Title:

Pollination across the diel cycle: a global meta-analysis

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Abstract

The daily transition between day and night, known as the diel cycle, is characterised by significant shifts in environmental conditions and biological activity, both of which can affect crucial ecosystem functions like pollination. Yet, despite over six decades of research into whether plant reproductive success varies between day and night, consensus remains elusive. We compiled and analysed the evidence of diel pollination differences from 135 studies with pollinator exclusion experiments across 139 angiosperms using phylogenetically controlled multilevel meta-analytic models and tested the influence of environmental conditions and plant functional traits. Our synthesis revealed an overall lack of difference in pollination success between day and night, suggesting generalization across the diel cycle. However, diel variation was partially explained by elevation, such that nocturnal pollination success was greater at low elevations, whereas diurnal pollination was more beneficial at higher elevations. Furthermore, plant traits related to pollinator attraction (odour, colour), and anthesis time influenced diel variation in pollination success. In the light of increasing anthropogenic pressures on biodiversity, as well as unique challenges for nocturnal biota, this synthesis underscores the complementarity of pollinators for flowering plants across the diel cycle, and the importance of considering both nocturnal and diurnal pollinators in conservation efforts.

Keywords: diel, diurnal, nocturnal, pollination, fruit set, seed set, meta-analysis

Background

Few environmental fluctuations are more consistent than the transition of day to night. The 24-hour (diel) cycle can see considerable variation in resources (e.g., sunlight), abiotic conditions (e.g., temperature), and biotic interactions (e.g., predation). Species have evolved suites of traits to exploit daily environmental fluctuations leading to diel differences in ecosystem function. In a review of five key ecosystem functions, Cox & Gaston (2023) concluded that our understanding of the distinct but linked processes of nocturnal and diurnal ecosystems are underdeveloped. A persistent diurnal bias in ecological research (Park 1940, Gaston 2019) is worth addressing for several reasons. First, nocturnality is widespread, with 30% of vertebrates and more than 60% of invertebrates exhibiting nocturnal activity (Hölker et al. 2010) and with approximately one-third of angiosperm families benefitting from nocturnal pollination (Borges et al. 2016). Second, diel-differentials exist for many anthropogenic pressures (Gaston et al. 2023), for example light or noise pollution (McMahon et al. 2017) or diel asymmetry in warming - minimum temperatures (often night occurring) are increasing at much greater rates than are maximum temperatures (Donat and Alexander 2012, Cox et al. 2020). It remains true that nocturnal ecology must be considered before our knowledge of a community, its functions, and its responses to global change can be considered complete (Park et al. 1931).

Pollination is a crucial ecosystem function for crops and wildflowers (Klein et al. 2007, Ollerton et al. 2011). The relative contribution to plant reproductive success varies extensively among pollinator groups (Herrera 1987, Wilson and Thomson 1991, Page & Nicholson et al. 2021), and is the product of 1) a plant's reliance on animal vectors for successful reproduction (i.e., pollination dependency (Eckert et al. 2010)), and 2) a pollinator's visitation rate and per visit pollen transfer efficiency (i.e., pollination effectiveness (Stebbins 1970)). Both nocturnal and diurnal flowering plants differ considerably in their pollination dependency and nocturnal and diurnal pollinators can differ considerably in their pollination effectiveness. Yet, a strong diurnal bias persists in pollination research (Macgregor and Scott-Brown 2020, Buxton et al. 2022), which limits our understanding and appreciation of diel variation in pollination outcomes.

There are well documented examples of pollination by nocturnal lepidoptera (Brantjes 1978, Anderson et al. 2023), beetles (Consiglio and Bourne 2001, Grant et al. 2021), and mammals

(Goldingay et al. 1991, Fleming et al. 2001), and many plant species are visited by a range of diurnal and nocturnal pollinators (Fleming and Holland 1998, Knop et al. 2018, Siqueira et al. 2018, Alison et al. 2022, Fijen et al. 2023). The contribution to reproductive success by nocturnal pollinators can be minimal for some plant species (e.g., Morse and Fritz 1983), such as for plants with low pollinator dependency, yet for other plants, nocturnal pollinators are the most effective and/or only pollen vector (e.g., Young 2002). Furthermore, disregarding nocturnal pollinators can lead to misleading inferences of plant species pollination requirements (Alison et al. 2022).

Associations between floral traits (e.g., scent, colour, floral morphology, heat generation) and nocturnal or diurnal pollinator functional groups (Baker 1961, Fenster et al. 2004, Faegri and van der Pijl 2013) may help explain diel pollination differences. These ‘pollination syndromes’ have precedent, as research has shown that specializing pollination on either temporal functional group can improve plant reproductive outcomes, for example greater pollen transfer from night-active moths with large foraging ranges (Kawakita and Kato 2004). Yet, the fallibility of syndromes is well known (Ollerton et al. 2009, but see Dellinger 2020). For example, plants conforming to the moth-pollination syndrome (i.e., white, fragrant, tubular flowers) are, in fact, pollinated by a diversity of nocturnal and diurnal insects (Slauson 2000, Funamoto and Ohashi 2017). Moreover, having temporally generalized pollination can increase visitation across a diel cycle and provide resilience against local pollinator extinctions (Walton et al. 2020, Shibata and Kudo 2023). Nonetheless, it remains widely assumed that specific floral traits are associated with nocturnal or diurnal pollination (Valdivia and Niemeyer 2006).

Abiotic conditions may also influence diel pollination differences. Natural nocturnal light levels can be several orders of magnitude lower than daytime levels (Borges et al. 2016). These low light conditions can affect plant signalling and pollinator attraction. Moreover, total daylight hours will vary with latitude and time of year, and research suggests the relative contribution from nocturnal pollinators could decrease with latitude (Sletvold et al. 2012, Chapurlat et al. 2015), where seasonal periods of pollinator activity coincide with increased daylength. In temperate and dry regions, night temperatures tend to be lower, and with minimum daily temperatures commonly occurring at night. Pollination rates are also known to vary altitudinally (Arroyo et al. 1985, Adedoja et al. 2018), potentially due to harsher environmental conditions at higher elevations (Cruden 1972, Dellinger et al. 2023). Nocturnal, diurnal, or crepuscular activity may be an adaptation to avoid these unfavourable conditions (Herrera 1992, Heinrich 1993, Willmer and Stone 1997). Alternatively, the arid hypothesis for nocturnal flowering and pollination (Borges et al. 2016) posits that plants in dry conditions should preferentially bloom at night since it reduces the water demands of flowering (e.g., Galen et al. 1999, Galen 2000). This is also reflected in evidence that nocturnal pollination is found in 67.8% of the 31 families with CAM photosynthesis (Borges et al. 2016). Although nighttime abiotic conditions will differ between latitude and climate zone, environmental diel variation may nonetheless create unique temporal niches to which plants and pollinators have adapted.

Numerous studies have directly tested the relative contribution of nocturnal and diurnal pollination through exclusion experiments, whereby plants or flowers are bagged to prevent either diurnal or nocturnal pollinator visitation. These treatment groups (night and day pollination) are often paired with additional pollination treatments, including control flowers (open pollination) or supplemental pollen addition (hand pollination). Although previous reviews of nocturnal pollination exist (Baker 1961, Borges et al. 2016, Macgregor and Scott-Brown 2020, Buxton et al. 2022), none synthesize evidence of the relative contribution of nocturnal and diurnal pollinators to plant reproductive success. Given these common experimental designs, we undertook a meta-analysis to investigate diel pollination differences, and the biotic or abiotic factors that may explain these differences. We ask the following questions:

1. Do day and night pollination contribute equally to plant reproductive success?
2. Are day or night pollination as effective as open (24 hr) pollination?
3. Are diel pollination differences explained by i) environmental conditions (i.e., daylength, daily temperature range, and elevation), and ii) plant life history traits?

Methods

Literature search and inclusion

We conducted our literature search in October 2023 using the following piloted search string: ("nocturnal*” OR "night*") and ("pollin*”) and ("success*" OR "pollen*" OR "fruit*" OR "seed*” OR "effic*" OR "effective*" OR “visit*”). This search string identified 1893 papers in the Web of Science (WoS) from 9 databases, including WoS Core Collection, CABI, BIOSIS Previews, ProQuest, SciELO, Zoological Record. In addition, we collated references from two recent reviews of nocturnal pollination (Macgregor and Scott-Brown 2020, Buxton et al. 2022), which yielded an additional 306 references. After removing duplicates, we used Rayyan (Ouzzani et al. 2016) to screen all 1950 unique bibliographic records. Through screening abstracts, we identified 275 papers as possible candidates for inclusion. After screening the full text of these papers, we identified 136 that contained potential data for meta-analysis. We included studies if they 1) conducted a pollinator exclusion experiment in which pollination was completely inhibited during both day and night; 2) measured pollination effectiveness as either fruit set, fruit mass, seed set, seed mass, or pollen deposition; 3) reported sample sizes and descriptive statistics (e.g., means, boxplots). Our first criteria excluded papers that used taxon-specific exclusion methods, (e.g., wire cages against night active mammals, (Kleizen et al. 2008)). Our second criteria excluded most measures of male fitness (e.g., pollen removal). A PRISMA inclusion chart (**Figure A1.1**) is provided in Appendix 1.

Data extraction

In addition to experimental exclusion of day and night pollination, we recorded responses to treatments where all pollinator visitation was excluded (i.e., autogamy, complete exclusion, or bagged treatments) and where no exclusion occurred (i.e., control or open pollination treatments). We extracted the sample size, mean and variance, including from figures when these values were not reported in text or tables using WebPlotDigitizer (Rohatgi 2015). When results were reported as boxplots, we used the function *metaDigitise* (Pick et al. 2019) to extract and estimate means and variance. Fruit set results were often reported without variance. When this was the case, we calculated the theoretical variance assuming a binomial distribution given the number of fruits set from a reported number of flowers. All variance measurements were converted to standard deviation.

Missing data imputation

We imputed missing variances for 29 comparisons from studies that did not report standard deviation, but for which we could extract sample sizes. Within each pollination outcome measure, we modelled standard deviation as a function of the sample size, mean pollination outcome, and treatment (day pollination, night pollination or open pollination), following (Bishop and Nakagawa 2021). For seed set, we included interactions among the predictors ($F_{6,525}$: 127.62, $R^2 = 0.71$), whereas for seed mass ($F_{5,23}$: 23.31, $R^2 = 0.79$) and pollen deposition ($F_{5,23}$: 25.04, $R^2 = 0.80$), we included only additive terms given the small sample sizes. There were two instances where the study year was not reported, and authors did not respond to email inquiry. For these missing years we used the studies' publication date and imputed a study year based on the average time between study date and publication date for all other articles (4.9 years).

Effect size calculation

We calculated effect sizes as the standardized mean difference (SMD), otherwise known as Hedges' g (Hedges 1981). We chose to use SMD over other effect sizes because can handle zeroes and includes a correction for small sample sizes (Nakagawa and Santos 2012), which occurred with our data. For each pollination effectiveness measure, we calculated SMD for three treatment comparisons: 1) between night and day pollination, 2) between day and open pollination, and 3) between night and open pollination. For the first comparison, effect sizes > 0 indicate night pollination was more effective than day pollination. While for the other comparisons effect sizes < 0 mean that day, or night pollination was less effective than open pollination (i.e., a day or night pollination deficit). Additionally, we calculated the SMD between closed and open pollination, to generate estimates of plant species pollination dependency. Our inclusion criteria ensured all studies contained a day vs. night comparison (n = 136), however open pollination was reported in 83.8% of studies (n = 114) and so the sample size for these treatment comparisons differs. In addition, 65.4% of studies (n = 89) reported both open and closed pollination, which we use to calculate pollination dependency (see below).We calculated effect sizes in R (R Core Development Team, 2020) using the escalc function in the ‘metafor’ package (v. 2.1-0, (Viechtbauer 2010)).

Moderators

We collected information on several moderator variables to explain heterogeneity in the data or to account for phylogenetic similarity. We directly extracted five variables from the included studies: 1) study location – if latitude and longitude were not reported, then coordinates were estimated based on place names or maps); 2) study year – for studies with field seasons that overlapped two years we used the first year; 3) study duration – start and end months of exclusion experiments; and 4) whether or not the plant is a crop.

We considered the SMD between closed and open pollination treatments ($n_{species} = 95$, $n_{study} = 89$, $n_{SMD} = 182$) as a measurement of study-level plant species pollination dependency. To improve sample coverage, we averaged across studies to generate species-level estimates (excluding one extreme effect size: SMD > 10), first, at the pollination effectiveness metric level, resulting in 56.7% coverage of day vs. night pollination effect sizes. We further supplemented missing values by generating non-metric specific estimates, which increased coverage to 70.3%, and finally using genera-level estimates, resulting in a total coverage of 82.8% of effect sizes, and 111 plant species.

We obtained additional information on moderator variables using external sources. To explore the influence of biogeography we obtained each study’s day length, daily temperature range and elevation. We use the CBM model (Forsythe et al. 1995) to calculate day length according to solar declination, a study’s latitude, and day of year based on the median date of the experiment’s start and end months. Using a study’s location, median date, and year, we extracted the month-long average of daily temperature ranges based on the Climatic Research Unit Time Series (CRU TS, v.4.07) dataset (Harris et al. 2020). Elevation was obtained for each study location by extracting point elevations from the Amazon Web Services Terrain Tiles using the elevatr R package (v.0.99.0, (Hollister and Shah 2017)).

Plant phenotype may influence diel pollination effectiveness. Following (Lanuza et al. 2023), we collected information on the following pollination-relevant plant traits (**Table S1**): plant lifespan, life form, photosynthetic pathway, breeding system, flower colour, flower symmetry, flower shape, anthesis time, nectar presence, odour presence, flower width (mm), flower length (mm), style length (mm), and plant height (m). The included studies reported many of these trait values, and we filled in missing values by searching the literature and referencing botanical keys. Where quantitative traits (e.g., flower width) could not be found we accessed herbarium specimens hosted on GBIF and measured dimensions of at least five flowers. When sex differences existed between quantitative traits (e.g., for dioecious plants), we took measurements from female flowers. We excluded one plant species (*Mitrastemon yamamotoi*, Mitrastemonaceae) prior to analyses, as it lacked photosynthesis, and could not be reliably imputed to either CAM or C_4 pathway. Furthermore, we re-classified the only two plant species with capitulum flowers (family Asteraceae) as open flowers, as well as one plant species with blue flowers (*Adenophora jasionifolia*), and one with brown flowers (*Cullenia exarillata*) as purple and yellow, respectively. Lastly, where anthesis time was unobtainable (n = 24 plant species), we classified these as having variable (“both”) anthesis.

We assessed correlations between continuous traits and environmental variables using Pearson’s correlation co-efficient. We further calculated measures of associations between pairs of nominal traits using Cramer’s V, and between continuous variables and nominal traits with the R^2 from linear regressions (**Figure A1.2**). Flower width, length and style length were found to be highly correlated. Thus, we elected to model only style length, as a measure of functional flower size related to pollination. In contrast, daylength, DTR and elevation were uncorrelated, and thus retained in our analyses.

Plants with traits associated with night or day pollination might have shared evolutionary history. After resolving species names to current nomenclature using the worldflora package (v.1.14-1, (Kindt 2020)), we constructed a phylogeny with the V.PhyloMaker2 package (v.0.1.0; (Jin and

Qian 2019)) by pruning a dated plant phylogeny (Smith and Brown 2018), and added unrepresented species using the default scenario (i.e., missing genera and species were placed at the basal node of the family or genus respectively). This time calibrated phylogeny allowed us to construct a phylogenetic covariance matrix. We use these phylogenies and covariance matrices in our meta-regression models (see below).

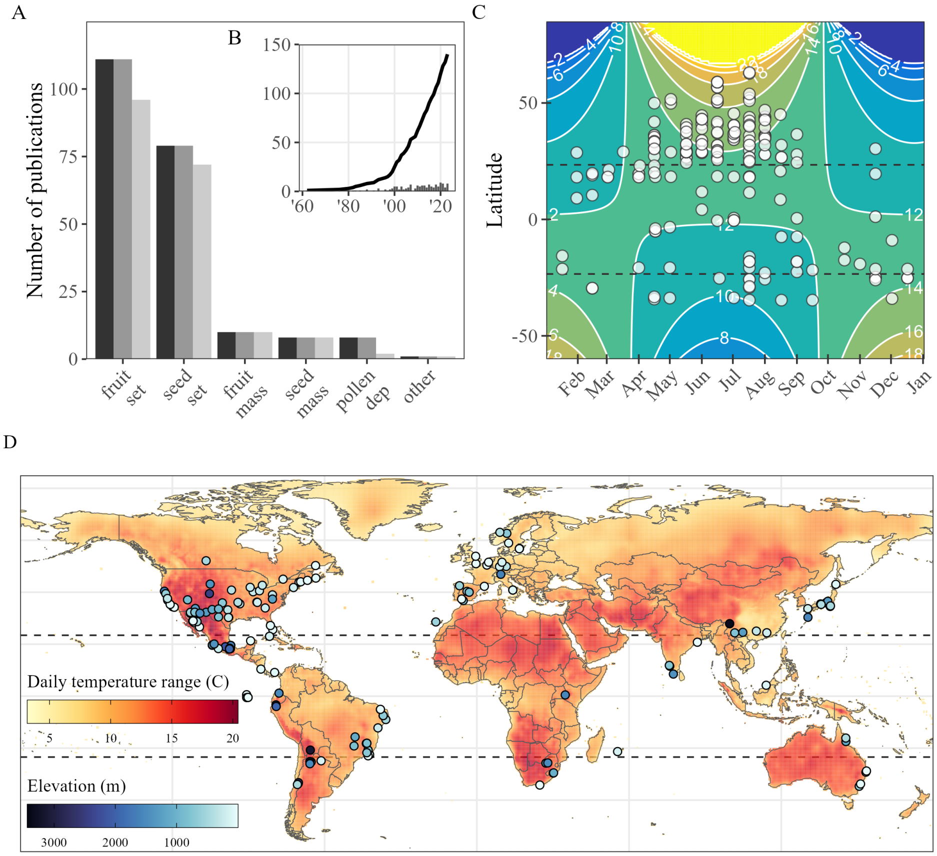

Figure 1 The research into diel pollination differences examined different pollination outcomes (A), progressed over time (B), occurred across a range of daylengths (C), temperature conditions, and elevations (D). The bar colour in (A) corresponds to the number of studies that report pollination effectiveness measures for night, day, and open pollination treatments, respectively (see Methods). The time series (B) shows the cumulative (line) and annual (bars) number of studies. Each study's daylength (C, hours) was computed using each study's location and median date. Daily temperature range and elevation (D) were extracted based on study location (see Methods).

Multi-level meta-analysis and regression

Meta-analysis and meta-regression were undertaken using the rma.mv function within the *metafor* package (v.4.4-0, (Viechtbauer 2010)). Prior to analyses, we removed five effect sizes (day vs. night: n = three, day vs. open: n = two), as these were extreme values (i.e., SMD > 10 or < -10). This yielded 1094 effect sizes (day vs. night: 400, day vs. open: 342, night vs. open: 352, open vs. closed: 182), which were distributed across different pollination effectiveness metrics and treatment comparisons (**Figure 1A**). Likewise, this resulted in a different number of analysed plant species for each treatment comparison (day vs. night: n = 138, day vs. open: n = 112, night vs. open = 112). We first fitted multi-level meta-analysis models to assess overall trends for each diel pollination difference (i.e., day vs night pollination, day vs open pollination, and night vs open pollination). Given the hierarchical structure of our dataset (i.e., including both multiple effect sizes resulting from the same study, different pollination measurements, as well as species with shared evolutionary history), we included five random effects, i) study ID, to account for multiple effect sizes resulting from the same study, ii) pollination effectiveness measurement type, iii & iv) phylogenetic and non-phylogenetic species effects, and v) an effect-level ID for residual heterogeneity among effect sizes. We estimated total heterogeneity in each diel pollination comparison and that associated with each random effect using I^2 (Higgins and Thompson 2002). Additionally, to assess differences among diel pollination effectiveness metrics, we fitted a meta-regression model with pollination effectiveness metric as a fixed effect, along with a reduced random effect structure (study ID, effect ID, and phylogenetic and non-phylogenetic species effects).

We then fitted univariate multi-level meta regression models to test our hypotheses related to the effect of traits and the environment. We took a univariate approach as the strong dependencies among multiple variables limited inference based upon multi-predictor models. For each diel pollination comparison, we modelled SMD in relation to each trait and environmental variable. We compared linear and quadratic terms for environmental variables to test for non-linear relationships. These models were specified with the same random structure as our meta-analytical models. We then compare the predictive power of each trait and environmental variable by comparing their goodness of fit (marginal R^2, (Nakagawa and Schielzeth 2013)), as well as Q-tests and ΔAIC relative to meta-analytic models. Model estimates were considered statistically significant if their 95% confidence intervals did not cross zero. We visualised our results using modified code from the orchard R package (v2.0, (Nakagawa et al. 2023)),

Publication bias, limitations, and sensitivity analysis

We tested for publication bias using three approaches. First, we first plotted SMD against its standard error (square-root of sampling variance), to look for asymmetry in funnel plots. Next, we used a modified version of the Egger's regression test (Egger et al. 1997) for multi-level meta-analytic models, which regresses the SMD on its standard error, whilst accounting for the random effect structure. Here, if the model intercept is significantly different from zero, this is indicative of publication bias or "small study effects". Finally, we tested for time-lag effect (Jennions and Møller 2002) by modelling SMD as a function of publication year, together with the random effect structure described above.

Results

Attributes of diel pollination studies

Our final dataset consisted of a total of 1094 effect sizes, from 135 studies, and 139 plant species (85 genera and 37 families), resulting in 400 comparisons between day vs. night pollination, 342 between day pollination and open pollination, and 352 between night and open pollination. Most studies reported pollination outcomes as fruit set (55.7%, 609 effect sizes), followed by seed set (35.5%, 388 effect sizes), and fruit mass (n = 48), seed mass (n = 30), and pollen deposition (n = 19) comprised a minority of data (8.8%; **Figure 1A**). Pollination experiments were conducted between 1962 and 2022 (**Figure 1B**), typically during summer months and with an average daylength of 13.34 hrs ± 1.56 (mean ± SD), daily temperature range of 12.69 C ± 3.69, and elevation of 678 m ± 749 (**Figure 1 C-D**). Research was conducted on every continent, with 4.44% of studies from Africa, 13.3% from Asia, 3.7% from Oceania, 14.8% from Europe, and 63.7% from the Americas (**Figure 1D**). The top three most represented plant families in terms of number of species were Cactaceae (n = 23), Caryophyllaceae (n = 11), and Asparagaceae (n = 11).

Day vs. night pollination

Phylogenetic meta-analysis revealed that there were no overall significant differences between day and night pollination (**Figure 2**, top panel). Total heterogeneity was high (I^2 = 98 %), with the most being attributed to the non-phylogenetic species effect (45%), followed by individual effects (25.4%), study (24%), measurement (2%) and species phylogeny (1.5%). We find that day or night pollination are generally less effective than a full 24-hour (open) pollination period, but henceforth focus on day vs. night pollination and report the full results for open pollination vs. day or night pollination in Appendix 2.

At the pollination measurement level, seed set resulting from night pollination was significantly greater than from day pollination (0.392, [0.114, 0.670]; **Figure 2**), whereas the SMD of all other outcomes (fruit mass, fruit set, pollen deposition and seed mass) did not differ from zero.

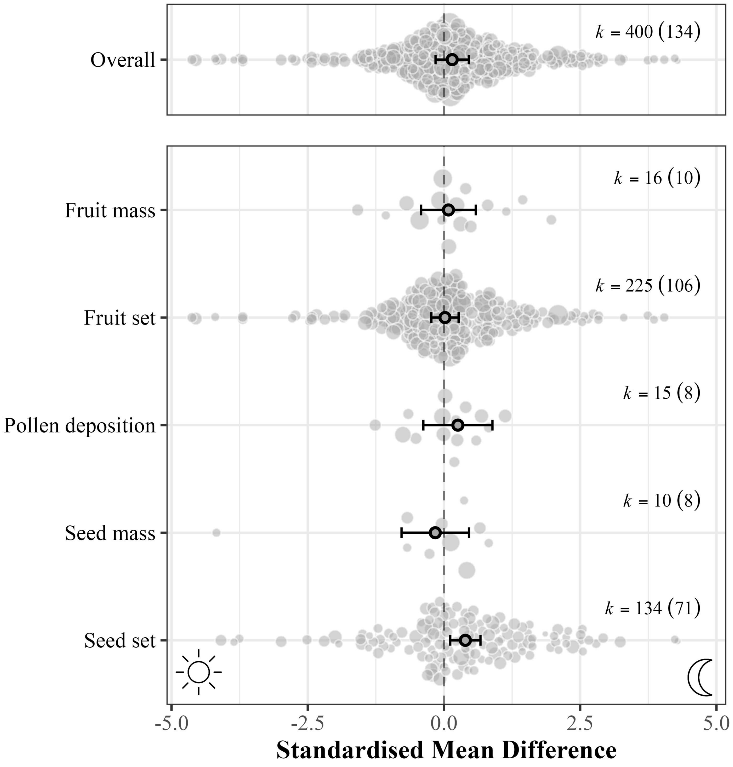

Figure 2. Standardized mean differences of the overall effect between day vs. night pollination for each pollination outcome measure, as well as the overall effect. Primary dots and error bars indicate marginal

mean estimates and 95% confidence intervals. Background points indicate individual effect sizes, in which size is proportional to the inverse of the standard error of the effect size.

Diel pollination differences in relation to environmental variables and plant traits

Comparison of the summary statistics (Omnibus Q test and ΔAIC, Table S2), as well as the explained variance (marginal R^2) in diel pollination outcomes (**Figure 3**) by each environmental and trait variable revealed that elevation was the only important tested environmental variable, whereas three plant functional traits, as well as species pollination dependency, explained a significant amount of variation.

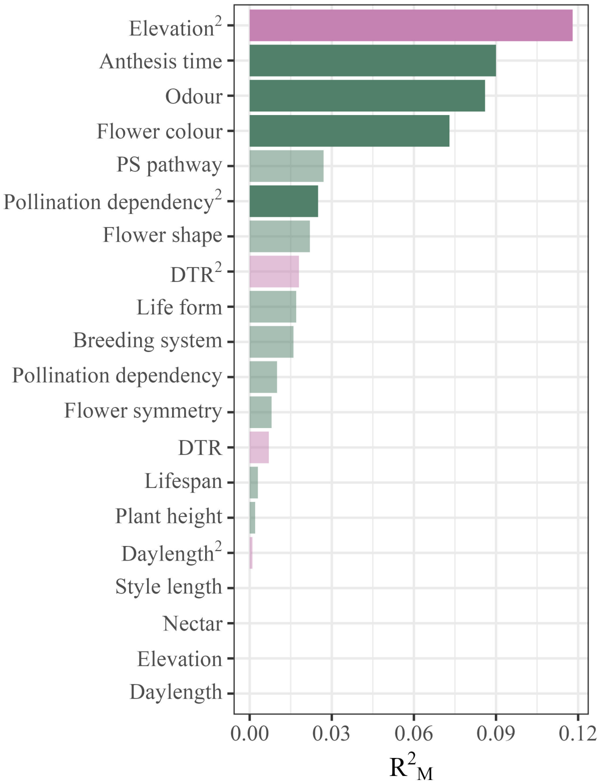

Figure 3. Coefficient of determination (marginal R^2) for each environmental (purple) and trait variable (green) in relation to each diel pollination comparison. Solid columns are those variables for which the omnibus test (Q_M) was significant ($p < 0.05$), whereas transparent columns were non-significant ($p > 0.05$).

We found that the success of nocturnal pollination relative to day pollination was highest at mid-elevations, before declining at higher elevations (linear term: z = 3.267, p = 0.001, quadratic term: z = -5.031, p < 0.0001, **Figure 4**).

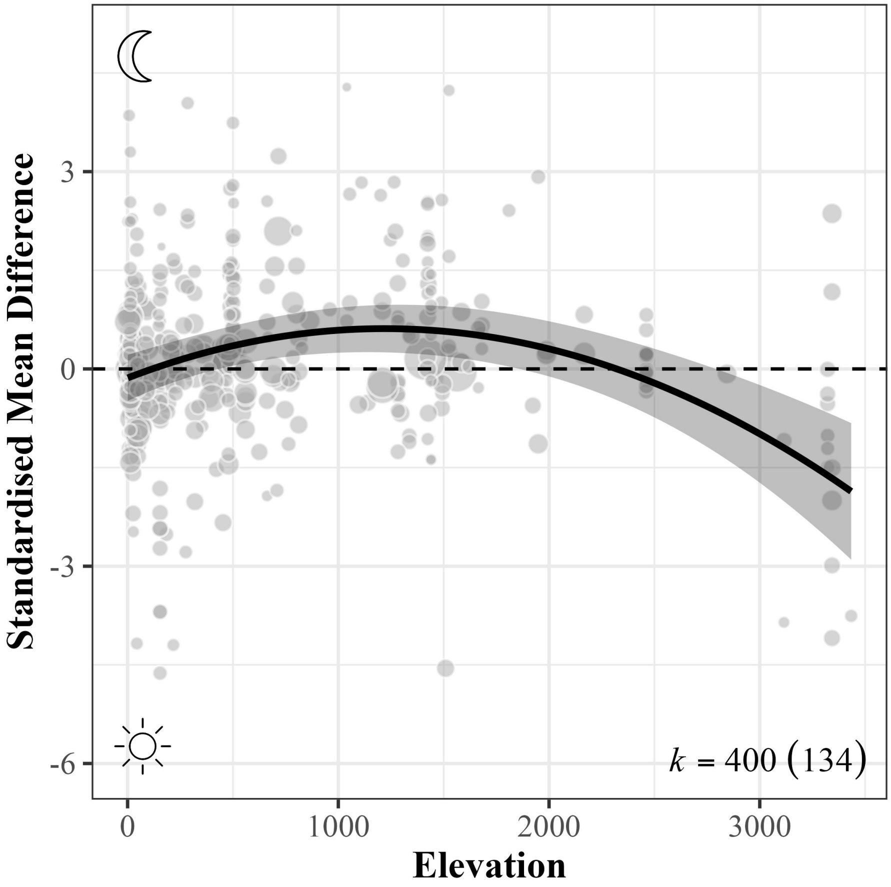

Figure 4. Standardized mean difference between diel pollination comparisons and elevation (m). Solid line and shaded ribbon indicate predicted line of best fit and 95% confidence intervals. Background points indicate individual effect sizes, in which size is proportional to the inverse of the standard error of the effect size.

Plant traits influenced diel pollination differences (**Figure 5**). Diurnal pollination success was higher, relative to nocturnal pollination, among species with flowers lacking discernible odour (-0.925, [-1.538, -0.382]), whereas the presence of odour led to the reverse (0.317, [0.007, 0.626]). In addition, nocturnally blooming plant species had significantly higher pollination success from nocturnal pollination relative to diurnal pollination (0.528, [0.188, 0.868]). Plants with orange and purple flowers exhibited greater pollination success from diurnal pollination relative to nocturnal pollination (orange: -1.559, [-2.718, -0.401]; purple: -1.142, [-2.175, -0.108]).

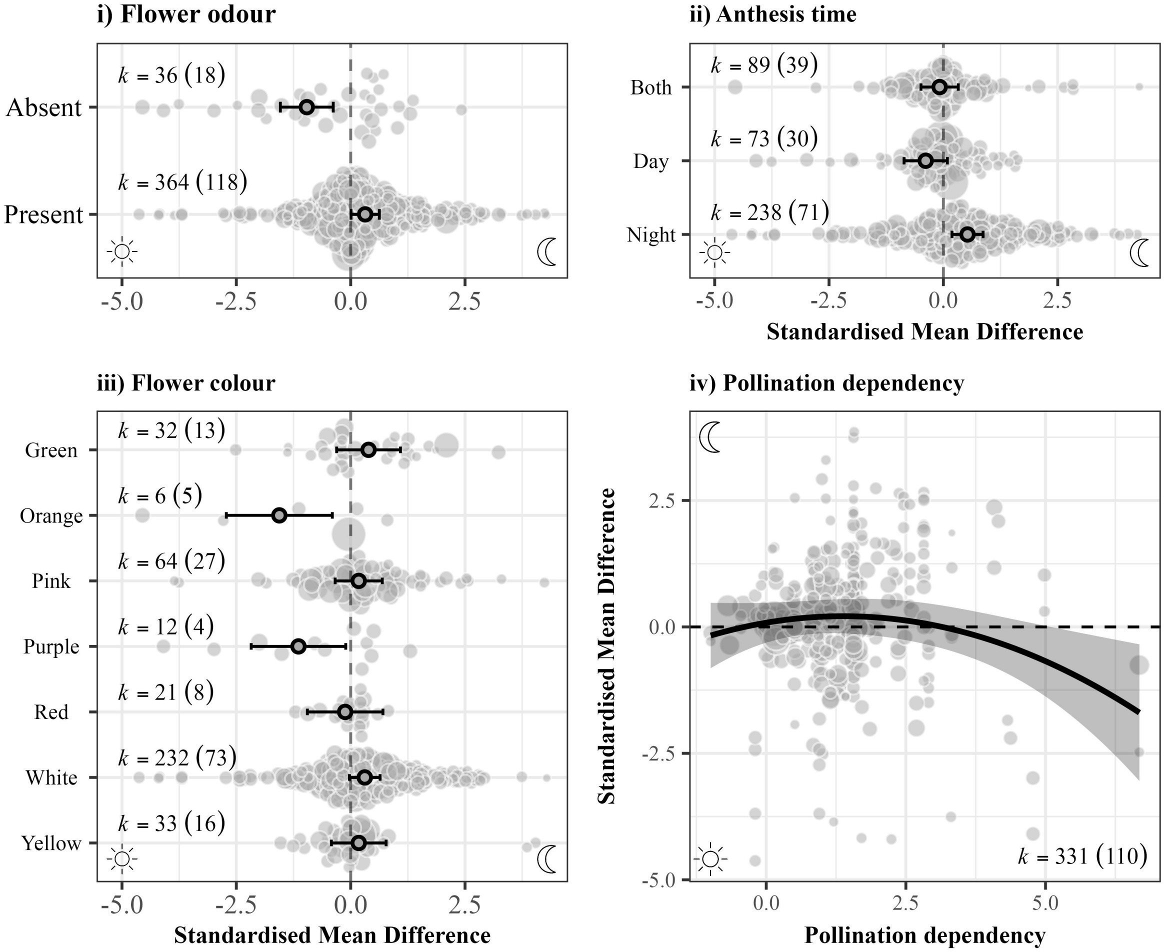

Figure 5. Standardized mean differences between diel pollination comparisons in relation to plant traits: i) flower odour, ii) anthesis time, iii) flower colour, and iv) pollination dependency. Primary dots and error bars (panels i-iii) indicate marginal mean estimates and 95% confidence intervals, and solid line and shaded ribbon indicate predicted line of best fit and 95% confidence intervals (panel iv). Background points indicate individual effect sizes, in which size is proportional to the inverse of the standard error of the effect size.

Influence of pollination dependency on diel pollination differences

We found that diurnal pollination was significantly better than nocturnal pollination for very high levels of pollination dependency (linear effect: z = 1.237, p = 0.216, quadratic term: z = -2.225, p = 0.026, **Figure 5**).

Publication bias and sensitivity analysis

The data showed little evidence of publication bias in terms of funnel plot asymmetry for the day vs. night pollination comparison (**Figure A1.3**). Results from the Egger's tests suggested there was no evidence for asymmetry (z = -0.892, p = 0.374). Additionally, we found no evidence for a time-lag effect (year effect: z = 0.573, p = 0.567).

Discussion

Through the most quantitative synthesis of pollination across the diel cycle, we present evidence of an overall lack of difference between day and night pollination. Adaptation to conditions in one part of the diel cycle may confer fitness disadvantages in other temporal periods. However, our results indicate diel generalization of pollination. Elevation and plant life history traits explained variation in diel pollination differences, but not plant phylogeny, daylength, or daily temperature range. Daytime and nighttime activity play an important role in temporal niche partitioning and ecosystem function. Given that pollination may be temporally generalized, important directions for future research include i) understanding the contribution and management of nocturnal crop pollinators (Buxton et al. 2022) and ii) understanding the magnitude and effect anthropogenic pressures on pollination in the nighttime environment, for example nighttime warming or light pollution (Tougeron and Sanders 2023).

Pollination success did not differ between day and night pollination, except for greater seed set from nocturnal pollination. For the plant species included in our analysis, authors hypothesized greater nocturnal pollination success was caused by increased dispersal of pollen (Young 2002, Barthelmess et al. 2006), more efficient pollen receipt or deposition (Miyake and Yahara 1998, Anderson et al. 2023), and the timing of anthesis or stigma receptivity (Groman and Pellmyr 1999, Young and Gravitz 2002), for example. Is the contribution of nocturnal pollinators to seed set detected here representative of angiosperm pollination more broadly? It’s unlikely because many studies chose plants for which there was an expectation of nocturnal pollination. Given this selection bias, perhaps the more surprising result is the general absence of diel pollination differences. These results, together with our findings that day or night pollination is often less effective than a full 24-hour pollination period (Appendix 2), point towards cathermality (activity during both daytime and nighttime) of plant reproductive strategies and pollination complementarity over time periods. Temporal complementarity, wherein both diurnal and nocturnal pollinators contribute to plant reproductive success (Jennersten and Morse 1991, Devoto et al. 2011, Amorim et al. 2013, Aguilar-Rodriguez et al. 2016, Funamoto and Sugiura 2021), provides functional redundancy across the diel cycle, and may provide resilience against pressures that disproportionately act during any one period (e.g., heat during the day, artificial light at night). Yet, substantial variation in the degree of diel pollination difference existed, and we found some support that this is explained by environmental variables and plant traits. We discuss these in turn.

Diel variation in pollination success was structured along an elevational gradient, such that nocturnal pollination was more beneficial among plant species at low - to - mid elevations (500 - 1500 m), whereas diurnal pollination was more effective at higher elevations (> 2750 m). The decline of nocturnal pollination success with altitude may be attributed to the reduced activity of night-active pollinators. For example, studies in the two cactus species *Oreocerus celsianus,* (Larrea-Alcazar and Lopez 2011) and *Echinopsis schnickendantzi* (Alonso-Pedano and Ortega-Baes 2012) at > 3000m demonstrated that diurnal pollination by hummingbirds or bees respectively, surpassed nocturnal pollination, owing to the infrequent presence of nocturnal pollinators. Interestingly, while *O. celsianus* exhibits floral traits suited for hummingbird pollination, those of *E. schnickendantzi* are suggestive of a moth pollination syndrome (e.g., presence of odour, white flowers), indicating the importance of flexibility of pollination syndromes for plant reproduction in harsh environments. Furthermore, previous studies have demonstrated elevational turnover in (sub-)tropical pollination systems, most notably from ectothermic invertebrates to endothermic vertebrates at high altitudes (Cruden 1972, Dellinger et al. 2023). As the environmental conditions at high altitudes associated with diurnal foraging activity are arguably less severe than nighttime conditions, our results suggest that altitudinal shifts in pollination systems can also result in diel turnover in pollination success across both vertebrate and invertebrate taxa.

The underlying causes of improved nocturnal pollination success at lower elevations remain ambiguous yet may reflect underlying elevational patterns in biodiversity. Both species and interaction diversity in plant-pollinator networks can peak at mid elevations (Hoiss et al. 2015), and diel network comparisons highlight that nocturnal pollination networks can be more species rich than diurnal networks (Walton et al. 2020). Thus, given that pollinator diversity can be linked with greater pollination success (Dainese et al. 2019), observed trends may indicate previously unappreciated diversity of nocturnal insects within a large proportion of studied pollination systems.

Our results support classical notions of pollination syndromes based on simple morphological traits. Nocturnal pollination success was higher, relative to diurnal pollination, for odour-producing flowers with night anthesis. Conversely, plants with scentless and orange or purple flowers with day anthesis benefitted more from diurnal pollination. Although pollinators use both visual and olfactory cues (Riffell and Alarcón 2013), odour can be a more reliable and longer ranging cue at night. Our results support the importance of odour as a critical stimulus for nocturnal pollinators. We hesitate to conclude on the adaptive significance of flower colour, given 1) small sample sizes (e.g., six effect sizes for orange flowers), 2) a prevalence of non-significant differences across all colours, and 3) flower pigment is often genetically correlated (e.g., through pleiotropy) with other traits that could be under selection (Mckinnon and Pierotti 2010, Wessinger and Rausher 2012).

We found a strong association between nocturnal pollination and increased pollination success in flowers that open at night. This association is suggestive of an adaptive response due to greater pollinator efficiency among nocturnally active pollinators compared to their diurnal counterparts. For instance, Young (2002) proposed that nyctinasty, where flowers open at night and close during the day, led to increased pollination success in *Silene alba,* as moths transported pollen across greater distances, leading to improved outcrossing rates, whilst simultaneously limiting pollination by less effective diurnal pollinators. In addition, synchronisation between flower anthesis timing and stigma receptivity has also been proposed as a potential mechanism for diel variation in pollination outcomes (Young and Gravitz 2002). However, Young & Gravitz found no evidence of this, and our results also do not support this notion as we found no corresponding pattern between diurnal pollination and daytime-blooming flowers. Furthermore, several studies indicate that the timing of pollination throughout the day has minimal impact on pollination outcomes, as demonstrated through timed hand pollination experiments (Haber and Franke 1982, Kwak and Jennersten 1986, Wolff et al. 2003, Martins et al. 2020). As such, our results contend that nocturnal anthesis likely represents an adaptive strategy, alongside other traits which affect pollinator preference such as odour and colour (Matsumoto et al. 2015) due to the improved pollinator efficiency of nocturnal pollinators for these plant species.

Our meta-analysis reveals blind spots in our understanding of pollination across the diel cycle. Given the importance of pollination for crop production, we were surprised that most studies (87%) focused on non-cultivated plants. Interestingly, a number of studies found no difference between day and night pollination for crop species expected to be primarily bee, which is to say day-pollinated (Cutler et al. 2012, Robertson et al. 2021, Fijen et al. 2023). This highlights the potential importance of night-time pollination and risk of yield gaps if nocturnal pollinators are not part of crop pollination management plans. However, diurnal and nocturnal pollinators may not respond equivalently to agricultural management. For example, planting herbaceous wildflowers to support pollinators may be effective for bees (Albrecht et al. 2020), yet moth communities are likely to benefit from increasing tree and shrub density (Bates et al. 2014, Ellis and Wilkinson 2021). One direction for future crop pollination research is to investigate the degree of nocturnal pollination dependency and what management practices can co-benefit diurnal and nocturnal pollinator communities.

Our meta-analysis has limitations. First, lunar cycles can regulate the activity of many insects (Warrant and Dacke 2010, Kronfeld-Schor et al. 2013), including pollinators (Kerfoot 1967, Young et al. 2021), but studies rarely reported lunar phase or date information at resolutions fine enough to examine this. Future experiments could consider lunar phase as an important covariate in the design and analysis of diel pollination research. Second, we focus on biotic pollination. Environmental factors that differ between day and night, such as air turbidity and humidity would likely affect abiotic pollination, for example wind pollination (Timerman and Barrett 2021). Last, we do not report the pollinator taxa responsible for nocturnal or diurnal pollination. Studies used a variety of methods (e.g., point counts, pan traps), sampled over a range of time periods (e.g., minutes to hours), and reported pollinator identity at different taxonomic resolutions. This lack of standardization is understandable. Conducting nighttime pollinator observations is demanding and logistically challenging, particularly when experiments require in person observation. Technological innovations in biodiversity monitoring, such as eDNA, acoustic recording devices, and cameras could overcome these challenges, provide more standardized monitoring, and adjust the diurnal bias in ecological research.

Conclusions

Diel variation in conditions, resources, and interactions can form the basis of temporal niches in which species have evolved traits to maximize fitness (Kronfeld-Schor and Dayan 2003). Temporal partitioning across a diel cycle may facilitate plant coexistence, for example through a reduction in competition for pollinators (e.g., Stone et al. 1997), but our results do not support the generalization of temporal specialization. Rather, plant reproductive success is often flexible to the timing of pollination. Where diel pollination differences do exist, that they are explained by flower colour, odour, and anthesis time will not surprise adherents of pollination syndromes. Nonetheless, our data show that exceptions to syndrome-based expectations are numerous, and thus we discourage assuming pollinator activity period based on plant traits alone. We did not find support for large-scale biogeographical patterns of diel pollination difference, for example across latitudinal gradients of daylength (Munguia-Rosas et al. 2009, Sletvold et al. 2012) or temperature range (Borges et al. 2016). Our meta-analysis resolves the ‘lack of strong experimental evidence’ of diel pollination differences (Buxton et al. 2022) and highlights where there is more to learn about the drivers, consequences, and responses to diurnal and nocturnal pollination. Diel variation in ecosystem functioning is a frontier of ecological research (Cox and Gaston 2023) and anthropogenic pressures on the nighttime environment are increasing (Gaston et al. 2023). Redressing a diurnal bias in ecological research will continue to yield novel insights and evidence needed to ensure ecosystem functioning in daytime and nighttime environments.

Author contributions

LKK and CCN contributed equally to study conception, design and methodology, data acquisition, data analysis, data interpretation, and writing.

Acknowledgements

The authors would like to thank Frida Rosengren and Johnny Jönsson from Lund University Biology Library for assistance developing our literature search, Hakim Abdi for his advice on global temperature databases, and Alexandra Klein for bearing witness to the coin toss that determined author order. Earlier versions of this manuscript benefitted from comments by Øystein Opedal and Hanna Thosteman.

Conflict of interest statement

The authors have no competing interests to declare.

Data availability statement

Data will be made available through an open GitHub repository.

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APPENDIX 1

Supporting information

Table S1. Trait values for plant species reported in included studies. Qualitative traits were scored based on flower symmetry (actinomorphic: A; zygomorphic: Z), life span (perennial: P; short-lived: S), life form, photosynthetic (PS) pathway, flower shape, breeding system (hermaphrodite: h, diecious: d; monoecious: m), anthesis time (day-blooming: D, night-blooming: N, both or unclear: B), the presence or absence (p vs. a) of nectar and odour, and colour (green: G; orange: O; pink: Pi; purple: Pu; red: R; white: W; yellow: Y). For quantitative traits, we converted all floral measurements to mm and all plant heights to m. Where values were reported as a range (e.g., 6-10 m) we used the midpoint. We include both the species name reported in study articles and the species name used to construct phylogenies based on (Smith and Brown 2018).

Reported species	**Current species**	**Plant family**	**Flower symmetry**	**life span**	**Life form**	**PS pathway**	**Flower shape**	**Breeding system**	**Anthesis time**	**nectar**	**odour**	**colour**	**Flower width (mm)**	**Flower length (mm)**	**Style length (mm)**	**Plant height (m)**
Abronia fragrans	Abronia fragrans	Nyctaginaceae	A	P	herb	C3	tube	h	N	p	p	Pi	8	25	15	0.7
Abronia umbellata	Abronia umbellata	Nyctaginaceae	A	S	herb	C3	tube	h	B	p	p	Pu	16	20	8	0.075
Echinopsis leucantha	Acanthocalycium leucanthum	Cactaceae	A	P	herb	CAM	tube	h	N	p	a	W	113.62	198.14	150	1.25
Adenophora capillaris	Adenophora capillaris	Campanulaceae	A	P	herb	C3	campanulate	h	N	p	p	W	4.95	13.9	27.25	0.75
Adenophora jasionifolia	Adenophora jasionifolia	Campanulaceae	A	P	herb	C3	campanulate	h	D	p	a	Pu	29.19	18.44	22.18	0.35
Adenophora khasiana	Adenophora khasiana	Campanulaceae	A	P	herb	C3	campanulate	h	N	p	a	Pu	24.65	20.59	25.37	1
Adenophora triphylla	Adenophora triphylla	Campanulaceae	A	P	herb	C3	campanulate	h	N	p	a	Pu	9.5	9.5	17	1.5
Aegiceras corniculatum	Aegiceras corniculatum	Primulaceae	A	P	tree	C3	brush	h	D	p	p	W	15	12	10.35	6
Agarista revoluta	Agarista revoluta	Ericaceae	A	P	tree	C3	campanulate	h	B	p	p	W	6.1	8.7	4.4	2.7
Agave angustifolia	Agave angustifolia	Asparagaceae	A	P	herb	CAM	tube	h	B	p	p	W	12.5	65	95	0.75

Agave chrysantha	Agave chrysantha	Asparagaceae	A	P	herb	CAM	tube	h	D	p	p	Y	12.5	40	57.5	1
Agave colorata	Agave colorata	Asparagaceae	A	P	herb	CAM	tube	h	D	p	p	G	12.5	47.5	65	2.5
Agave horrida	Agave horrida	Asparagaceae	A	P	herb	CAM	tube	h	N	p	p	Y	17.5	40	55	0.45
Agave macroacantha	Agave macroacantha	Asparagaceae	A	P	herb	CAM	tube	h	N	p	p	G	9	57.5	62.5	0.45
Agave palmeri	Agave palmeri	Asparagaceae	A	P	herb	CAM	tube	h	D	p	p	G	17.5	40	50	0.45
Agave subsimplex	Agave subsimplex	Asparagaceae	A	P	herb	CAM	tube	h	B	p	p	Y	15	37.5	52.5	0.275
ManfRa virginica	Agave virginica	Asparagaceae	A	P	herb	CAM	tube	h	B	p	p	G	4	20	32.5	1
Aloe peglerae	Aloe peglerae	Asphodelaceae	A	S	herb	CAM	tube	h	N	p	a	Y	13	30	55	0.4
Asclepias syriaca	Asclepias syriaca	Apocynaceae	A	P	herb	C3	open	h	B	p	p	Pi	12.5	9	0.41	1.5
Asclepias verticillata	Asclepias verticillata	Apocynaceae	A	P	herb	C3	open	h	B	p	p	Pi	4.2	3.33	0.375	0.45
Banksia ericifolia	Banksia ericifolia	Proteaceae	A	P	shrub	C3	brush	h	B	p	p	O	57.5	150	25	6
Billbergia horrida	Billbergia horrida	Bromeliaceae	A	P	herb	CAM	tube	h	N	p	p	G	55	25	50	0.4
Durio grandiflorus	Boschia grandiflora	Malvaceae	A	P	tree	C3	open	h	D	a	p	W	60	15	25	11.5
Brunsvigia gregaria	Brunsvigia gregaria	Amaryllidaceae	A	P	herb	C3	tube	h	B	p	a	R	35	40	40	0.185
Calliandra longipedicellata	Calliandra longipedicellata	Fabaceae	A	P	shrub	C3	brush	h	N	p	p	R	60	50	60	2
Carnegiea gigantea	Carnegiea gigantea	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	24.9	112.2	53.9	8
Castilleja citrina	Castilleja purpurea var. citrina	Orobanchaceae	Z	P	herb	C3	tube	h	B	p	p	Y	3.5	32.5	34.5	0.25
Castilleja lindheimeri	Castilleja purpurea var. lindheimeri	Orobanchaceae	Z	P	herb	C3	tube	h	B	p	p	O	2.5	37.5	40.5	0.3
Castilleja sessiliflora	Castilleja sessiliflora	Orobanchaceae	Z	P	herb	C3	tube	h	B	p	p	W	3	42.5	44.5	0.22
Cipocereus crassisepalus	Cipocereus crassisepalus	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	55.9	55.7	84	3
Cipocereus minensis	Cipocereus minensis	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	32.8	46.1	27.4	2
Clerodendrum izuinsulare	Clerodendrum izuinsulare	Lamiaceae	A	P	tree	C3	tube	h	B	p	p	W	11.47	26.25	33.47	7.5
Clerodendrum trichotomum	Clerodendrum trichotomum	Lamiaceae	A	P	tree	C3	tube	h	D	p	p	W	14.67	25.29	42.81	7.5
Clerodendrum molle	Clerodendrum villosum	Lamiaceae	A	P	shrub	C3	tube	h	B	p	p	W	1.75	25	25	3.25

Cordia lutea	Cordia lutea	Boraginaceae	A	P	shrub	C3	tube	h	D	p	p	Y	30	30	20	8
Cullenia exarillata	Cullenia exarillata	Malvaceae	A	P	tree	C3	tube	h	D	p	p	brown	13.5	45	54	27.5
Daphne jezoensis	Daphne jezoensis	Thymelaeaceae	A	P	shrub	C3	tube	d	B	p	p	Y	10.8	6.4	2.7	0.2
Durio kutejensis	Durio kutejensis	Malvaceae	A	P	tree	C3	open	h	N	p	p	R	110	40	72.5	12
Durio oblongus	Durio oblongus	Malvaceae	A	P	tree	C3	open	h	D	p	p	W	95	37.5	67.5	25
Echium simplex	Echium simplex	Boraginaceae	A	P	herb	C3	tube	h	D	p	p	W	5	12.5	17.5	3
Encholirium spectabile	Encholirium spectabile	Bromeliaceae	A	P	herb	CAM	tube	h	N	p	p	G	20	15	10	2.5
Escallonia myrtoidea	Escallonia myrtoidea	Escalloniaceae	A	P	tree	C3	campanulate	h	B	p	p	W	85	65	65	6
Eupatorium perfoliatum	Eupatorium perfoliatum	Asteraceae	A	P	herb	C3	capitulum	h	B	p	p	W	3	5	6	1
Faramea cyanea	Faramea occidentalis	Rubiaceae	A	P	tree	C3	tube	h	N	p	p	W	14	17	9	9
Grazielia intermedia	Grazielia intermedia	Asteraceae	A	P	herb	C3	capitulum	d	D	p	p	W	2	4	6	2.5
Grevillea robusta	Grevillea robusta	Proteaceae	Z	P	tree	C3	brush	h	D	p	p	O	2	23	17.5	17.5
Guettarda scabra	Guettarda scabra	Rubiaceae	A	P	shrub	C3	tube	h	N	p	p	W	11.66	15.1	16.9	3.25
Gymnadenia conopsea	Gymnadenia conopsea	Orchidaceae	Z	P	herb	C3	papilionaceous	h	D	p	p	Pi	10.34	15	1.5	0.237
Inga ingoides	Inga ingoides	Fabaceae	A	P	tree	C3	brush	h	D	p	p	W	5	14	73	20
Inga striata	Inga striata	Fabaceae	A	P	tree	C3	brush	h	D	p	p	W	4	10	71	20
Inga vera	Inga vera	Fabaceae	A	P	tree	C3	brush	h	D	p	p	W	6	14	45	20
Ipomoea carnea	Ipomoea carnea	Convolvulaceae	A	P	shrub	C3	tube	h	B	p	p	Pi	88.6	79.1	18.8	1.5
Ipomoea habeliana	Ipomoea habeliana	Convolvulaceae	A	P	vine	C3	tube	h	N	p	p	W	60	110	150	8
Ipomoea marcellia	Ipomoea marcellia	Convolvulaceae	A	P	vine	C3	tube	h	D	p	p	W	22.7	57.5	55.94	1.75
Ipomopsis aggregata	Ipomopsis aggregata	Polemoniaceae	A	S	herb	C3	tube	h	N	p	p	R	2.5	32.5	25.5	0.9
Isertia laevis	Isertia laevis	Rubiaceae	A	P	tree	C3	tube	h	N	p	p	W	32.4	41	42	15
Jatropha curcas	Jatropha curcas	Euphorbiaceae	A	P	tree	CAM	campanulate	m	D	p	p	G	8.47	4.44	7.59	12.5
Lagenaria siceraria	Lagenaria siceraria	Cucurbitaceae	A	S	vine	C3	tube	m	N	p	p	W	95	9.4	3.5	9
Leptocereus scopulophilus	Leptocereus scopulophilus	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	36	53	37	4

Echinopsis chiloensis	Leucostele chiloensis	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	85	150	90.4	4.5
Echinopsis terscheckii	Leucostele terscheckii	Cactaceae	A	P	herb	CAM	tube	h	N	p	a	W	163.8	177.7	153.9	15
Lilium auratum	Lilium auratum	Liliaceae	A	P	herb	C3	open	h	D	p	p	W	140	110	120	2.5
Lilium formosanum	Lilium formosanum	Liliaceae	A	P	herb	C3	open	h	B	p	p	W	110	130	140.5	1.4
Lonicera etrusca	Lonicera etrusca	Caprifoliaceae	Z	P	vine	C3	tube	h	N	p	p	W	2.5	32.9	42.7	4
Marginatocereus marginatus	Lophocereus marginatus	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	R	15.7	34.7	22.88	8.5
Lophocereus schottii	Lophocereus schottii	Cactaceae	A	P	herb	CAM	tube	h	N	a	p	Pi	6.1	30	50	3
Luculia pinceana	Luculia pinceana	Rubiaceae	A	P	shrub	C3	tube	h	B	p	p	Pi	30	27.5	33	6
Luehea seemannii	Luehea seemannii	Malvaceae	A	P	tree	C3	open	m	N	p	p	W	15	7.5	10	22.5
Luffa acutangula	Luffa acutangula	Cucurbitaceae	A	S	herb	C3	tube	m	N	p	p	Y	52.2	11	3.5	6
Lyonia lucida	Lyonia lucida	Ericaceae	A	P	shrub	C3	campanulate	h	B	p	p	Pi	3.5	7	6	3.75
Mabea fistulifera	Mabea fistulifera	Euphorbiaceae	A	P	tree	C3	open	m	N	p	p	R	13	26.6	26.6	6.5
Macleania bullata	Macleania bullata	Ericaceae	A	P	shrub	C3	tube	h	B	p	a	O	5	42	43.8	3
Malus domestica	Malus domestica	Rosaceae	A	P	tree	C3	open	h	B	p	p	W	35	15	12.5	3.5
Mitrastemon yamamotoi	Mitrastemon yamamotoi	Mitrastemonaceae	A	P	herb	NA	open	h	B	p	p	W	20	15	25	0.025
Ipomoea aff. Marcellia	Ipomoea aff. Marcellia	Convolvulaceae	A	P	vine	C3	tube	h	N	p	p	W	18.42	22.73	42.33	1.75
Narcissus papyraceus	Narcissus papyraceus	Amaryllidaceae	A	P	herb	C3	tube	h	B	p	p	W	30	14.5	16	0.375
Nicotiana attenuata	Nicotiana attenuata	Solanaceae	A	S	herb	C3	tube	h	N	p	p	W	12.5	35	30	1.25
Nicotiana rustica	Nicotiana rustica	Solanaceae	A	S	herb	C3	tube	h	D	p	p	Y	6.9	18	23	1.06135
Ochroma pyramidale	Ochroma pyramidale	Malvaceae	A	P	tree	C3	tube	h	N	p	p	W	200	115	150	30
Oreocereus celsianus	Oreocereus celsianus	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	Pi	60	78.1	75	6
Pachycereus pecten-aboriginum	Pachycereus pecten-aboriginum	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	62	77	45	8
Pachycereus pringlei	Pachycereus pringlei	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	24.2	102.2	53.2	7
Pedicularis siphonantha	Pedicularis siphonantha	Orobanchaceae	Z	P	herb	C3	papilionaceous	h	D	p	a	Pi	55	50.6	11	0.15

Phlox drummondii	Phlox drummondii	Polemoniaceae	A	S	herb	C3	tube	h	D	p	p	Pu	21	15	1.56	0.225
Pilosocereus chrysacanthus	Pilosocereus chrysacanthus	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	Pi	36.41	93.94	75.17	4
Platanthera hologlottis	Platanthera hologlottis	Orchidaceae	Z	P	herb	C3	papilionaceous	h	B	p	p	W	11	15	2	0.6
Putoria calabrica	Plocama calabrica	Rubiaceae	A	P	shrub	C3	tube	h	B	p	a	Pi	6.29	14.09	28.33	0.11
Polaskia chichipe	Polaskia chichipe	Cactaceae	A	P	herb	CAM	tube	h	D	p	p	G	35	30	14	3
Prunus persica	Prunus persica	Rosaceae	A	P	tree	C3	open	h	B	p	p	Pi	27.5	15	12	5
Tillandsia macropetala	Pseudalcantarea macropetala	Bromeliaceae	A	P	herb	C3	tube	h	N	p	p	G	107	30	104	1.525
Psittacanthus robustus	Psittacanthus robustus	Loranthaceae	A	P	vine	C3	tube	h	D	p	a	Y	5	110	100	7
Pterocereus gaumeri	Pterocereus gaumeri	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	Y	51	50	40	8
Randia itatiaiae	Randia itatiaiae	Rubiaceae	A	P	shrub	C3	tube	m	N	p	p	W	20.8	16.6	13	6.5
Rubus chamaemorus	Rubus chamaemorus	Rosaceae	A	P	herb	C3	open	d	D	a	a	W	19	2.52	4.39	0.175
Salix caprea	Salix caprea	Salicaceae	A	P	shrub	C3	brush	d	N	p	p	G	13.9	30.3	0.2	9
Hylocereus costaricensis	Selenicereus costaricensis	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	250	260	200	4
Hylocereus polyrhizus	Selenicereus monacanthus	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	70	135	200	4
Hylocereus undatus	Selenicereus undatus	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	136	345	200	4
Silene caroliniana	Silene caroliniana	Caryophyllaceae	A	P	herb	C3	tube	h	D	p	a	Pi	1.9	21.2	24.1	0.15
Silene ciliata	Silene ciliata	Caryophyllaceae	A	P	herb	C3	tube	h	N	p	a	Pi	4	12.5	13.5	0.02
Silene latifolia	Silene latifolia	Caryophyllaceae	A	P	herb	C3	tube	d	N	p	p	W	24	27	17	0.45
Silene alba	Silene latifolia subsp. alba	Caryophyllaceae	A	P	herb	C3	tube	d	N	p	p	W	9	22.3	28	0.65
Silene lemmonii	Silene lemmonii	Caryophyllaceae	A	P	herb	C3	tube	h	N	a	a	W	3	8	16	0.55
Silene nutans	Silene nutans	Caryophyllaceae	A	P	herb	C3	tube	d	N	p	p	W	3	10.9	14.5	0.42
Silene sennenii	Silene sennenii	Caryophyllaceae	A	P	herb	C3	tube	h	N	a	p	Pi	5	11	10	0.55
Silene stellata	Silene stellata	Caryophyllaceae	A	P	herb	C3	tube	h	N	a	p	W	8	9.8	20.1	1.2
Silene virginica	Silene virginica	Caryophyllaceae	A	P	herb	C3	tube	h	D	p	a	R	3.6	24.1	31.3	0.3

Viscaria vulgaris	Silene viscaria	Caryophyllaceae	A	P	herb	C3	tube	h	B	p	p	Pi	20	12	15	0.375
Silene vulgaris	Silene vulgaris	Caryophyllaceae	A	P	herb	C3	tube	h	B	p	p	Pi	20	12	15	0.375
Echinopsis schickendantzii	Soehrensia schickendantzii	Cactaceae	A	P	herb	CAM	tube	h	N	a	p	W	175	180	115	2
Echinopsis thelegona	Soehrensia thelegona	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	142.1	182.5	133	2.5
Sonneratia caseolaris	Sonneratia caseolaris	Lythraceae	A	P	tree	C3	open	h	N	p	p	W	55	57.5	82	15
Stachyurus praecox	Stachyurus praecox	Stachyuraceae	A	P	shrub	C3	campanulate	d	B	p	p	Y	8	5	5	2.9
Stenocereus queretaroensis	Stenocereus queretaroensis	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	48	88.77	70.03	10
Stenocereus quevedonis	Stenocereus quevedonis	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	43	75	40	6
Stenocereus stellatus	Stenocereus stellatus	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	Pi	35	67.5	37.5	4
Stenocereus thurberi	Stenocereus thurberi	Cactaceae	A	P	herb	CAM	tube	h	N	p	p	W	18.7	79.2	58	3.4
Syzygium laetum	Syzygium laetum	Myrtaceae	A	P	tree	C3	brush	h	B	p	p	R	60.3	56.4	44.9	10
Syzygium mundagam	Syzygium mundagam	Myrtaceae	A	P	tree	C3	brush	h	B	p	p	W	43.8	37.1	24.8	15
Syzygium sayeri	Syzygium sayeri	Myrtaceae	A	P	tree	C3	brush	h	D	p	a	W	4.47	29.48	16.19	22.5
Tilia americana	Tilia americana	Malvaceae	A	P	tree	C3	open	h	N	p	p	Y	12	4	4	27.5
Tilia cordata	Tilia cordata	Malvaceae	A	P	tree	C3	open	h	N	p	p	Y	7	4	4	30
Tilia platyphyllos	Tilia platyphyllos	Malvaceae	A	P	tree	C3	open	h	N	p	p	Y	14.5	4	4	30
Tillandsia heterophylla	Tillandsia heterophylla	Bromeliaceae	A	P	herb	C3	tube	h	N	p	p	W	14	10	70	1.5
Tournefortia rufo-sericea	Tournefortia rufo-sericea	Boraginaceae	A	P	shrub	C3	tube	h	B	p	p	W	4	5	2	2.5
Trichosanthes anguina	Trichosanthes cucumerina	Cucurbitaceae	A	S	herb	C3	tube	m	N	p	p	W	37.5	27.5	27.5	2.5
Trichosanthes kirilowii	Trichosanthes kirilowii	Cucurbitaceae	A	S	herb	C3	tube	m	N	p	p	W	25	12	12	6
Trifolium pratense	Trifolium pratense	Fabaceae	Z	S	herb	C3	papilionaceous	h	B	p	p	Pi	3.5	16	16	0.5
Vaccinium angustifolium	Vaccinium angustifolium	Ericaceae	A	P	shrub	C3	campanulate	h	B	p	p	W	5	5	4	0.325
Vitis rotundifolia	Vitis rotundifolia	Vitaceae	A	P	vine	C3	open	d	B	p	p	G	3.5	3.5	1	21
Yucca aloifolia	Yucca aloifolia	Asparagaceae	A	P	herb	CAM	campanulate	h	N	a	p	W	55	35	17.5	2

Yucca elata	Yucca elata	Asparagaceae	A	P	herb	CAM	campanulate	h	N	a	p	W	59.5	44.5	10	5
Yucca filamentosa	Yucca filamentosa	Asparagaceae	A	P	herb	C3	campanulate	h	N	a	p	W	35	35	25	2.75
Fragaria x ananassa	Fragaria ananassa	Rosaceae	A	P	herb	C3	open	h	B	p	p	W	31.2	31.2	1	0.2
Fontainea picrosperma	Fontainea picrosperma	Euphorbiaceae	A	P	tree	C3	open	d	B	a	p	W	19.5	6.5	4	25
Rubus fruticosus	Rubus fruticosus	Rosaceae	A	P	shrub	C3	open	h	B	p	p	W	22.5	7.5	4	2.5
Clarkia concinna	Clarkia concinna	Onagraceae	Z	S	herb	C3	open	h	B	p	p	Pi	56.9	17.5	14.6	0.22
Clarkia breweri	Clarkia breweri	Onagraceae	Z	S	herb	C3	open	h	B	p	p	Pi	48.4	12.5	23.1	0.175
Habenaria dentata	Habenaria dentata	Orchidaceae	Z	P	herb	C3	papilionaceous	h	D	p	a	W	6.97	44.9	2	0.575
Lonicera japonica	Lonicera japonica	Caprifoliaceae	Z	P	vine	C3	tube	h	N	p	a	W	15	40	40	10
Banksia spinulosa	Banksia spinulosa	Proteaceae	A	P	shrub	C3	brush	h	B	p	p	Y	65	105	22.5	2

Table S2. Summary statistics for each univariate meta-regression day vs. night pollination in relation to environmental and plant trait variables. ΔAIC: Difference in AIC relative to the meta-analytic model. Q_M: Omnibus (Wald-type) test statistic for each moderator, along with its degree of freedom and p-value. R^2_M and R^2_C: Marginal and conditional R^2. QE: test statistic for residual heterogeneity, along with degrees of freedom and p-value. Variables are in descending order of R^2_M. ΔAIC is not shown for pollination dependency, as this model was formulated on a subset of the dataset.

Variable	ΔAIC	Q_M	df	p-value	R^2_M	R^2_C	QE	df	p-value
Elevation^2	**-26,717**	**25,319**	2	*<0,001*	**0,118**	0,763	6157,708	397	<0,001
Anthesis time	-16,823	15,249	2	*<0,001*	0,090	0,749	5947,952	397	<0,001
Odour	-19,197	19,351	1	*<0,001*	0,086	0,744	6100,98	398	<0,001
Flower colour	-22,77	17,576	6	*0,007*	0,073	0,744	**5549,994**	393	<0,001
PS pathway	-4,684	3,331	1	0,068	0,027	0,745	5993,103	398	<0,001
Pollination dependency^2	NA	7,148	1	0,028	0,025	0,671	3995,044	328	<0,001
Flower shape	-8,062	3,756	4	0,44	0,022	0,748	5979,118	395	<0,001
DTR^2	-5,535	4,277	2	0,118	0,018	0,737	6284,907	397	<0,001
Life form	-5,721	3,303	3	0,347	0,017	0,744	6308,643	396	<0,001
Breeding system	-5,216	3,051	2	0,218	0,016	0,746	6287,106	397	<0,001
Pollination dependency	NA	2,249	1	0.134	0,01	0,676	4033,452	329	<0,001
Flower symmetry	-2,487	1,292	1	0,256	0,008	0,744	6300,742	398	<0,001
DTR	-2,297	1,467	1	0,226	0,007	0,734	6296,897	398	<0,001
Lifespan	-1,738	0,35	1	0,554	0,003	0,744	6336,999	398	<0,001
Plant height	-1,428	0,414	1	0,52	0,002	0,744	6336,731	398	<0,001
Daylength^2	-2,56	0,099	2	0,952	0,001	0,744	6225,039	397	<0,001
Daylength	-1,241	0,021	1	0,886	0	0,742	6257,82	398	<0,001
Nectar	-1,345	0,011	1	0,915	0	0,742	6188,07	398	<0,001
Style length	-1,445	0,006	1	0,937	0	0,743	6303,569	398	<0,001
Elevation	-1,25	0,001	1	0,979	0	0,742	6337,012	398	<0,001

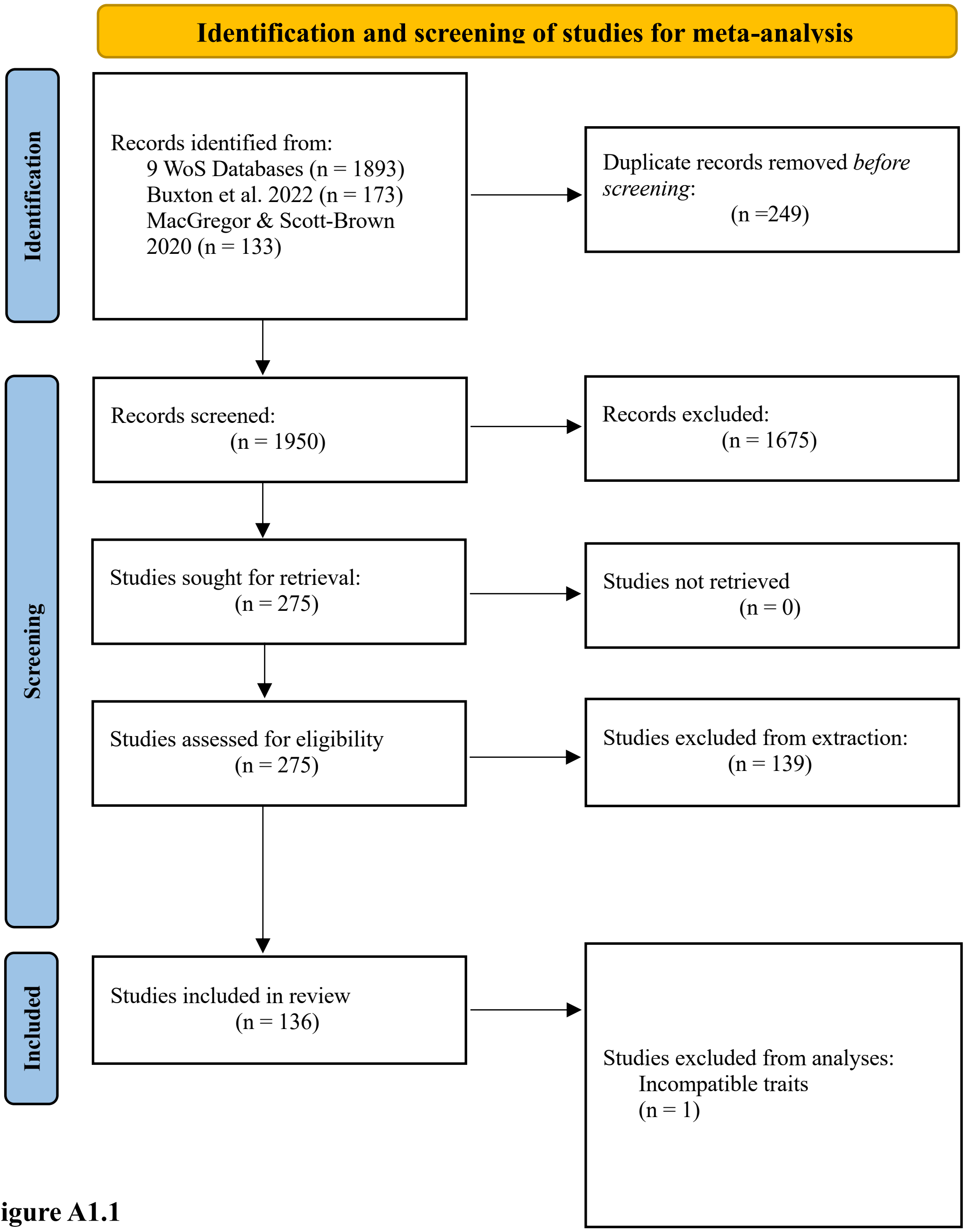
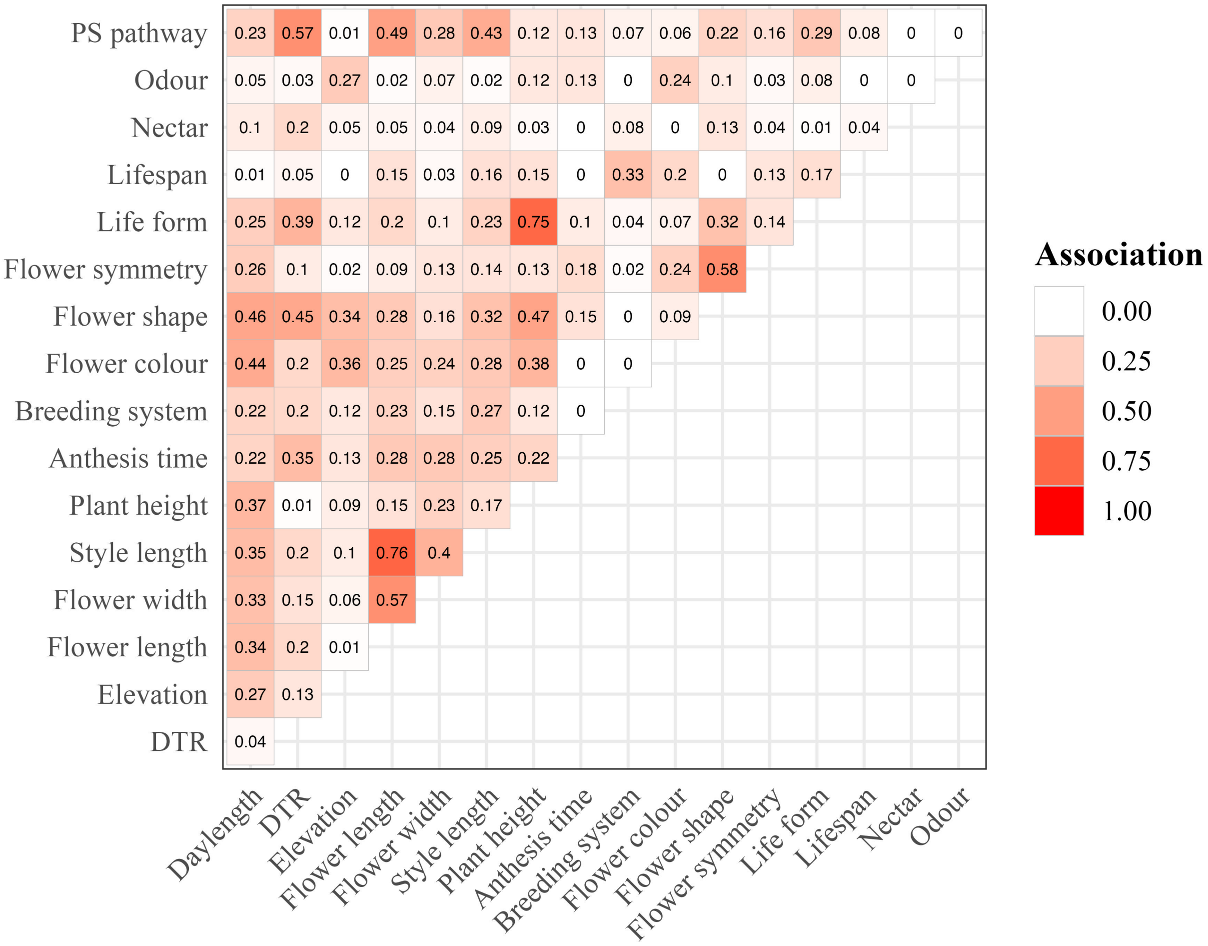

Identification and screening of studies for meta-analysis
Identification
Screening
Included
Records identified from:
9 WoS Databases (n = 1893)
Buxton et al. 2022 (n = 173)
MacGregor & Scott-Brown 2020 (n = 133)
Duplicate records removed *before screening*:
(n =249)
Records screened:
(n = 1950)
Records excluded:
(n = 1675)
Studies sought for retrieval:
(n = 275)
Studies not retrieved
(n = 0)
Studies assessed for eligibility
(n = 275)
Studies excluded from extraction:
(n = 139)
Studies included in review
(n = 136)
Studies excluded from analyses:
Incompatible traits
(n = 1)

Figure A1.1



	Daylength	DTR	Elevation	Flower length	Flower width	Style length	Plant height	Anthesis time	Breeding system	Flower colour	Flower shape	Flower symmetry	Life form	Lifespan	Nectar	Odour
PS pathway	0.23	0.57	0.01	0.49	0.28	0.43	0.12	0.13	0.07	0.06	0.22	0.16	0.29	0.08	0	0
Odour	0.05	0.03	0.27	0.02	0.07	0.02	0.12	0.13	0	0.24	0.1	0.03	0.08	0	0	
Nectar	0.1	0.2	0.05	0.05	0.04	0.09	0.03	0	0.08	0	0.13	0.04	0.01	0.04		
Lifespan	0.01	0.05	0	0.15	0.03	0.16	0.15	0	0.33	0.2	0	0.13	0.17			
Life form	0.25	0.39	0.12	0.2	0.1	0.23	0.75	0.1	0.04	0.07	0.32	0.14				
Flower symmetry	0.26	0.1	0.02	0.09	0.13	0.14	0.13	0.18	0.02	0.24	0.58					
Flower shape	0.46	0.45	0.34	0.28	0.16	0.32	0.47	0.15	0	0.09						
Flower colour	0.44	0.2	0.36	0.25	0.24	0.28	0.38	0	0							
Breeding system	0.22	0.2	0.12	0.23	0.15	0.27	0.12	0								
Anthesis time	0.22	0.35	0.13	0.28	0.28	0.25	0.22									
Plant height	0.37	0.01	0.09	0.15	0.23	0.17										
Style length	0.35	0.2	0.1	0.76	0.4											
Flower width	0.33	0.15	0.06	0.57												
Flower length	0.34	0.2	0.01													
Elevation	0.27	0.13														
DTR	0.04															

Figure A1.2. Pairwise associations between plant species traits and study environmental variables. The value of association is either Cramer's V for pairs of nominal variables, Pearson's correlation co-efficient for pairs of continuous variables, or R^2 between nominal – continuous pairs. Rows are ordered with categorical traits first, then continuous traits and lastly environmental variables.

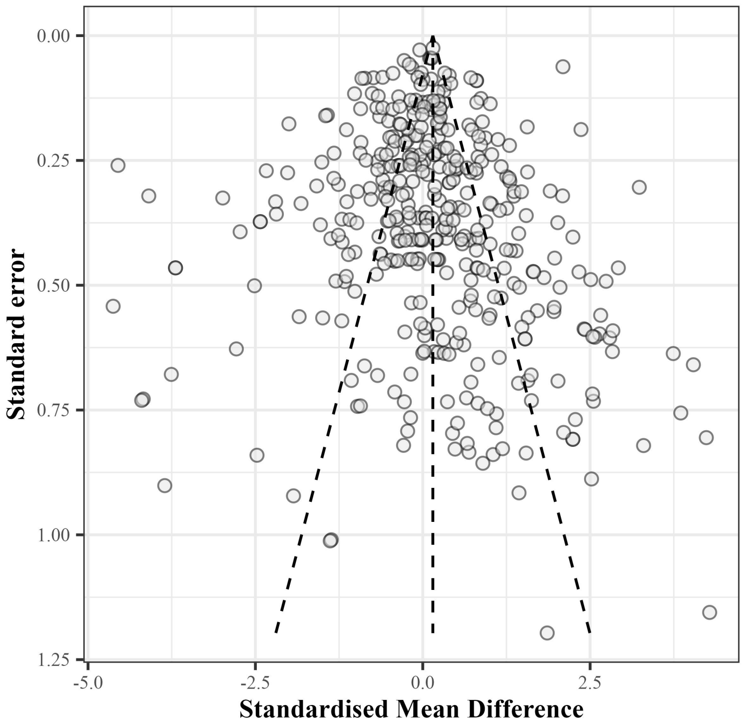


Figure A1.3. Funnel plots showing the relationship between the standardized mean difference and standard error for each diel pollination comparison. Dashed line and background color indicate 95% pseudo-confidence intervals (i.e., 1.96 ± SE).

APPENDIX 2

Supplemental results for comparisons between day and night pollination and open pollination

Table A2.1. Total heterogeneity (I^2) in effect sizes and partial heterogeneity attributable to each random effect in the meta-analytic model for each diel ~ open pollination comparison.

Comparison	I^2_{total}	I^2_{effect}	$I^2_{measure}$	I^2_{phylo}	$I^2_{species}$	I^2_{study}
Day vs. open	96.0	34.1	25.3	6.1	14.0	16.5
Night vs. open	96.4	26.6	12.5	5.2	49.1	3.0

Phylogenetic meta-analysis revealed that there were no overall significant differences between either day or night pollination and open pollination (Figure A2.1, top panels). Total heterogeneity for each comparative dataset was high (~ 96 %, Table A2.1), with varying amounts attributable to each random effect, depending on the contrast.

At the pollination measurement level, fruit set and seed set resulting from day pollination were significantly lower than open pollination (fruit set: -0.426, [-0.627, -0.226], seed set: -0.472, [-0.692, -0.251]) and seed mass was significantly higher than open pollination (0.591, [0.0.125, 1.057]) and fruit set resulting from night pollination was significantly less than open pollination (-0.470, [-0.679, -0.262]).

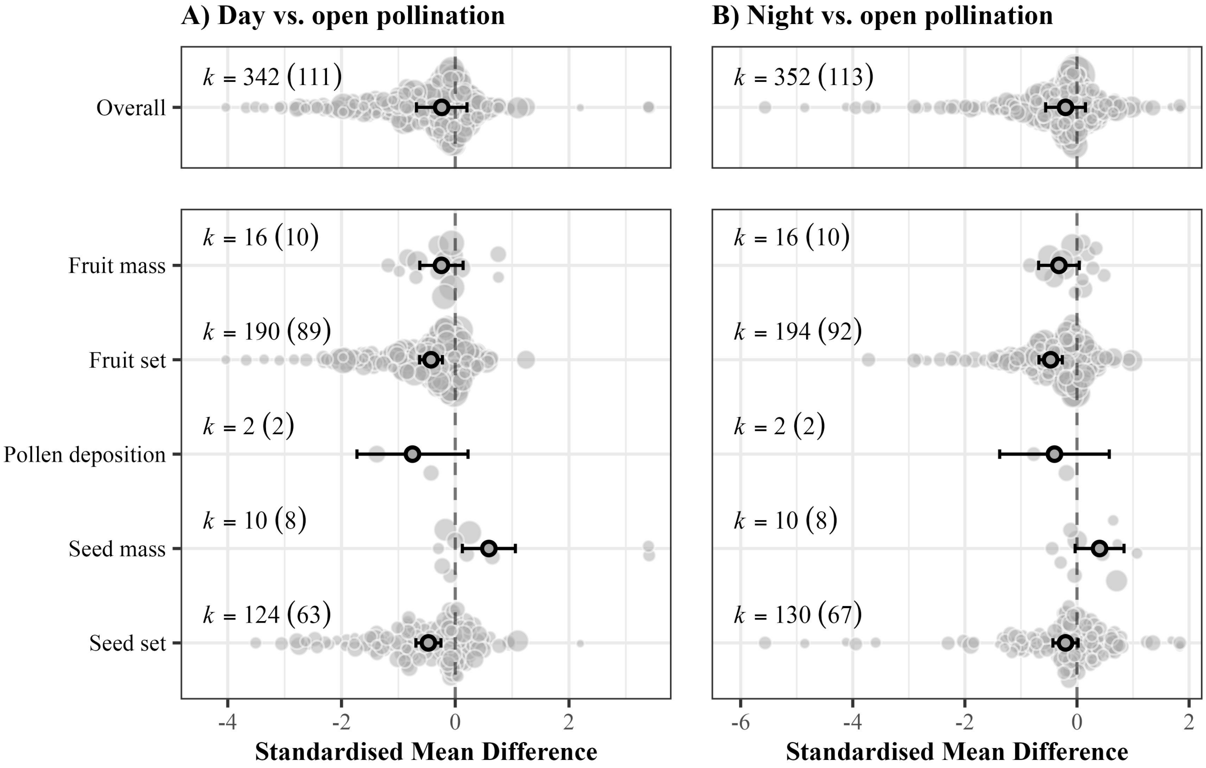


Figure A2.1. Standardized mean differences of the overall effect between day vs. open pollination (A) and night vs. open pollination (B) for each pollination outcome measure, as well as the overall effect. Primary dots and error bars indicate marginal mean estimates and 95% confidence intervals. Background points indicate individual effect sizes, in which size is proportional to the inverse of the standard error of the effect size.

Diel pollination differences in relation to environmental variables and plant traits

Table A2.2. Summary statistics for each univariate meta-regression of environmental and plant trait variables in each diel ~ open pollination comparison. ΔAIC: Difference in AIC relative to the meta-analytic model for each comparison. QM: Omnibus (Wald-type) test statistic for each moderator, along with its degree of freedom and p-value. R^2_M and R^2_C: Marginal and conditional R^2 . QE: test statistic for residual heterogeneity, along with degrees of freedom and p-value.

Comparison	Variable	ΔAIC	Q_M	df	p-value	R^2_M	R^2_C	QE	df	p-value
	Flower colour	**-14,306**	**18,046**	6	*0,006*	**0,065**	0,678	2827,7	335	<0,001
	Life form	-9,448	14,486	3	*0,002*	0,056	0,655	3062,919	338	<0,001
	Flower shape	-7,77	11,67	4	*0,02*	0,055	0,642	2825,951	337	<0,001
Day vs. open	Anthesis time	-6,681	7,978	2	*0,019*	0,045	0,652	2930,981	339	<0,001

	Elevation^2	-5,899	6.045	2	0,049	0,027	0,653	3217,858	339	<0,001
	PS pathway	-3,821	3,964	1	*0,046*	0,035	0,645	**2785,755**	340	<0,001
	Odour	-2,712	3,215	1	0,073	0,013	0,655	3224,908	340	<0,001
	Style length	-1,837	1,955	1	0,162	0,011	0,653	3163,886	340	<0,001
	Nectar	-1,158	1,16	1	0,282	0,006	0,637	3075,672	340	<0,001
	Lifespan	-1,228	1,156	1	0,282	0,006	0,647	3225,863	340	<0,001
	Breeding system	-0,743	0,89	2	0,641	0,004	0,651	3210,095	339	<0,001
	Plant height	-0,507	0,519	1	0,471	0,003	0,647	3114,049	340	<0,001
	Elevation	-0,267	0,301	1	0,583	0,002	0,647	3212,498	340	<0,001
	Daylength	-0,268	0,159	1	0,69	0,001	0,649	3198,549	340	<0,001
	DTR^2	-0,003	0,389	2	0,823	0,001	0,647	3135,473	339	<0,001
	Daylength^2	-0,391	0,208	2	0,901	0,001	0,651	3173,979	339	<0,001
	Flower symmetry	-0,283	0,026	1	0,871	0	0,648	3215,518	340	<0,001
	DTR	-0,086	0,013	1	0,91	0	0,646	3144,143	340	<0,001
Night vs. open	Odour	**-29,954**	**32,756**	1	*<0,001*	**0,153**	0,723	**2464,814**	350	<0,001
	Elevation^2	-28,873	32,42	2	*<0,001*	0,152	0,718	2507,992	349	<0,001
	Flower colour	-14,492	14,831	6	*0,022*	0,079	0,733	2510,353	345	<0,001
	Flower shape	-8,984	8,373	4	0,079	0,057	0,737	2657,366	347	<0,001
	Life form	-8,549	8,792	3	*0,032*	0,054	0,739	2544,335	348	<0,001
	Elevation	-7,586	8,179	1	*0,004*	0,044	0,7	2726,036	350	<0,001
	Anthesis time	-5,99	5,61	2	*0,061*	0,039	0,738	2640,112	349	<0,001
	Plant height	-6,835	7,179	1	*0,007*	0,036	0,727	2607,041	350	<0,001
	Breeding system	-4,291	4,055	2	0,132	0,026	0,727	2629,291	349	<0,001
	DTR^2	-3,525	3,995	2	0,136	0,018	0,724	2684,902	349	<0,001
	Style length	-2,427	2,267	1	0,132	0,016	0,724	2714,558	350	<0,001
	Flower symmetry	-2,374	1,894	1	0,169	0,015	0,73	2722,122	350	<0,001
	Nectar	-1,742	1,312	1	0,252	0,01	0,727	2721,774	350	<0,001
	DTR	-1,742	1,661	1	0,197	0,009	0,725	2695,473	350	<0,001
	PS pathway	-1,706	0,652	1	0,42	0,009	0,729	2722,467	350	<0,001
	Daylength^2	-1,426	1,078	2	0,583	0,006	0,734	2720,187	349	<0,001
	Lifespan	-0,69	0,227	1	0,634	0,002	0,727	2716,544	350	<0,001
	Daylength	-0,464	0,15	1	0,698	0,001	0,725	2720,267	350	<0,001

Comparison of the summary statistics (Omnibus Q test and ΔAIC, Table SX), as well as the explained variance (Figure A2.2) by each environmental and trait variable (marginal R^2) revealed that elevation was the only important tested environmental variable for predicting differences between either day or night pollination and open pollination, whereas five plant functional traits explained a significant amount of variation for day vs. open pollination, and four traits explained a significant amount of variation for night vs open pollination.

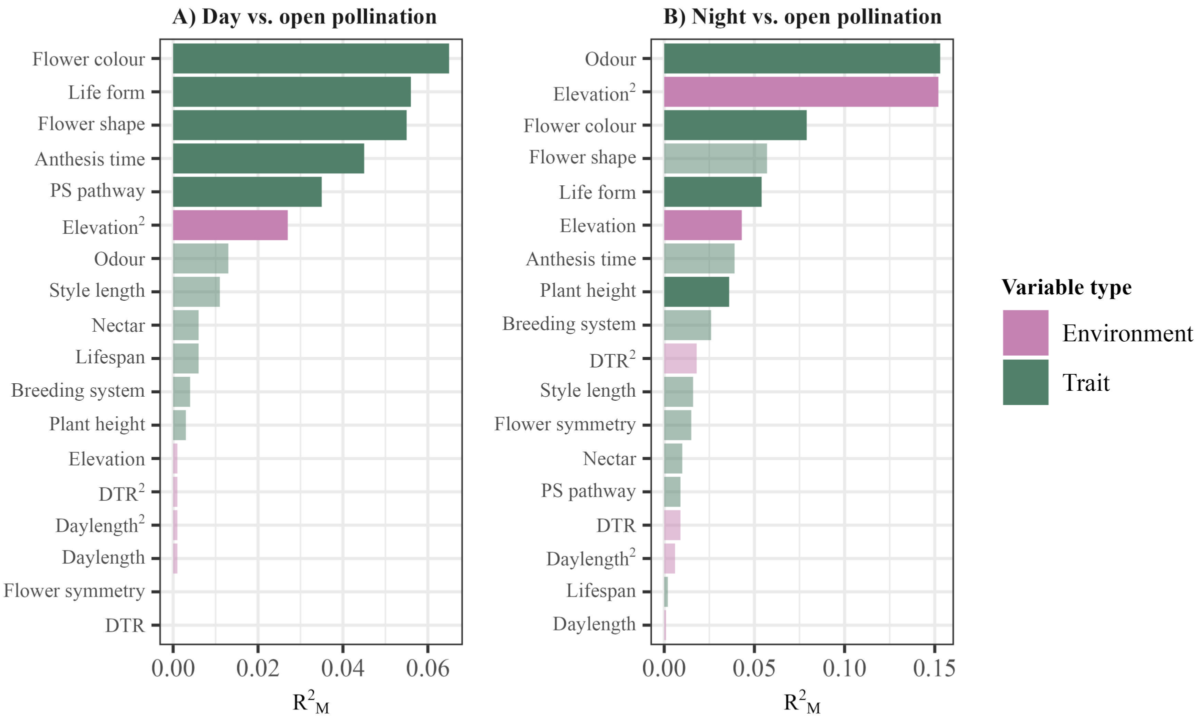


Figure A2.2. Coefficient of determination (marginal R^2) for each environmental and trait variable in relation to each diel pollination comparison. Solid columns are those variables for which the omnibus test (Q_M) was significant ($p < 0.05$), whereas transparent columns were non-significant ($p > 0.05$).

There was a significantly positive quadratic relationship between the SMD between day and open pollination and elevation (linear term: $z = -2.056$, $p = 0.039$, quadratic term: $z = 2.405$, $p = 0.016$), however, the 95% confidence intervals overlapped zero across the entirety of the range of elevational values (Figure A2.3A). In contrast, we found a significant negative quadratic relationship between the SMD between night and open pollination and elevation (linear term: $z = 1.046$, $p = 0.29$, quadratic term: $z = -4.827$, $p < 0.0001$), such that the success of nocturnal pollination relative to open pollination declined at higher elevations (> 2000 m) (Figure A2.3B).

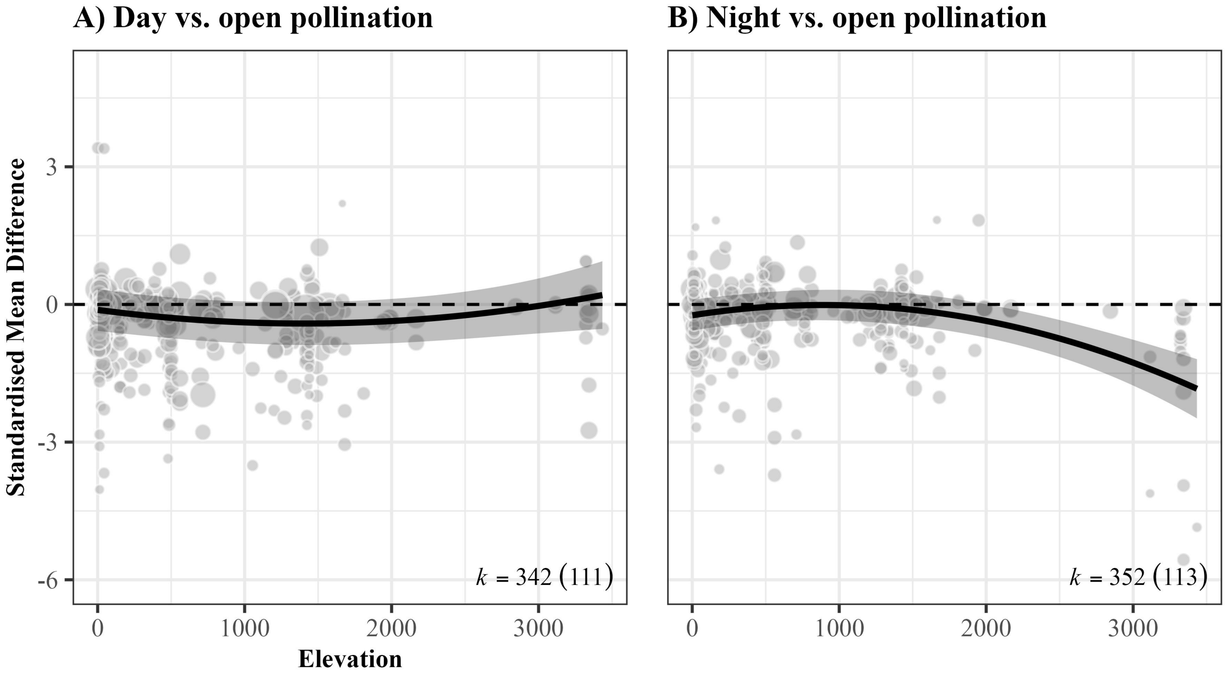
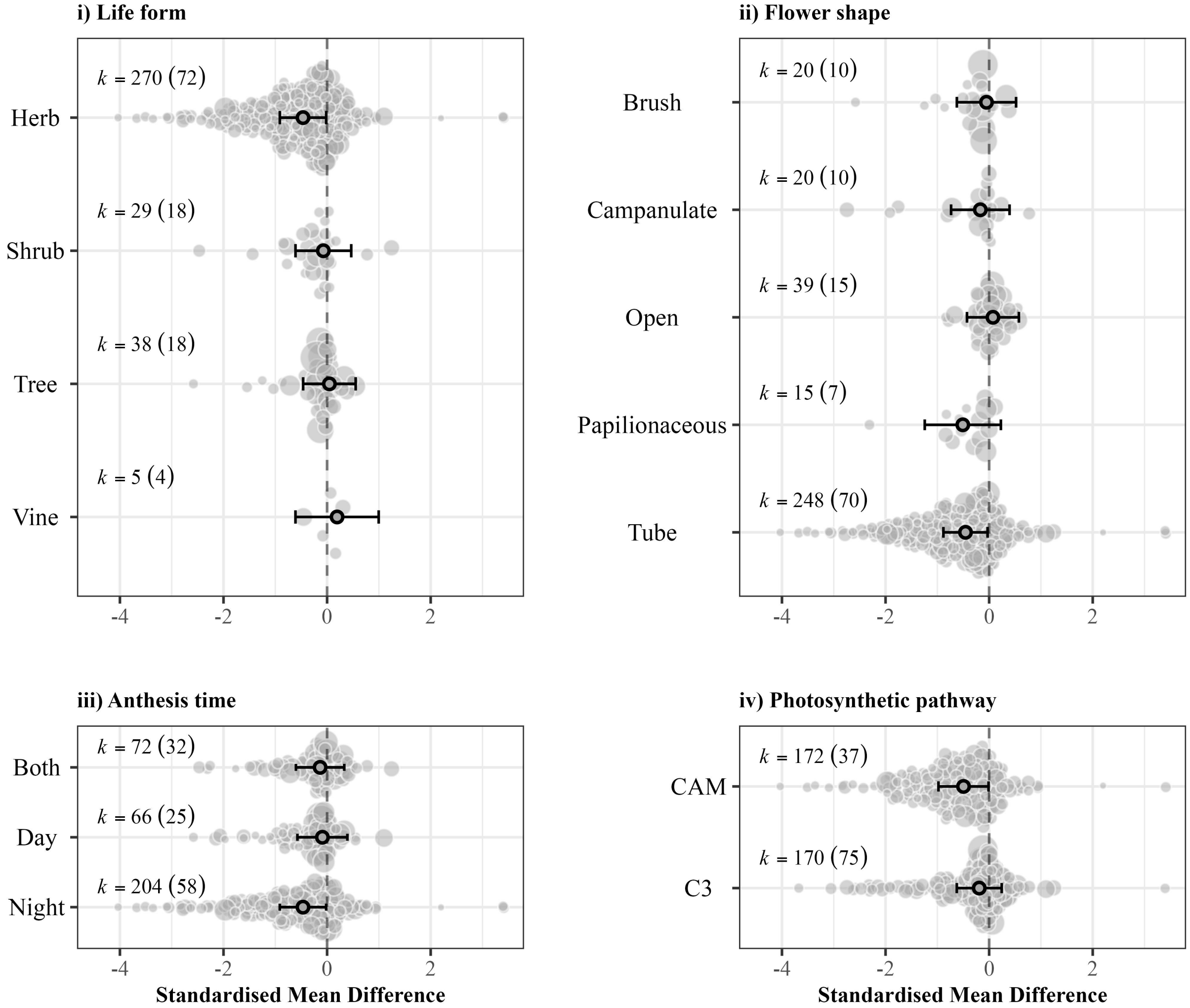


Figure A2.3. Standardized mean difference between diel pollination comparisons and elevation (m). Solid line and shaded ribbon indicate predicted line of best fit and 95% confidence intervals. Background points indicate individual effect sizes, in which size is proportional to the inverse of the standard error of the effect size. Solid lines and ribbons indicate significant trends from the Omnibus test (see Table SX) between SMD and elevation for the day vs. night and night vs open pollination comparisons.

Herbs had significantly lower pollination success from diurnal pollination relative to the entire 24-hour period (-0.465, [-0.913, -0.017], Figure A2.4). Tubular flowers and night blooming species had significantly lower pollination success with diurnal pollination relative to open pollination (tubular flowers: -0.456 [-0.883, -0.03]; night-blooming species (-0.466, [-0.913, -0.018]). Furthermore, plant species with a CAM photosynthetic pathway had significantly lower pollination success from diurnal pollination relative to open pollination (-0.495 [-0.978, -0.011]). Despite describing a significant amount of variation in the SMD between day and open pollination, the SMD of no single flower colour type was significantly different from zero.



i) Life form

ii) Flower shape

iii) Anthesis time

iv) Photosynthetic pathway

Figure A2.4. Standardized mean differences between day pollination and open pollination in relation to plant functional traits: i) life form, ii) flower shape, iii) anthesis time and iv) photosynthetic pathway. Primary dots and error bars indicate marginal mean estimates and 95% confidence intervals. Background points indicate individual effect sizes, in which size is proportional to the inverse of the standard error of the effect size.

Flowers without odour had significantly lower pollination success from nocturnal pollination, relative to open pollination (-1,164, [-1.62, -0.709]) (Figure A2.5). Purple flowers had worsened pollination outcomes from nocturnal pollination relative to open pollination (-1.209, [-1.910, -0.507]). Furthermore, the difference between nocturnal pollination and open pollination was positively related to plant height (z = 2.679, p = 0.007). Despite describing a significant amount of variation in the SMD between nocturnal and open pollination, the SMD of no single life form type was significantly different from zero.

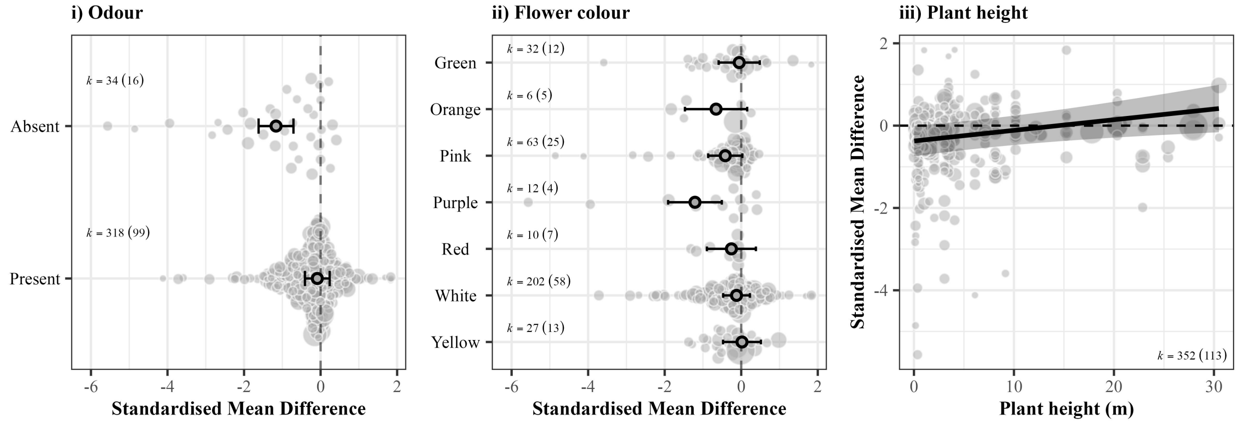


Figure A2.5. Standardized mean differences between night pollination and open pollination in relation to plant functional traits: i) flower odour, ii) flower colour, and iii) plant height. Primary dots and error bars (panels i & ii) indicate marginal mean estimates and 95% confidence intervals, and solid line and shaded ribbon indicate predicted line of best fit and 95% confidence intervals (panel iii). Background points indicate individual effect sizes, in which size is proportional to the inverse of the standard error of the effect size.

Publication bias and sensitivity analysis

Although there was some evidence for asymmetry in comparisons between diurnal or nocturnal pollination and open pollination (Figure A2.6), results from the Egger's tests suggested there was no evidence for asymmetry in comparisons with open pollination (day vs. open: z = 0.668, p = 0.503; night vs. open: z = 0.498, p = 0.618) and we found no evidence for a time-lag effect (year effect: day vs. open: z = -1.254, p = 0.210; night vs. open: z = -1.3236, p = 0.1856).

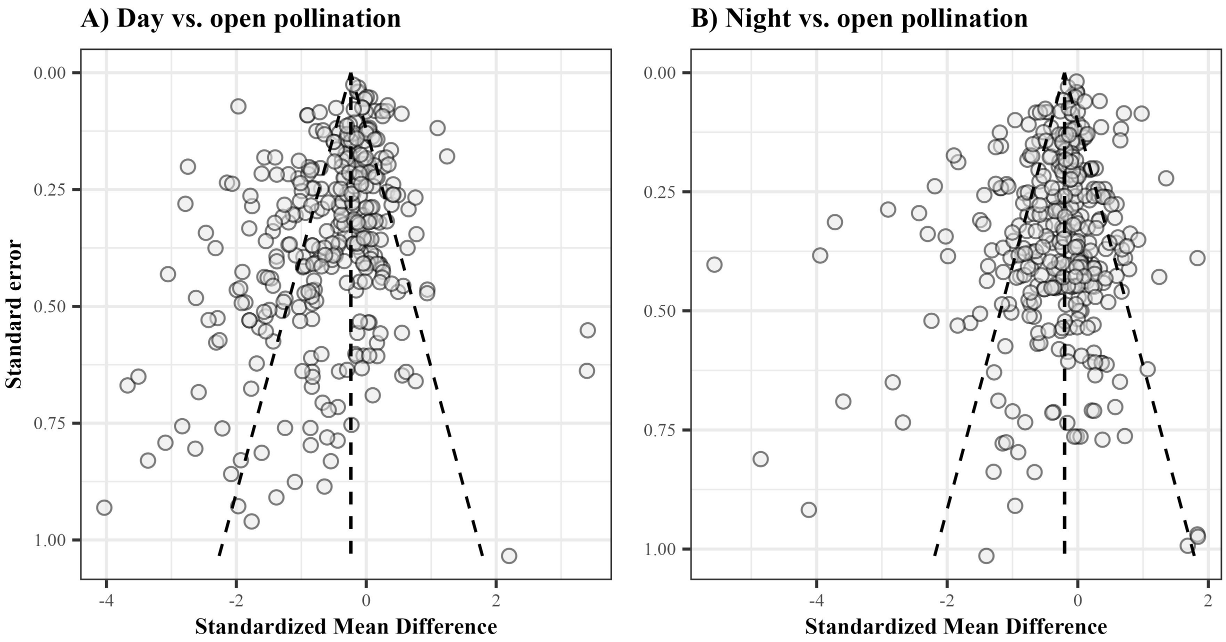


Figure A2.6. Funnel plots showing the relationship between the standardized mean difference and standard error for each diel pollination comparison with open pollination. Dashed line and background color indicate 95% pseudo-confidence intervals (i.e., 1.96 ± SE).