002\)083\[1006:GTINSO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1006:GTINSO]2.0.CO;2).
- El-Keblawy, A., 2017. Germination response to light and temperature in eight annual grasses from disturbed and natural habitats of an arid Arabian desert. *J. Arid Environ.* 147, 17–24. <https://doi.org/10.1016/j.jaridenv.2017.08.002>.
- 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. *Sci. Adv.* 2 (6), e1600377. <https://doi.org/10.1126/sciadv.1600377>.
- Feltham, H., Park, K., Minderman, J., Goulson, D., 2015. Experimental evidence that wildflower strips increase pollinator visits to crops. *Ecol. Evol.* 5 (16), 3523–3530. <https://doi.org/10.1002/ece3.1444>.
- French-Constant, R.H., Somers-Yeates, R., Bennie, J., Economou, T., Hodgson, D., Spalding, A., McGregor, P.K., 2016. Light pollution is associated with earlier tree budburst across the United Kingdom. *Proc. R. Soc. B Biol. Sci.* 283 (1833), 20160813. <https://doi.org/10.1098/rspb.2016.0813>.
- Forrest, J.R.K., 2015. Plant-pollinator interactions and phenological change: what can we learn about climate impacts from experiments and observations? *Oikos* 124 (1), 4–13. <https://doi.org/10.1111/oik.01386>.
- Franks, S.J., Sim, S., Weis, A.E., 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. Natl. Acad. Sci.* 104 (4), 1278–1282. <https://doi.org/10.1073/pnas.0608379104>.
- Garner, W.W., Allard, H.A., 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *Mon. Weather Rev.* 48 (7), 415. [https://doi.org/10.1175/1520-0493\(1920\)48<415b:EOTRLO>2.0.CO;2](https://doi.org/10.1175/1520-0493(1920)48<415b:EOTRLO>2.0.CO;2).
- Gaston, K.J., de Miguel, A.S., 2022. Environmental impacts of artificial light at night. *Annu. Rev. Environ. Resour.* 47 (2022), 373–398. <https://doi.org/10.1146/annurev-environ-112420-014438>.
- Gaston, K.J., Bennie, J., Davies, T.W., Hopkins, J., 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. *Biol. Rev.* 88 (4), 912–927. <https://doi.org/10.1111/bvr.12036>.
- Gaston, K.J., Ackermann, S., Bennie, J., Cox, D.T.C., Phillips, B.B., Sánchez de Miguel, A., Sanders, D., 2021. Pervasiveness of biological impacts of artificial light at night. *Integr. Comp. Biol.* 61 (3), 1098–1110. <https://doi.org/10.1093/icb/ibab145>.
- Gezon, Z.J., Inouye, D.W., Irwin, R.E., 2016. Phenological change in a spring ephemeral: implications for pollination and plant reproduction. *Glob. Chang. Biol.* 22 (5), 1779–1793. <https://doi.org/10.1111/gcb.13209>.
- Grass, I., Albrecht, J., Jauker, F., Diekötter, T., Warzecha, D., Wolters, V., Farwig, N., 2016. Much more than bees—wildflower plantings support highly diverse flower-visitor communities from complex to structurally simple agricultural landscapes. *Agric. Ecosyst. Environ.* 225, 45–53. <https://doi.org/10.1016/j.agee.2016.04.001>.
- Grognez, V., Landolt, F., Curty, J., Knop, E., 2025. Slugs hide in the dark: artificial light at night alters fitness and activity of dominant herbivores with consequences for ecosystem functioning. *iScience* 28 (6), 112770. <https://doi.org/10.1016/j.isci.2025.112770>.
- Guarnieri, M., 2018. An Historical Survey on Light Technologies. *IEEE Access* 6, 25881–25897. <https://doi.org/10.1109/ACCESS.2018.2834432>.
- Haaland, C., Naisbit, R.E., Bersier, L.-F., 2011. Sown wildflower strips for insect conservation: a review: wildflower strips for insect conservation. *Insect Conserv. Divers.* 4 (1), 60–80. <https://doi.org/10.1111/j.1752-4598.2010.00098.x>.
- Haas, S.M., Lortie, C.J., 2020. A systematic review of the direct and indirect effects of herbivory on plant reproduction mediated by pollination. *PeerJ* 8, e9049. <https://doi.org/10.7717/peerj.9049>.
- Halket, A.C., 1931. The flowers of *Silene saxifraga*, L.; an inquiry into the cause of their day closure and the mechanism concerned in effecting their periodic movements. *Ann. Bot.* os-45 (1), 15–36. <https://doi.org/10.1093/oxfordjournals.aob.a090264>.
- Han, B.-H., Kim, J.-Y., Kwak, J.-I., Choi, T.-Y., 2015. Correlation between the illuminance and the flowering and leaf growth of trees at night in case of downtown from Jamsil Station to Olympic Park, Seoul. *Kor. J. Environ. Ecol.* 29 (3), 441–453. <https://doi.org/10.13047/KJEE.2015.29.3.441>.
- Hayama, R., Coupland, G., 2003. Shedding light on the circadian clock and the photoperiodic control of flowering. *Curr. Opin. Plant Biol.* 6 (1), 13–19. [https://doi.org/10.1016/S1369-5266\(02\)00011-0](https://doi.org/10.1016/S1369-5266(02)00011-0).
- Hegland, S.J., Nielsen, A., Lázaro, A., Bjørknes, A., Totland, Ø., 2009. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* 12 (2), 184–195. <https://doi.org/10.1111/j.1461-0248.2008.01269.x>.
- Heide, O.M., 1994. Control of flowering and reproduction in temperate grasses. *New Phytol.* 128 (2), 347–362. <https://doi.org/10.1111/j.1469-8137.1994.tb04019.x>.
- Heinen, R., 2021. A spotlight on the phytobiome: plant-mediated interactions in an illuminated world. *Basic Appl. Ecol.* 57, 146–158. <https://doi.org/10.1016/j.baae.2021.10.007>.
- Hölker, F., Moss, T., Griefahn, B., Kloas, W., Voigt, C.C., Henckel, D., Hänel, A., Kappeler, P.M., Völker, S., Schwöpe, A., Franke, S., Uhrlandt, D., Fischer, J., Klenke, R., Wolter, C., Tockner, K., 2010. The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecol. Soc.* 15 (4). <https://www.jstor.org/stable/26268230>.
- Iler, A.M., CaraDonna, P.J., Forrest, J.R.K., Post, E., 2021. Demographic consequences of phenological shifts in response to climate change. *Annu. Rev. Ecol. Syst.* 52 (1), 221–245. <https://doi.org/10.1146/annurev-ecolsys-011921-032939>.
- Inouye, D.W., 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89 (2), 353–362. <https://doi.org/10.1890/06-2128.1>.
- Johansson, M., Staiger, D., 2015. Time to flower: interplay between photoperiod and the circadian clock. *J. Exp. Bot.* 66 (3), 719–730. <https://doi.org/10.1093/jxb/eru441>.
- Ke, M., Gao, Z., Chen, J., Qiu, Y., Zhang, L., Chen, X., 2018. Auxin controls circadian flower opening and closure in the waterlily. *BMC Plant Biol.* 18 (1), 143. <https://doi.org/10.1186/s12870-018-1357-7>.
- Khurana, E., Singh, J.S., 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. *Environ. Conserv.* 28 (1), 39–52. <https://doi.org/10.1017/S0376892901000042>.
- Kimball, S., Angert, A.L., Huxman, T.E., Venable, D.L., 2010. Contemporary climate change in the Sonoran Desert favors cold-adapted species. *Glob. Chang. Biol.* 16 (5), 1555–1565. <https://doi.org/10.1111/j.1365-2486.2009.02106.x>.
- Knop, E., Dominoni, D., 2024. Sensory pollution by artificial light: implications for ecology and evolution. *Basic Appl. Ecol.* 78, 39–40. <https://doi.org/10.1016/j.baae.2024.04.005>.
- Kudo, G., Cooper, E.J., 2019. When spring ephemerals fail to meet pollinators: mechanism of phenological mismatch and its impact on plant reproduction. *Proc. R. Soc. B Biol. Sci.* 286 (1904), 20190573. <https://doi.org/10.1098/rspb.2019.0573>.
- Kwiatkowska, M., Bohdanowicz, J., Cubala, M., Słomka, A., Żabicka, J., Żabicki, P., Migdalek, G., Marcussen, T., Thiele, K., Kuta, E., 2019. A new pollination system in non-cleistogamous species of *Viola* results from nyctinastic (night-closing) petal movements – a mixed outcrossing-selfing strategy. *Flora* 253, 1–9. <https://doi.org/10.1016/j.flora.2019.01.007>.

- Lavorel, S., 2013. Plant functional effects on ecosystem services. *J. Ecol.* 101 (1), 4–8. <https://doi.org/10.1111/1365-2745.12031>.
- Liu, Y., Reich, P.B., Li, G., Sun, S., 2011. Shifting phenology and abundance under experimental warming alters trophic relationships and plant reproductive capacity. *Ecology* 92 (6), 1201–1207. <https://doi.org/10.1890/10-2060.1>.
- Long, R.L., Gorecki, M.J., Renton, M., Scott, J.K., Colville, L., Goggin, D.E., Commander, L.E., Westcott, D.A., Cherry, H., Finch-Savage, W.E., 2015. The ecophysiology of seed persistence: a mechanistic view of the journey to germination or demise. *Biol. Rev.* 90 (1), 31–59. <https://doi.org/10.1111/brv.12095>.
- Luna, B., Moreno, J.M., 2010. Range-size, local abundance and germination niche-breadth in Mediterranean plants of two life-forms. *Plant Ecol.* 210 (1), 85–95. <https://doi.org/10.1007/s11258-010-9740-y>.
- Macgregor, C.J., Pocock, M.J.O., Fox, R., Evans, D.M., 2019. Effects of street lighting technologies on the success and quality of pollination in a nocturnally pollinated plant. *Ecosphere* 10 (1), e02550. <https://doi.org/10.1002/ecs2.2550>.
- Maglianesi, M.A., Hanson, P., Brenes, E., Benadi, G., Schleuning, M., Dalsgaard, B., 2020. High levels of phenological asynchrony between specialized pollinators and plants with short flowering phases. *Ecology* 101 (11), e03162. <https://doi.org/10.1002/ecy.3162>.
- McClung, C.R., 2001. Circadian Rhythms in Plants. *Plant Cell* 18 (4), 792–803.
- McClung, C.R., 2006. Plant circadian rhythms. *Plant Cell* 18 (4), 792–803.
- McKinney, A.M., CaraDonna, P.J., Inouye, D.W., Barr, B., Bertelsen, C.D., Waser, N.M., 2012. Asynchronous changes in phenology of migrating Broad-tailed Hummingbirds and their early-season nectar resources. *Ecology* 93 (9), 1987–1993. <https://doi.org/10.1890/12-0255.1>.
- Memmott, J., Craze, P.G., Waser, N.M., Price, M.V., 2007. Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* 10 (8), 710–717. <https://doi.org/10.1111/j.1461-0248.2007.01061.x>.
- Meng, L., Zhou, Y., Román, M.O., Stokes, E.C., Wang, Z., Asrar, G.R., Mao, J., Richardson, A.D., Gu, L., Wang, Y., 2022. Artificial light at night: an underappreciated effect on phenology of deciduous woody plants. *PNAS Nexus* 1 (2), pgac046. <https://doi.org/10.1093/pnasnexus/pgac046>.
- Milberg, P., Andersson, L., Thompson, K., 2000. Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Sci. Res.* 10 (1), 99–104. <https://doi.org/10.1017/S0960258500000118>.
- Mondoni, A., Daws, M.I., Belotti, J., Rossi, G., 2009. Germination requirements of the alpine endemic *Silene elisabethae* Jan: effects of cold stratification, light and GA3. *Seed Sci. Technol.* 37 (1), 79–87. <https://doi.org/10.15258/sst.2009.37.1.10>.
- Muroya, M., Oshima, H., Kobayashi, S., Miura, A., Miyamura, Y., Shiota, H., Onai, K., Ishiura, M., Manabe, K., Kutsuna, S., 2021. Circadian clock in *Arabidopsis thaliana* determines flower opening time early in the morning and dominantly closes early in the afternoon. *Plant Cell Physiol.* 62 (5), 883–893. <https://doi.org/10.1093/pcp/pcab048>.
- Plos, C., Stelbrink, N., Römermann, C., Knight, T.M., Hensen, I., 2023. Abiotic conditions affect nectar properties and flower visitation in four herbaceous plant species. *Flora* 303, 152279. <https://doi.org/10.1016/j.flora.2023.152279>.
- Prieto-Benítez, S., Dötterl, S., Giménez-Benavides, L., 2016. Circadian rhythm of a *Silene* species favours nocturnal pollination and constrains diurnal visitation. *Ann. Bot.* 118 (5), 907–918. <https://doi.org/10.1093/aob/mcw136>.
- Prokop, P., Fedor, P., 2016. Why do flowers close at night? Experiments with the Lesser celandine *Ficaria verna* Huds (Ranunculaceae). *Biol. J. Linn. Soc.* 118 (3), 698–702. <https://doi.org/10.1111/bij.12752>.
- Prokop, P., Jersáková, J., Fančovičová, J., Pipíška, M., 2019. Flower closure enhances pollen viability in *Crocus discolor* G. Reuss. *Flora* 250, 68–71. <https://doi.org/10.1016/j.flora.2018.11.019>.
- R Core Team, 2021. R: the R project for statistical computing. <https://www.r-project.org/>.
- Rafferty, N.E., Ives, A.R., 2012. Pollinator effectiveness varies with experimental shifts in flowering time. *Ecology* 93 (4), 803–814. <https://doi.org/10.1890/11-0967.1>.
- Robbirt, K.M., Roberts, D.L., Hutchings, M.J., Davy, A.J., 2014. Potential disruption of pollination in a sexually deceptive orchid by climatic change. *Curr. Biol.* 24 (23), 2845–2849. <https://doi.org/10.1016/j.cub.2014.10.033>.
- Samarakoon, U.C., Peiris, S.E., 2005. Control of circadian rhythm-regulated nyctinastic movement in water lily (*Nymphaea stellata* Willd.) flowers. *J. Horticult. Sci. Biotechnol.* 80 (2), 167–170. <https://doi.org/10.1080/14620316.2005.11511911>.
- Sanders, D., 2021. A Meta-analysis of Biological Impacts of Artificial Light at Night, p. 5. <https://doi.org/10.1098/rstb.2022.0356>.
- Seymour, B., Dell, A., Höfker, F., Kalinkat, G., 2023. A framework for untangling the consequences of artificial light at night on species interactions. *Philos. Trans. R. Soc. B* 378 (1892), 20220356. <https://doi.org/10.1098/rstb.2022.0356>.
- Shim, J.S., Kubota, A., Imaizumi, T., 2017. Circadian clock and photoperiodic flowering in arabidopsis: CONSTANS is a hub for signal integration. *Plant Physiol.* 173 (1), 5–15. <https://doi.org/10.1104/pp.16.01327>.
- Sidhu, C.S., Joshi, N.K., 2016. Establishing wildflower pollinator habitats in agricultural farmland to provide multiple ecosystem services. *Front. Plant Sci.* 7. <https://doi.org/10.3389/fpls.2016.00363>.
- Sivasankar, J., Thimmaiah, A., 2021. Lunar rhythms in agriculture—review on scientific perspectives. *Int. J. Complement. Alt. Med.* 14 (2), 81–85. <https://doi.org/10.15406/ijcam.2021.14.00536>.
- Škvareninová, J., Tuhárska, M., Škvarenina, J., Babálová, D., Slobodníková, L., Slobodník, B., Středová, H., Mindáš, J., 2017. Effects of light pollution on tree phenology in the urban environment. *Morav. Geogr. Rep.* 25 (4), 282–290. <https://doi.org/10.1515/mgr-2017-0024>.
- Thieurmel, B., Elmarhraoui, A., 2017. sunalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase, p. 0.5.1. [10.32614/CRAN.package.suncalc](https://cran.r-project.org/web/packages/suncalc/index.html).
- Van Doorn, W.G., 2003. Flower opening and closure: a review. *J. Exp. Bot.* 54 (389), 1801–1812. <https://doi.org/10.1093/jxb/erg213>.
- Van Doorn, W.G., Kamdee, C., 2014. Flower opening and closure: an update. *J. Exp. Bot.* 65 (20), 5749–5757. <https://doi.org/10.1093/jxb/eru327>.
- Vázquez-Ramírez, J., 2025. Climate change may alter seed and seedling traits and shift germination and mortality patterns in alpine environments. *Ann. Bot.* 00, 1–17.
- Walters, R.G., 2004. Towards an understanding of photosynthetic acclimation. *J. Exp. Bot.* 56 (411), 435–447. <https://doi.org/10.1093/jxb/eri060>.
- Wang, S., Wang, Z., Xiao, L., Zhang, H., Liu, Y., 2022. Artificial light at night advances reproductive phenology and reduces reproductive capacity of a wild plant. *Ecology*. <https://doi.org/10.1101/2022.12.11.519667>.
- Waser, N.M., Price, M.V., 2016. Drought, pollen and nectar availability, and pollination success. *Ecology* 97 (6), 1400–1409. <https://doi.org/10.1890/15-1423.1>.
- Webb, A.A.R., 2003. The physiology of circadian rhythms in plants. *New Phytol.* 160 (2), 281–303. <https://doi.org/10.1046/j.1469-8137.2003.00895.x>.
- Wilson, P., Thomson, J.D., 1991. Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. *Ecology* 72 (4), 1503–1507. <https://doi.org/10.2307/1941124>.
- Wolfe, J.D., Ralph, C.J., Wiegardt, A., 2017. Bottom-up processes influence the demography and life-cycle phenology of Hawaiian bird communities. *Ecology* 98 (11), 2885–2894. <https://doi.org/10.1002/ecy.1981>.
- Woolley, J.T., Stoller, E.W., 1978. Light penetration and light-induced seed germination in soil. *Plant Physiol.* 61 (4), 597–600. <https://doi.org/10.1104/pp.61.4.597>.
- Xia, Q., Ando, M., Seiwa, K., 2016. Interaction of seed size with light quality and temperature regimes as germination cues in 10 temperate pioneer tree species. *Funct. Ecol.* 30 (6), 866–874. <https://doi.org/10.1111/1365-2435.12584>.
- Yanovsky, M.J., Kay, S.A., 2003. Living by the calendar: how plants know when to flower. *Nat. Rev. Mol. Cell Biol.* 4 (4), 265–276. <https://doi.org/10.1038/nrm1077>.
- You, L., Tuo, W., Dai, Z., Wang, H., Ahmad, S., Peng, D., Wu, S., 2023. Effects of light intensity, temperature, and circadian clock on the nyctinastic movement of *Oxalis triangularis* 'Purpurea'. *Technol. Horticult.* 3 (1), 0. <https://doi.org/10.48130/THH-2023-0011>.