

Research



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Evolutionary biology

Empidine dance flies pollinate the woodland geranium as effectively as bees

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Most flowering plants species rely on insects for pollination, a successful mutualism allowing them to reproduce over wide areas while flower-visitors are rewarded with food. This association is so conspicuous in the case of bees that other groups of potential pollinators, especially flies, have long been underestimated. However, visitors are not always pollinators. While the importance of flies in plant–visitor networks is now acknowledged, their pollination effectiveness has hardly been investigated. In this study, we assessed the pollination effectiveness of *Geranium sylvaticum* flower-visitors using single-visit seed set experiments, in a subalpine meadow where flies are predominant. We found that: (i) empidine dance flies were the most frequent visitors of *G. sylvaticum*; (ii) a single-visit by an empidine dance fly produced the same average number of seeds as a visit by a bee; (iii) large pollinators were more efficient than small pollinators irrespective of their identity. As a conclusion, large empidines were the main pollinators of *G. sylvaticum*. Considering the high diversity and abundance of flower-visiting fly species, such results showing their ability to be as effective pollinators as bees should encourage further studies to develop a better understanding on their role in plant–pollinator networks.

1. Introduction

Insect pollination is a key ecological interaction, involved in the reproduction of more than 80% of angiosperms [1] and about 75% of world crop production [2]. Until recently, most of the studies addressing the role of insects as pollinators focused on bees, but the awareness of the collapse of their populations has sparked a growing interest in other flower-visiting insects (non-bee Hymenoptera, Diptera, Coleoptera, Lepidoptera) as potential pollinators [3]. However even in agricultural landscapes, where wild insects have proven efficient pollinators by increasing fruit set independently of honeybees' abundance [4], studies measuring pollination effectiveness of non-bee flower-visiting insects are very scarce. Consequently, despite the proliferating new knowledge on flower–visitor networks, the actual role played by most anthophilous insects in the pollination of flowering plants remains largely unknown.

Flies (Diptera) represent the most conspicuous group of flower-visitors and potential pollinators after bees [5–7], especially in cool to cold habitats of high altitude or latitude where wild bees become naturally scarcer [8–14]. However, most studies including dipterans address only flower visitation frequencies, which King *et al.* [15] consider a poor proxy for pollinator effectiveness. Visitors are indeed not always pollinators, a visit being likely to enhance the

reproductive success of a plant only when it results in conspecific pollen deposition on its stigma. Therefore, direct measures of pollinator effectiveness and plant reproductive success should be performed, respectively, through single-visit stigmatic pollen deposition and seed set after single-visit experiments [16,17]. To our knowledge, very few studies include such experiments on flower-visiting Diptera, although some of them challenge the common assumption that bees are the best pollinators: e.g. hoverflies can pollinate strawberries as efficiently as bees [18], and a blowfly (Calliphoridae) was shown to be as efficient as honeybees and other flower-visitors together in pollinating hybrid carrots [19]. Moreover, the first study comparing syrphids with other Diptera found no differences in pollen-loads or specialization [20]. Those results cast light on the lack of knowledge about the role played by most flower-visiting fly families in the pollination of angiosperms.

To assess the effectiveness of dipterans as pollinators of a wild plant relative to other foraging insects, we used *Geranium sylvaticum* L. and its flower-visitors as a model, in a subalpine environment where wild bees are scarce. Our objectives were: (i) to quantify the visitor cortege of *G. sylvaticum*; (ii) to assess the pollination effectiveness of the main flower-visitors using single-visit seed set experiments; (iii) to test whether pollination effectiveness was related to species identity or species traits, such as body size and visit duration.

2. Material and methods

(a) Study site

The study was conducted from 15 June to 15 July 2015 in the north of Mercantour National Park, France. The site is a largely flat, semi-open subalpine area at 1800 m altitude (6°46'33.8" E, 44°23'59.1" N), which consists of large meadows dotted with larches (*Larix decidua*). Near bushes and under larches thrive numerous populations of *G. sylvaticum*, some of them reaching several hundred individuals. Snow cover usually lasts from November until May and mowing occurs twice, in late summer.

(b) Study model: *Geranium sylvaticum* and its flower-visiting insects

Geranium sylvaticum is a rhizomatous, perennial, gynodioecious and protandrous plant that occurs in meadows, in woodlands and on roadsides. It is widely distributed in Europe and temperate Asia; in France, its populations are confined to mountainous areas, the east and the north of the country. Three main sexual types, depending on their number of functional stamens—female (=male-sterile = pistillate) (0), intermediate (1–9) and hermaphrodite (10)—have been identified [21]. All our experiments were restricted to hermaphrodites, as pistillate plants were rare at the study site and previous studies found that seed set could vary depending on the sexual type [21–23]. Newly opened flowers first undergo a male phase, lasting approximately half a day, during which the 10 stamens release the pollen; then a female phase of a few hours, during which the five lobes of the hitherto immature stigma unfold and become receptive for pollen. The ovary is composed of five carpels, each containing two ovules, but only one ovule of each pair develops into a seed. Thus, each flower produces between zero and five seeds. At the study site, flowers of *G. sylvaticum* are mainly visited by dipterans, especially empidines [13].

(c) Monitoring of visits

Flower-visitors were recorded between 19 June and 1 July 2015 by monitoring 18 groups of 10 flowers for 10 min. The 18 monitoring sessions were divided into three different conditions: full sun, dappled sun and full shade. To test whether visitors to *G. sylvaticum* change with the time of day, we divided the sessions of each condition between morning and afternoon (half-day factor). The 18 sessions were all performed between 10.00 and 16.00 on non-rainy days with a temperature above 18°C. For each insect visitor that came into contact with the reproductive parts of the flower, the following information was recorded: hour of the visit, taxonomic group (order and family at least; see electronic supplementary material, table S1) and size class (A: ≥ 10 mm or B: < 10 mm).

(d) Pollination regime experiments

For all the following bagging experiments, including those of §2(e), we used organza bags with a very fine mesh of about 0.16 mm². Fruits were harvested just before dehiscence, around three or four weeks after bagging depending on weather conditions.

To assess the dependence on pollinators of *G. sylvaticum*, we selected 36 healthy plants for which a different pollination regime was applied to three flowers: (1) self-pollination, to test if the protandry succeeded in preventing self-fertilization; the flower was bagged just before blooming. The expected number of seeds was 0; (2) open-pollination, to get the number of seeds produced by entomogamy in natural conditions; the flower was bagged after the stigma became unreceptive, when the petals started dropping; (3) hand-pollination, to get the maximal number of seeds in the local conditions at the study site; a receptive stigma was pollinated with freshly harvested pollen from distant *G. sylvaticum* flowers, then the flower was bagged.

(e) Single-visit seed set experiments

To assess the pollination effectiveness of the main flower-visitors, 32 flowers were bagged between male and female phase to prevent pollen contamination of the bag. The day after bagging, we unbagged the flower when the stigma was freshly receptive and waited for the first visit of a foraging insect. Its taxonomic group (see electronic supplementary material, table S2) and size class (A: ≥ 10 mm or B: < 10 mm), as well as the duration of the visit were recorded.

(f) Statistical analyses

All statistical analyses were performed with R software v. 3.2.5 [24]. To test if the number of visits by empidine flies was significantly higher than the number of visits by the other insects altogether, we used a non-parametric Wilcoxon two-sample paired rank test (count data with non-normal distribution).

We analysed the seed sets of single-visits (proportion data) using a generalized linear model ('glm' procedure) that included an effect of taxonomic group (empidine or bee), size and visit duration (log-transformed to obtain homoscedasticity), with quasi-binomial error distribution to account for overdispersion. Because single-visit seed set experiments involving flower-bagging are time-consuming and difficult to carry out properly in the field, our sample size was limited, preventing us from testing for interactions among effects. A power analysis by simulation indicated that given our sample size, our analysis allows us to detect a difference of one seed between size categories in 77% of cases, and between bees and empidines in 81% of cases. The power of our analysis to detect a visit duration effect of 0.092, corresponding to an increase of one seed for a visit duration of 150 s—equivalent to the observed median of visit duration—averages at 40%.

To test the effects of taxonomic group, size, exposure (full sun, dappled sun, shadow), half-day and all their interactions on the number of visits by each group of visitors, we used a linear mixed-effects model ('lme' procedure of 'nlme' library) that incorporated a random effect of the session, a session representing a 10-flower patch monitored for 10 min.

For both analyses, we performed a stepwise model simplification: at each step, we dropped the least significant variable or interaction based on p -value, and we tested for difference between the model's Akaike information criterion (AIC). For each model, the normality of the residuals and homoscedasticity of variance were checked visually.

3. Results

(a) Visitors to *Geranium sylvaticum*

We recorded 329 visits; 80.6% were made by Diptera and 18.2% by Hymenoptera. The remaining 1.2% included butterflies and beetles. The number of visits by empidine dance flies, representing 74.2% of all visits, was significantly higher than the number of all the visits by other insects considered together (Wilcoxon test, $p < 0.005$). They were not equally distributed by size classes: one large species, *Empis pandellei* Daugeron, was responsible for 62% of all visits by empidines. Bees made 17% of all visits; 86% were honeybees (*Apis mellifera* L.) and the remaining 14% were solitary bees smaller than 10 mm.

When restricting analyses to bees and empidines (98.8% of the visits), frequency of visits was significantly influenced by visitor size, taxonomic group and time of the day. The most frequent visitors were empidines, and for both groups, large visitors were predominant. There were more visitors in the afternoon than in the morning, and exposure had a near-significant effect: the number of visits increased with sunlight and no visit by bees was observed in the shade (table 1 and figure 1).

(b) Pollination regime experiments

None of the flowers tested for auto-fertilization produced seed (mean = 0, $N = 36$). Hand-pollinated flowers produced 93 seeds, as did the flowers under the open-pollination treatment (hand-pollinated: 2.58 ± 0.32 per flower, open-pollinated: 2.58 ± 0.24 per flower; mean \pm s.e., $N = 36$).

(c) Single-visit seed set

Twenty-nine single-visits from empidines ($N = 18$) or bees ($N = 11$) were recorded. When considering all visits together, average number of seeds was 2.16 ± 0.28 per single-visit (mean \pm s.e., $N = 32$) and was not significantly different from the seed set of open-pollinated or hand-pollinated flowers (unpaired two-sample Wilcoxon test, $p > 0.05$). Size of the visitor had a significant effect, as visits by large-sized flies and bees (greater than or equal to 10 mm) produced more seeds than visits by smaller ones ($F_{1,27} = 5.25$, $p = 0.03$; figure 2). Taxonomic group (bee or empidine) and duration of the visit did not influence the seed set, although the average duration of visits by empidines (335 ± 60 s) was much longer than the average duration of visits by bees (54 ± 17 s).

Table 1. ANOVA table of mixed-effects model testing the influence of taxonomic group, exposure, half-day, size of the insect and all their interactions on the number of visits to *Geranium sylvaticum* flowers, after stepwise simplification.

| | numDF | denDF | F | p-value |
|----------|-------|-------|-------|---------|
| group | 1 | 52 | 45.76 | <0.0001 |
| exposure | 2 | 14 | 3.58 | 0.055 |
| half-day | 1 | 14 | 7.47 | 0.016 |
| size | 1 | 52 | 5.90 | 0.018 |

4. Discussion

(a) Insect visitation to *Geranium sylvaticum* is necessary for pollination

Our results confirm that sexual reproduction of *G. sylvaticum* depends on flower-visiting insects, as flowers under the auto-fertility treatment produced no seed. This is likely due to the protandry of the flowers, as this plant species was reported to be self-compatible [21]. Among its visitors, empidine dance flies were the most frequent. The proportions of flies (80.6%) and empidines (74.2%) that visited *G. sylvaticum* were consistent with the results of a previous study conducted in 2012 in the same area [13].

(b) The influence of abiotic conditions on *Geranium sylvaticum* visitors and pollinators

As only visits by flies were recorded in the shade, and *G. sylvaticum* is a partial-shade species growing in cool habitats, its main visitors and pollinators could be predicted by their functional traits like the ability to forage at lower temperature or to detect flowers without direct sunlight. Compared with bees, flies can thrive in colder and damper conditions, both of these parameters increasing with altitude. It is likely that over a large part of its range, *G. sylvaticum* is pollinated mainly by empidine dance flies, as they share the same habitats. Effects of sun exposure-related factors observed in this study at a local scale, like temperature, also exist at a much larger scale along the altitudinal gradient, partially explaining the predominance of flies at altitude [14].

(c) Pollination efficiency, visitor size and foraging behaviour

Large visitors were the most efficient pollinators regardless of their taxonomic group, which might be explained by their foraging behaviour. In relation to the morphology of the flower, the size of the flower-visiting insect determines whether and how it can access the food source: during a visit, large species like *Empis pandellei* or *Apis mellifera* place their body upon the sexual parts of the flower, as allowed by their long legs and mouthparts, resulting in many contacts with the anthers and the stigma. Smaller species usually land on a petal and then access the nectaries, on the base of the stamens, by passing under the sexual parts of the flower. Such a relationship between the size of a pollinator and its pollinating effectiveness has already been documented in bumblebees [25]. As visits by large bees or empidines

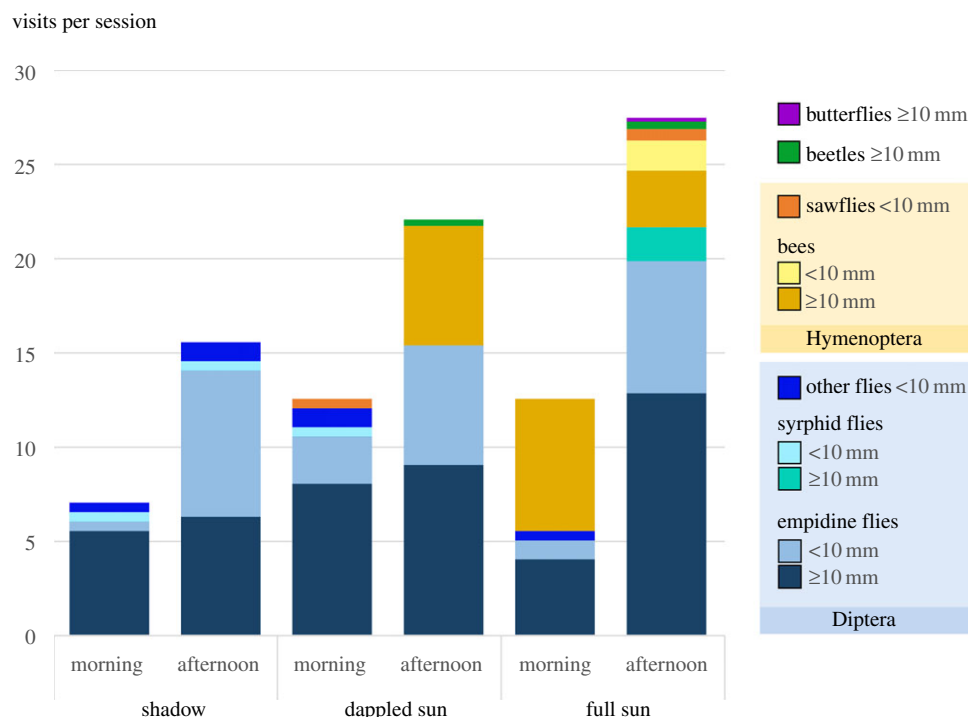


Figure 1. Average number of visitors to *Geranium sylvaticum* per observation session (10 flowers monitored for 10 min) under three different conditions of exposure, in the morning and in the afternoon.

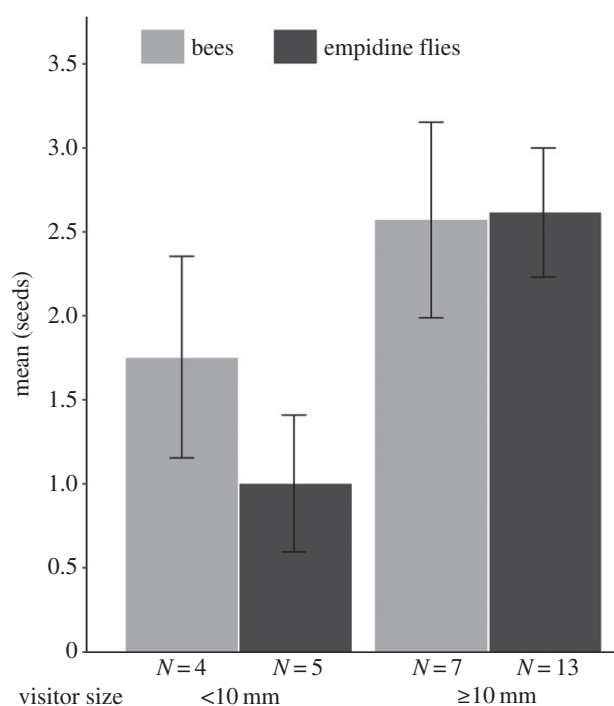


Figure 2. Number of seeds produced by *Geranium sylvaticum* flowers after single-visits by small (left) and large (right) bees (light grey) and empidines (dark grey), respectively (mean \pm s.e.).

resulted in the same average number of seeds, and the latter were the most frequent visitor with 46% of all visits, empidines were the most efficient pollinators of *G. sylvaticum* at the study site.

It may seem surprising that large visitors are so efficient that only one visit is enough to produce the same average number of seeds as open-pollinated flowers. This is likely inherent to flower-bagging: insects spent a much longer time foraging in freshly unbagged, nectar-rich flowers than

in recently visited flowers. While moving into the flower to access each of the nectaries, they increased pollen deposition on the stigma.

(d) The *Geranium sylvaticum*–empidines model: a drop in the ocean

Considering how frequently interactions between empidines and numerous flowering plant species have been reported in the literature since Darwin [13,26–36], it is surprising that their role in the reproductive success of those plants had never been addressed. They are obligate floral-visitors with more than 2000 described species worldwide which, contrary to the commonly accepted assumptions that they are generalists and poor pollinators, could reveal high levels of specialization and the same pollination efficiency as bees. Their high abundance and diversity throughout the favourable season suggest that they are important pollinators in mountains and at high latitudes [14]. Like empidine dance flies, numerous species of calliphorids, conopids, muscids, anthomyids, tabanids and many other fly families depend on nectar and pollen for feeding. In habitats where bees are unable to thrive, flies often represent the predominant biotic vector carrying pollen grains from one flower to another, and therefore the main potential pollinators.

Data accessibility. Data are available from the Dryad Digital Repository at: <https://doi.org/10.5061/dryad.4fq833s> [37].

Authors' contributions. All authors conceived the study and designed the experiments. V.L. performed fieldwork, analysed the data with the help of C.F., and drafted the manuscript. All authors contributed to its final version, approved it, and agree to be held accountable for the content therein. C.D. obtained funding.

Competing interests. We declare we have no competing interests.

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