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RESEARCH PAPER

Pollen load, pollen species diversity and conspecific pollen carried by pollinators across 24-hour cycles

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ABSTRACT

Plant-pollinator interactions are key for the reproduction of wild plants and for food security. However, the role nocturnal pollinators play in wild plant communities is not yet clear. Specifically, it has rarely been studied whether nocturnal pollinators are comparable to diurnal ones in the pollination services they deliver in plant communities. We tested whether nocturnal pollinators have the potential to provide high pollination services to the plants they visit by carrying high conspecific pollen loads. We studied pollen loads carried by nocturnal and diurnal pollinators captured over 24-hour cycles in co-flowering plant communities in Swiss ruderal meadows. Pollen load was less diverse at night, and the proportion of conspecific pollen carried by nocturnal pollinators was higher than that of diurnal ones. Because the majority of plant species visited at night were also visited during the day, floral resource availability could drive the observed patterns in pollen load and amount of conspecific pollen. Nevertheless, nocturnal pollinators do not only carry pollen but can remove and potentially deposit conspecific pollen to the plants they visit. Therefore, pollinators active at night might be an important pollination vector for more plant species than previously thought and should not be neglected in pollination studies.

Introduction

Plant-pollinator interactions are key mutualisms for the reproduction of wild plants and for food security. About half of all flowering plant species depend on pollinators for more than 80% of their seed production (Rodger et al., 2021). Furthermore, more than 80% of crops including vegetables, fruits and stimulants depend on pollinators (Klein et al., 2007). However, declines in pollinating insects associated with global change drivers such as climate change, land-use change, agricultural intensification, urbanization, invasive species, and spread of pathogens are widespread (Ellis et al., 2023; Potts et al., 2010). Recent evidence suggests that increasing light pollution which disproportionally affects nocturnal insects adds to the drivers of pollinator declines and their pollination service (Giavi et al., 2021; Knop et al., 2017). As pollinators face the threats of many global change drivers, declines in pollinator abundance and diversity can have cascading impacts on plant communities (Clough et al., 2014). Since studies on plant-pollinator interactions are largely biased towards diurnal interactions, we specifically lack knowledge of nocturnal interactions in a community context (Knop et al., 2018, 2017; Macgregor et al., 2017). In particular, it is unclear which roles nocturnal pollinators play for wild plant communities (Hahn & Brühl, 2016).

Previous studies on nocturnal interactions were limited to very specialized interactions or involving specific groups of pollinators or plants, and most studies were done in tropical regions (Alonso-Pedano & Ortega-Baes, 2012; Balducci et al., 2019). The importance of nocturnal pollination by insects in temperate regions has only been recognized recently. A few previous studies in temperate regions focus on moths and

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Table 1

Results of four generalized linear mixed models testing how pollen load, pollen species diversity, the amount of conspecific pollen, and the proportion of conspecific pollen carried by pollinators depend on time of day or night (t in radians). Significant model parameters are highlighted in bold ($p < 0.05$), and marginally significant ones in italics ($p \geq 0.05$).

Response variables	Pollen load	Pollen species diversity	Amount of conspecific pollen	Proportion of conspecific pollen
Fixed terms	Estimate (standard error)			
Intercept	**5.162 (0.244)**	**1.497 (0.059)**	**4.637 (0.199)**	**−0.496 (0.124)**
sin(t)	**0.777 (0.057)**	**0.105 (0.023)**	**0.696 (0.101)**	**−0.274 (0.067)**
cos(t)	**−0.192 (0.074)**	**−0.117 (0.029)**	−0.223 (0.143)	−0.030 (0.090)
sin(2^*t)	0.043 (0.053)	**0.045 (0.020)**	0.017 (0.094)	−0.070 (0.065)
cos(2^*t)	*0.088 (0.049)*	0.022 (0.017)	0.128 (0.096)	−0.053 (0.057)
Total number of pollen grains		**0.240 (0.009)**		
Random terms	Standard deviation			
Site	0.418	0.136	0.170	0.134
Date	0.861	0.123	0.737	0.446
Residuals	1.000	0.929	0.881	0.375
Marginal r^2	0.093	0.240	0.065	
Conditional r^2	0.547	0.351	0.293	
N	2789	2789	2740	2740

suggest their potential roles in plant-pollinator networks by showing that moths captured in light traps carry pollen. Three to 10% of captured moths in a boreal forest in Scotland (Devoto et al., 2011), 76% of captured moths in a biodiversity hotspot in Portugal (Banza et al., 2015) and 20.7% of captured moths in the Balearic Islands (Ribas-Marquès et al., 2022) carried pollen. In the Himalayas, 65% of settling moths from which pollen was extracted from proboscices were considered potential pollinators (Singh et al., 2022). To promote plant reproduction by outcrossing, moths must not only carry pollen but also transfer it to conspecific plants. As heterospecific pollen transfer can interfere with the fertilization of ovules by conspecific pollen by mechanical clogging and allelopathy, and can reduce seed production (Ashman & Arceo-Gómez, 2013), a higher proportion of conspecific pollen transfer can be more beneficial for plants. In an experiment using fluorescent pollen-tracker powder, Buxton et al. (2022) showed that moths can transfer pollen among flowers of the same species. But we still lack knowledge of conspecific pollen transfer by nocturnal pollinators at the community level.

Due to the difference in abiotic conditions (e.g. cooler temperature and darker conditions at night), pollinator communities and therefore plant-pollinator interactions differ notably between day and night (Souza et al., 2022). In Swiss ruderal meadows, including sites studied here, Knop et al. (2018) found that the dominant groups of pollinators at night (defined based on whether they carried pollen or not) were Lepidoptera and Coleoptera, whereas diurnal pollinators were mostly Diptera and Hymenoptera. Also, fewer pollinator species and individuals visited flowers at night than during the day: 16% of pollinator species visited flowers only at night, and 9% did so during both night and day (Knop et al., 2018). However, whether nocturnal pollinators interact with a more or less diverse set of plant species than diurnal ones has not been studied yet.

Pollen carried externally by pollinators can reflect the assemblage of plant species that they visit (Kearns & Inouye, 1993; Walton et al., 2020). Moreover, conspecific pollen removal by the pollinator as well as the potential for conspecific pollen deposition can be derived from the proportion of pollen grains from the visited flower that are observed on the pollinator body. To our knowledge, no study compared pollen loads carried by nocturnal and diurnal pollinators in co-flowering plant communities and studied the variation of conspecific pollen carried by pollinator communities across 24-hour cycles. Here, we compared pollen loads carried on the body of nocturnal and diurnal flower-visiting insects in Swiss ruderal meadows during 24-hour cycles. Specifically, we asked whether the pollen load, the diversity of pollen species, the amount and proportion of conspecific pollen carried by pollinators vary across a 24-hour cycle.

Materials and methods

Pollen dataset

We used a dataset of pollen load carried by flower visitors captured over 24-hour cycles in Swiss ruderal meadows located in eight sites between 709 and 851 m a.s.l. (Appendix A: Table 1, Knop et al., 2018, 2017). Between June and August 2014, we observed and captured insects actively visiting open flowers along one 50-m transect per site during 24-hour cycles. During each cycle, we sampled flower visitors every 30 min. During each round of 30 min, we walked along the 50-m transect, and sampled all flower visitors within 1 m on both sides of the transect. Over the course of the three-month sampling period, we visited each site up to six times on days and nights without rain and strong wind. Since sunset occurred at around 22:00 and sunrise around 05:59, we refer to nocturnal interactions when flower visits occurred between 22:00 and 05:59 h.

We sampled flower visitors using sweep nets (Streifkescher V2A A7d, Bioform, Germany). We only considered insects touching the reproductive parts of the plant as flower visitors (i.e., excluded the ones destroying the petals or sleeping in the flower). During the night, we randomly alternated each of two methods, using night-vision goggles (BIG25-CV, Vectronix, Switzerland) or LED head torches (873,155 Intertronic, Interdiscount, Switzerland). We brought caught insects to the laboratory for identification. For each caught flower visitor, we identified the visited plant in the field.

Using a 5 × 5 mm^2 fuchsin-stained (3256.1, Roth, Switzerland) glycerin gel (1.04094.1000, Merck KGaA, Germany), we removed the pollen from the insect bodies by swabbing the body areas carrying pollen which are available for pollination (i.e. excluded specialized pollen-carrying structures such as corbicula) (Forup & Memmott, 2005; Kearns & Inouye, 1993). We identified pollen species under light microscope using our own pollen reference database. To build the pollen reference database, before each 24-hour sampling cycle, we collected flowers with viable stamens of all flowering species in an area within 10 m from the transect.

We collected pollen load data from 3,626 insects belonging to 500 species and morphospecies from 98 families and 10 orders, caught visiting flowers of 90 plant species. On the flower visitors, we could determine 89.18% of pollen grains to species level, 99.89% to genus level, 0.07% to higher taxonomic levels than genus (grass and tree). We could not determine 0.04% of pollen grains. We classified the undetermined pollen grains at the morphospecies level. In total, we identified pollen grains of 128 morphospecies, referred to as pollen species hereafter.

Data analysis

To differentiate potential pollinators from mere flower visitors and to account for pollen-contamination, we classified all insect individuals that carried five or more pollen grains of any plant species as potential pollinators (Devoto et al., 2011; Knop et al., 2017). Pollen load was defined as the number of pollen grains carried by an individual pollinator. To analyze the variation in pollen load over 24-hour cycles, we ran a generalized linear mixed model with a negative binomial distribution using the glmer.nb function of the lme4 package (Bates et al., 2015) in R version 4.3.0 (R-Core-Team, 2023). To account for the cyclical nature of time of day or night, we used the sine and cosine of both t and $2*t$ as explanatory variables, where t is time in units of radians (Knop et al., 2018). To account for potential variations due to site characteristics and abiotic conditions, we included site and date of capture as random variables.

Pollen species diversity was defined as the total number of pollen species carried by an individual pollinator. To study pollen species diversity across 24-hour cycles, we ran a generalized linear mixed model with a Poisson distribution using the glmer function of the lme4 package. As in the previous model, we included the sine and cosine of time of day or night in radians as explanatory variables. To account for potential bias due to variation in pollen quantity carried by different pollinators, we included the log-tranformed total number of pollen grains on each pollinator as a covariate. We also included site and date as random variables.

The amount of conspecific pollen was defined as the number of pollen grains counted on an individual pollinator that originated from the plant species on which the pollinator was caught. To analyze the variation in the amount of conspecific pollen carried by individual pollinators, we ran a generalized linear mixed model with a negative binomial distribution using the glmer.nb function of the lme4 package. As in the previous models, we included the sine and cosine of time of day or night in radians as explanatory variables. We also included site and date as random variables. To study the variation of the proportion of conspecific pollen carried by pollinators across 24-hour cycles, we ran a generalized linear mixed model with a betabinomial distribution using the R package glmmTMB (Brooks et al., 2017). As response variable, we included the proportion of conspecific pollen grains carried by each individual pollinator. As in the previous models, we included the sine and cosine of time of day or night in radians as explanatory variables, and site and date as random variables. Again, we considered only pollinators (carrying > 5 pollen grains of any given plant species) in this analysis. To check the fit of all models, we used the simulateResiduals function in the DHARMa package (Hartig, 2022). For all models, we reported the marginal and conditional r^2 (Nakagawa et al., 2017).

Results

We identified 1,322,737 pollen grains carried by 3,626 flower

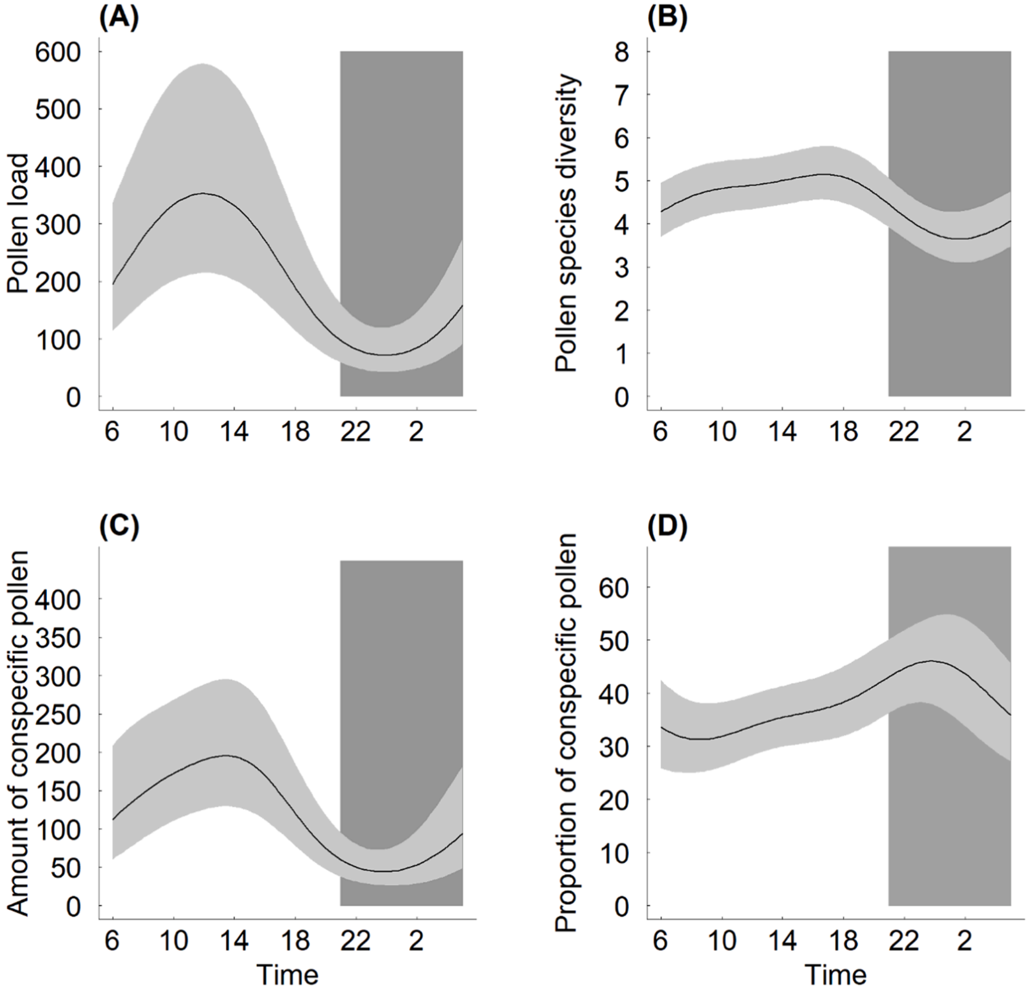

Fig. 1. Time of day or night affects (A) pollen load, (B) pollen species diversity, (C) the amount of conspecific pollen, and (D) the proportion of conspecific pollen carried by pollinators in Swiss ruderal meadows. Black curves are predictions of generalized linear mixed models and grey areas are 95% confidence intervals. Dark rectangles indicate nighttime.

visitors of which 523 (14.34%) were captured at night and 3,103 (85.66%) during the day. We captured an average of 7 individual flower visitors (ranging from 1 to 384) per species. Among plants, 4 (4.44%) species were visited only at night, 55 (61.11%) species only during the day and 31 (34.44%) species during night and day (Appendix A: Table 2). Thus, 88.57% of plant species visited at night were also visited during the day. Each flower visitor carried between 0 and 20,742 pollen grains from up to 18 plant species. Pollen load significantly depended on time of day or night over a 24-hour cycle (Table 1). Pollinators carried fewer pollen grains at night (Fig. 1A).

Time of day or night significantly affected variation in pollen species diversity carried by pollinators (Table 1). Over a 24-hour cycle, pollen species diversity slowly increased from 06:00 and peaked in the afternoon, then decreased to reach minimal values at night (Fig. 1B). However, this effect was rather weak, as the difference between the minimal and the maximal values was approximatively two pollen species (Fig. 1B). Overall, 72% of the pollinators carried conspecific pollen, i.e. pollen from the same plant species they visited and on which they were caught. Time of day or night significantly affected variation in amount and proportion of conspecific pollen (Table 1). Pollinators carried less conspecific pollen at night (Fig. 1C). Over a 24-hour cycle, proportion of conspecific pollen was always larger than 25%, and peaked at night (Fig. 1D).

Discussion

Our analysis of pollen loads carried by pollinators showed that pollen load fluctuated substantially across a 24-hour cycle, with fewer and less diverse pollen carried at night. A lower pollen diversity at night suggests that nocturnal pollinators have less diverse interactions in plant-pollinator networks and play therefore a different role than diurnal pollinators. Nevertheless, the effect of time of day or night on pollen species diversity was weak. Also, the amount of conspecific pollen carried by nocturnal pollinators was lower than that of diurnal ones but the probability that a pollen grain was conspecific was higher at night. As 88.57% of plant species visited at night in our study were also visited during the day, our results suggest that nocturnal pollinators are efficient pollen vectors for the plants they visit, and may provide additional pollination services to diurnally pollinated plants.

Low pollen load and pollen diversity at night

The finding that fewer pollen were collected at night is in accordance with Borges et al. (2016), who suggest that the majority of nocturnal pollinators feed on nectar, whereas only few collect pollen. A smaller and less diverse pollen load at night could be explained by the variation of floral resources available to flower-visiting insects over 24 h. As most temperate plants open new flowers during the day, available floral resources at night are mainly nectar and pollen of flowers which have been already exposed to diurnal pollinators (Willmer, 2011). While plants can adjust nectar production in response to consumption (Heil, 2011), pollen is not replenished (Hargreaves et al., 2009). Furthermore, many plant species close their flowers at night (van Doorn & van Meeteren, 2003), limiting the access to floral resources for nocturnal insects, which might be due to temporal niche partitioning among pollinators, and an avoidance of heterospecific pollen transfer among plants (Fründ et al., 2011). However, we did not collect data on the temporal dynamics of the quantities of nectar and pollen provided by the plants across 24 h.

The finding that nocturnal pollinators carried a less diverse pollen load, even after accounting for variations due to pollen abundance (i.e. smaller pollen load at night), may be explained by variations in insect size and insect-plant trait matching. Generally, larger insects are considered to carry more pollen (e.g. Földesi et al., 2021). However, as we do not have data on body mass, we cannot test this. Also, as moths and beetles were the dominant pollinator groups at night, we do not believe that this was the main explanation as both groups contain many large-sized species. Moths that visit bee flowers at night did not touch the anthers with body parts other than their probosces, and therefore may not have removed pollen as it was suggested by Willmer (2011). For example, the Geometridae moth *Perizoma alchemillata* was caught visiting the flower of *Stachys sylvatica* (Lamiaceae) at night but did not carry the pollen of this plant species. On the other hand, during the day *Bombus pascuorum* (Apidae) visited and carried the pollen of *S. sylvatica*, as was expected for Lamiaceae of which flowers usually present a bilabiate floral structure adapted to pollination by bees (Claßen-Bockhoff, 2007). Because the lack of mechanical fit between the nocturnal insects and flowers of diurnally visited flowers might limit their ability to remove or deposit pollen, it could be that only pollen grains from perfectly matching plant species were found on nocturnal pollinators.

High proportion of conspecific pollen at night

Proportion of conspecific pollen in the pollen load can provide information on pollinator performance, as it should positively affect plant reproduction and fitness. At night, lepidopteran pollinators including mainly *Alcis repandata* carried the highest proportion of conspecific pollen mainly from *Cirsium oleraceum* and *Valeriana officinalis*. During the day, dipteran pollinators including *Rhinophora lepida* and *Episyrphus balteatus* carried the highest proportion of conspecific pollen mainly from *Erigeron annuus*. Both at night and during the day, the highest conspecific pollen loads were from mostly generalized plants with easily accessible flowers (e.g. *Cirsium oleraceum, Erigeron annuus*). The pattern of variation in proportion of conspecific pollen over a 24-hour cycle in our study can thus partly be attributed to the pollinator communities. Specifically, the highest proportion of conspecific pollen at night corresponded to the peak of Lepidoptera visits (Knop et al., 2018). Thus, nocturnal pollinators can remove or deposit conspecific pollen for the plants visited at night at least as well as diurnal pollinators do for plants visited during the day.

Nocturnal pollinators may play a complementary role to diurnal ones to achieve higher pollination output in plants. Such a complementarity among diurnal and nocturnal pollinators has been shown for single plant species (Blüthgen & Klein, 2011). In the arid regions of Mexico, to alleviate competition for bat visitation with other coflowering species at night, the cactus *Marginatocereus marginatus* is also pollinated by hummingbirds during the day (Dar et al., 2006). In the common milkweed *Asclepias syriaca* in the temperate meadows of North America, low-frequency high-quality pollination (with outcross-pollen) by moths at night is complemented by low-quality pollination by bumblebees during the day, which have more frequent visitation and remove more pollinia, but transfer more self-pollen (Jennersten & Morse, 1991). In the tropical cloud forests of Ecuador, high-frequency bat pollination at night frequently accompanied with heterospecific pollen transfer in *Aphelandra acanthus* is complemented by pollination by hummingbirds during the day (Muchhala et al., 2009). In the Swiss pre-alps, Knop et al. (2017) found that a reduction of nocturnal pollinators of *Cirsium oleraceum* due to artificial light at night could not be compensated by the diurnal pollinators. Similarly, in the Swiss alps, Alison et al. (2022) found that the clover *Trifolium pratense* is visited by bumblebees during the day and by moths at night, and that both moth and bumblebee visitation increased seed set. However, more studies are needed to find out to what extent nocturnal and diurnal pollinators are indeed complementary in a community context.

Recommendations for future studies

Pollen carried on pollinator bodies alone does not provide information on effective pollination. Quantifying pollen deposition rates and characterizing pollen on stigmas of plants visited at night should further advance our understanding of nocturnal pollination interactions. To fully assess the importance of nocturnal pollinators for plant reproduction, future research should include manipulative experiments that temporally exclude nocturnal and diurnal pollinators and quantify seed set mediated by nocturnal pollinators. Studies that quantify the availability of floral resources in plant communities across 24-hour cycles will help disentangle whether low pollen load at night is due to few available resources or a high specialization.

Conclusions

Nocturnal pollinators do not only carry pollen but can remove and deposit conspecific pollen for plants flowering at night. Plant communities may rely on the functional and environmental complementarity between diurnal and nocturnal pollinators for pollination assurance. Given the worldwide pollinator decline and specific risks to nocturnal pollinators (such as light pollution), there is thus an urgent need for studies clarifying the contribution of nocturnal and diurnal pollinators to plant reproduction.

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.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.04.008.

References

Alison, J., Alexander, J. M., Diaz Zeugin, N., Dupont, Y. L., Iseli, E., Mann, H. M. R., et al. (2022). Moths complement bumblebee pollination of red clover: A case for day-and-night insect surveillance. *Biology Letters, 18*, Article 20220187. https://doi.org/10.1098/rsbl.2022.0187

Alonso-Pedano, M., & Ortega-Baes, P. (2012). Generalized and complementary pollination system in the Andean cactus *Echinopsis schickendantzii*. *Plant Systematics and Evolution, 298*, 1671–1677. https://doi.org/10.1007/s00606-012-0668-7

Ashman, T.-L., & Arceo-Gómez, G. (2013). Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. *American Journal of Botany, 100*, 1061–1070. https://doi.org/10.3732/ajb.1200496

Balducci, M. G., Martins, D. J., & Johnson, S. D. (2019). Pollination of the long-spurred African terrestrial orchid *Bonatea steudneri* by long-tongued hawkmoths, notably *Xanthopan morganii*. *Plant Systematics and Evolution, 305*, 765–775. https://doi.org/10.1007/s00606-019-01605-2

Banza, P., Belo, A. D. F., & Evans, D. M. (2015). The structure and robustness of nocturnal Lepidopteran pollen-transfer networks in a Biodiversity Hotspot. *Insect Conservation and Diversity, 8*, 538–546. https://doi.org/10.1111/icad.12134

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*, 1–48. https://doi.org/10.18637/jss.v067.i01

Blüthgen, N., & Klein, A.-M. (2011). Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology, 12*, 282–291. https://doi.org/10.1016/j.baae.2010.11.001

Borges, R. M., Somanathan, H., & Kelber, A. (2016). Patterns and Processes in Nocturnal and Crepuscular Pollination Services. *The Quarterly Review of Biology, 91*, 389–418. https://doi.org/10.1086/689481

Brooks, M. E., Kristensen, K., Benthem, K. J.van, Magnusson, A., Berg, C. W., Nielsen, A., et al. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal, 9*, 378. https://doi.org/10.32614/RJ-2017-066

Buxton, M., Anderson, B., & Lord, J. (2022). Moths can transfer pollen between flowers under experimental conditions. *New Zealand Journal of Ecology, 46*, 1–5. https://doi.org/10.20417/nzjecol.46.7

Claßen-Bockhoff, R. (2007). Floral construction and pollination biology in the lamiaceae. *Annals of Botany, 100*, 359–360. https://doi.org/10.1093/aob/mcm157

Clough, Y., Ekroos, J., Báldi, A., Batáry, P., Bommarco, R., Gross, N., et al. (2014). Density of insect-pollinated grassland plants decreases with increasing surrounding land-use intensity. *Ecology Letters, 17*, 1168–1177. https://doi.org/10.1111/ele.12325

Dar, S., Arizmendi, Ma.del C., & Valiente-Banuet, A. (2006). Diurnal and nocturnal pollination of marginatocereus marginatus (Pachycereeae: Cactaceae) in central Mexico. *Annals of Botany, 97*, 423–427. https://doi.org/10.1093/aob/mcj045

Devoto, M., Bailey, S., & Memmott, J. (2011). The 'night shift': Nocturnal pollen-transport networks in a boreal pine forest. *Ecological Entomology, 36*, 25–35. https://doi.org/10.1111/j.1365-2311.2010.01247.x

Ellis, E. E., Edmondson, J. L., Maher, K. H., Hipperson, H., & Campbell, S. A. (2023). Negative effects of urbanisation on diurnal and nocturnal pollen-transport networks. *Ecology Letters, 26*, 1382–1393. https://doi.org/10.1111/ele.14261

Földesi, R., Howlett, B. G., Grass, I., & Batáry, P. (2021). Larger pollinators deposit more pollen on stigmas across multiple plant species—A meta-analysis. *Journal of Applied Ecology, 58*, 699–707. https://doi.org/10.1111/1365-2664.13798

Forup, M. L., & Memmott, J. (2005). The Restoration of Plant–Pollinator interactions in hay meadows. *Restoration Ecology, 13*, 265–274. https://doi.org/10.1111/j.1526-100X.2005.00034.x

Fründ, J., Dormann, C. F., & Tscharntke, T. (2011). Linné's floral clock is slow without pollinators – flower closure and plant-pollinator interaction webs. *Ecology Letters, 14*, 896–904. https://doi.org/10.1111/j.1461-0248.2011.01654.x

Giavi, S., Fontaine, C., & Knop, E. (2021). Impact of artificial light at night on diurnal plant-pollinator interactions. *Nature communications, 12*, 1690. https://doi.org/10.1038/s41467-021-22011-8

Hahn, M., & Brühl, C. A. (2016). The secret pollinators: An overview of moth pollination with a focus on Europe and North America. *Arthropod-Plant Interactions, 10*, 21–28. https://doi.org/10.1007/s11829-016-9414-3

Hargreaves, A. L., Harder, L. D., & Johnson, S. D. (2009). Consumptive emasculation: The ecological and evolutionary consequences of pollen theft. *Biological Reviews, 84*, 259–276. https://doi.org/10.1111/j.1469-185X.2008.00074.x

Hartig, F., 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level /Mixed) Regression Models. R package version 0.4.5.

Heil, M. (2011). Nectar: Generation, regulation and ecological functions. *Trends in Plant Science, 16*, 191–200. https://doi.org/10.1016/j.tplants.2011.01.003

Jennersten, O., & Morse, D. H. (1991). The quality of pollination by diurnal and nocturnal insects visiting common milkweed, asclepias syriaca. *The American Midland Naturalist, 125*, 18–28. https://doi.org/10.2307/2426365

Kearns, C.A., Inouye, D.W., 1993. Techniques for pollination biologists. Techniques for pollination biologists.

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., et al. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences, 274*, 303–313. https://doi.org/10.1098/rspb.2006.3721

Knop, E., Gerpe, C., Ryser, R., Hofmann, F., Menz, M. H. M., Trösch, S., et al. (2018). Rush hours in flower visitors over a day–night cycle. *Insect Conservation and Diversity, 11*, 267–275. https://doi.org/10.1111/icad.12277

Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., & Fontaine, C. (2017). Artificial light at night as a new threat to pollination. *Nature, 548*, 206–209. https://doi.org/10.1038/nature23288

Macgregor, C. J., Evans, D. M., Fox, R., & Pocock, M. J. O. (2017). The dark side of street lighting: Impacts on moths and evidence for the disruption of nocturnal pollen transport. *Global Change Biology, 23*, 697–707. https://doi.org/10.1111/gcb.13371

Muchhala, N., Caiza, A., Vizuete, J. C., & Thomson, J. D. (2009). A generalized pollination system in the tropics: Bats, birds and Aphelandra acanthus. *Annals of Botany, 103*, 1481–1487. https://doi.org/10.1093/aob/mcn260

Nakagawa, S., Johnson, P. C. D., & Schielzeth, H. (2017). The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface, 14*, Article 20170213. https://doi.org/10.1098/rsif.2017.0213

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution, 25*, 345–353. https://doi.org/10.1016/j.tree.2010.01.007

R-Core-Team, 2023. A language and environment for statistical computing. r foundation for statistical computing, Vienna, Austria. https://www.R-project.org/.

Ribas-Marquès, E., Díaz-Calafat, J., & Boi, M. (2022). The role of adult noctuid moths (Lepidoptera: Noctuidae) and their food plants in a nocturnal pollen-transport network on a Mediterranean island. *J Insect Conserv, 26*, 243–255. https://doi.org/10.1007/s10841-022-00382-7

Rodger, J. G., Bennett, J. M., Razanajatovo, M., Knight, T. M., Kleunen, M.van, Ashman, T.-L., et al. (2021). Widespread vulnerability of flowering plant seed production to pollinator declines. *Science Advances, 7*. https://doi.org/10.1126/sciadv.abd3524

Singh, N., Lenka, R., Chatterjee, P., & Mitra, D. (2022). Settling moths are the vital component of pollination in Himalayan ecosystem of North-East India, pollen transfer network approach revealed. *Scientific reports, 12*, 2716. https://doi.org/10.1038/s41598-022-06635-4

Souza, C. S., Oliveira, P. E., Rosa, B. B., & Maruyama, P. K. (2022). Integrating nocturnal and diurnal interactions in a Neotropical pollination network. *Journal of Ecology, 110*, 2145–2155. https://doi.org/10.1111/1365-2745.13937

van Doorn, W. G., & van Meeteren, U. (2003). Flower opening and closure: A review. *Journal of Experimental Botany, 54*, 1801–1812. https://doi.org/10.1093/jxb/erg213

Walton, R. E., Sayer, C. D., Bennion, H., & Axmacher, J. C. (2020). Nocturnal pollinators strongly contribute to pollen transport of wild flowers in an agricultural landscape. *Biology Letters, 16*, Article 20190877. https://doi.org/10.1098/rsbl.2019.0877

Willmer, P. (2011). *Pollination and floral ecology, pollination and floral ecology*. Princeton University Press. https://doi.org/10.1515/9781400838943