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ORIGINAL ARTICLE

The Neglected Pollinators: Understanding the Importance of Lesser-Known Insect Taxa in Pollination

Butterflies, bumblebees and hoverflies are equally effective pollinators of *Knautia arvensis* (Caprifoliaceae), a generalist plant species with compound inflorescences

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Abstract

Plant-pollinator interactions exist along a continuum from complete specialisation to highly generalised, that may vary in time and space. A long-held assumption is that large bees are usually the most effective pollinators of generalist plants. We tested this by studying the relative importance of different groups of pollinators of *Knautia arvensis* (L.) Coult. (Caprifoliaceae: Dipsacoideae). This plant is suitable for such a study because it attracts a diversity of flower visitors, belonging to different functional groups. We asked whether all functional groups of pollinators are equally effective, or if one group is most effective, which has been documented in other species with apparently generalised pollination systems. We studied two subpopulations of *K. arvensis*, one at low and one at high density in Northampton, UK. To assess pollinator importance we exposed unvisited inflorescences to single visits by different groups of pollinators (butterflies, bumblebees, hoverflies and others) and assessed the proportion of pollinated stigmas. We then multiplied the effectiveness of each pollinator group with their proportional visitation frequency in five different years. For each group we also compared time spent on flowers and flight distance between visits. The relative importance of each pollinator group varied between years, as did their flight distances between flower visits. Butterflies were the best pollinators on a per visit basis (in terms of the proportion of stigmas pollinated) and flew further after visiting an inflorescence. Different measures and proxies of pollinator effectiveness varied between taxa, subpopulations, and years, and no one group of pollinators was consistently more effective than the others. Our results demonstrate the adaptive value of generalised pollination strategies when variation in relative abundance of different types of pollinators is considered. Such strategies may have buffered the ability of plants to reproduce during past periods of environmental change and may do so in the future.

KEYWORDS
adaptation, bees, environmental change, flies, floral evolution, generalisation, Lepidoptera, pollination, pollinator effectiveness

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1 | INTRODUCTION

There is a continuum of specialist to generalist interactions between plants and pollinators that can be highly complex and dynamic over space and time (e.g. Alarcón et al., 2008; Amorim et al., 2013; Gómez, 2002; Herrera, 1988; Lamborn & Ollerton, 2000; Muchhala et al., 2008; Ollerton, 2021; Rech et al., 2018) and can vary enormously even among closely related plant species (Ollerton et al., 2019). For most plant species, a number of flower visitors can potentially act as pollinators, though visitation frequency per se is no guarantee of pollinator effectiveness (Watts et al., 2012; Sakamoto et al., 2012; but see Ballantyne et al., 2017). There is also a general assumption that, because of their size, hairiness and behaviour, large bees are often the most effective pollinators (Ballantyne et al., 2017; Roquer-Beni et al., 2022) but this has rarely been tested in generalist plants with small flowers in compound inflorescences.

Quantifying the relative effectiveness of each flower visitor as a pollinator is difficult for small flowered species, and studies have mainly been undertaken in plants that have relatively large flowers, presented singly or in few-flowered inflorescences (for example de Brito et al., 2017; Kiepiel et al., 2022; Rocha et al., 2019; Waser & Price, 1990; Watts et al., 2012). This has to some extent biased our understanding of the ecology and evolution of plant-pollinator relationships, with plant families that are characterised by very small flowers and/or compound inflorescences being underrepresented in meta-analyses of pollinator effectiveness (Ollerton et al., 2015; Page et al., 2021; Waser et al., 1996). Assessing pollinator effectiveness in plants with compound inflorescences is especially difficult, yet such plants belong to large, diverse families such as Asteraceae, Eriocaulaceae and Apiaceae that play ecologically important roles in many plant communities because of the abundant floral resources that they provide to flower visitors (Biella et al., 2017; Del-Claro et al., 2019; Lack, 1982a, 1982b; Olsen, 1997; Oriani et al., 2009).

Theory suggests that plants should generalise on a range of different, equally effective pollinators when any one type of pollinator is infrequent or otherwise unreliable, for example, due to a highly dynamic environment (Waser et al., 1996). Such generalisation of pollination systems has been frequently suggested for members of families with compound inflorescences and open flowers but has rarely been properly tested (Ollerton, Killick, et al., 2007). Although plants within families such as Asteraceae and Apiaceae often possess what appear to be highly generalised pollination systems involving diverse groups of flower visitors (Torres & Galetto, 2002; Zych, 2007), studies of the role of these different taxa as pollinators often use indirect proxies of effectiveness such as visitation rate and insect pollen loads (e.g. Davila & Wardle, 2008; Lamborn & Ollerton, 2000; Lindsey, 1984; Niemirski & Zych, 2011; Ollerton, Stott, et al., 2007; Zych, 2002, 2007; Zych et al., 2019). There are few published studies that have assessed the direct consequences of insect visitation for pollen deposition on stigmas in plants with compound inflorescences (though see King et al., 2013, which we discuss in detail later) or that have looked at distances flown between compound inflorescences by pollinators, which can reduce geitonogamy in such plants (Eckert, 2000; Vange, 2002).

We studied pollinator effectiveness in the apparently generalist *Knautia arvensis* (L.) Coult. (Caprifoliaceae: Dipsacoideae), a common grassland species. All members of the subfamily Dipsacoideae (formerly family Dipsacaceae) possess compound inflorescences similar to Asteraceae that (at least in the few species studied to date) attract a wide taxonomic diversity of flower visitors. Specifically, we addressed the question of whether all types ("functional groups" sensu Ollerton, Killick, et al., 2007) of flower visitors are equally effective as pollinators, as one would expect from a true generalist (Waser et al., 1996), or whether only a sub-group of visitors is actually effective, as has been found for other plants with apparently generalised pollination systems (e.g. Fishbein & Venable, 1996; Ollerton, Killick, et al., 2007; Zych, 2007). In addition, we monitored the relative abundance of flower visitors over different seasons to understand how the most effective pollinators might change from year to year in this population.

2 | MATERIALS AND METHODS

2.1 | Study sites and species

Field observations and experimental manipulations were conducted during the late summers of 2001, 2006–2008, and 2012 on the Quarry Field and Scrub Field areas of the Bradlaugh Fields site in Northampton, central England (52.26962 N, 0.87999 W). The sites are a matrix of mesotrophic grassland with calcareous floristic elements, overlying Jurassic (Great Oolite) limestone. The site is managed by the Wildlife Trust for Bedfordshire, Cambridgeshire and Northamptonshire. The study species (*K. arvensis*) varied considerably in density between the Quarry Field and the Scrub Field, a feature that was used as the basis for a natural experiment on pollinator movements between inflorescences (see below).

Knautia arvensis (L.) Coult. (Caprifoliaceae: Dipsacoideae) is a common herbaceous perennial grassland plant, with a wide natural distribution across Eurasia and Scandinavia. It is considered invasive in some regions, such as North America. Compound inflorescences of protandrous, self-compatible flowers with single ovules are produced in late summer (Larsson, 2005; Tutin et al., 1976).

2.2 | Floral biology

In order to establish some basic parameters of the floral biology of *Knautia arvensis*, in 2001 we measured and counted the following traits for a sample of randomly selected inflorescences: mean inflorescence diameter (using an electronic calliper), number of ray florets, and number of disc florets. Measurements and counts were made and running means were calculated until the mean values

stabilised at $n = 28$ inflorescences. In addition, we assessed how the sexual state of the flowers changed from male to female and measured the amount of nectar standing crop present in flowers using microcapillary tubes, as per Dafni et al. (2005). Nectar concentration was measured using a Bellingham & Stanley sugar refractometer, up to a maximum of 50% sucrose equivalents (the limit of the refractometer we were using at the time). Fieldwork on Bradlaugh Fields over this period showed that the *K. arvensis* sub-population on the Scrub Field was consistently at higher density compared to the Quarry Field. To quantify floral density at the two sites in 2012, we took 24 photographs of the plants on the ground associated with a reference scale (Appendix A). Using ImageJ software (Abramoff et al., 2004), we calculated the precise photographed area and the number of flower heads per m^2.

2.3 | Pollinator observations

All observations of pollinators, including the single-visit experiments (Section 2.4), were carried out on warm, sunny days with low wind speed, in line with recommendations for surveying diurnal flower-visiting insects such as butterflies (Dafni et al., 2005; Pollard, 1977). Previous studies of *K. arvensis* have indicated many different groups of flower visitors potentially acting as pollinators in different parts of its natural range (Knuth, 1898a, 1898b, 1898c, Lack, 1982a, Jennersten, 1984, Larsson, 2005, Biella et al., 2019). Lack (1982a) found strong differences in the assemblages of these flower visitors between 2 years of observation, and Larsson (2005) demonstrated differences in pollinators' capacities for pollen deposition. Building on these studies, we directly measured pollen deposition by visitors to *K. arvensis* flowers as a measure of pollinator quality sensu Herrera (1987). This was then combined with data on visitation frequency in different years, interpreted in light of insect residence times on inflorescences and inter-plant pollinator movements, to assess the extent of annual variation in pollinator importance for *K. arvensis*.

During the flowering period of the *K. arvensis* population, transects were walked at intervals in order to record flower visitors across the whole population, typically one survey per week for 12 weeks. The exact position and lengths of the transects varied because of the patchy and dynamic nature of flowering in this species in a relatively small site and followed a zig-zag or spiral shape across the site of c. 500 m for >1 hour duration. During these walks, flower visitors were recorded as they were observed on flower heads and identified to the lowest possible taxonomic level in the field (see Appendix C). The most frequent visitors were then categorised into broad functional types to assess the relative abundance of different groups as pollinators. These groups were bumblebees (*Bombus* spp.), butterflies and day-flying moths (Lepidoptera), and hoverflies (Syrphidae). Taxa that were infrequent visitors were placed in the category 'Others', and included beetles (Coleoptera), solitary bees such as species of *Andrena* and *Megachile*, honeybees (*Apis mellifera*), non-Syrphidae flies (Diptera), and scorpionflies (Mecoptera).

2.4 | Residence time and flight distances of flower visitors

During the flowering season of 2012 we recorded the residence time for every flower visitor of *K. arvensis*. Time was recorded from the landing of the flower visitor on the inflorescence until its departure. We also measured the average distance flown by the three most frequent groups of flower visitors (butterflies, bumblebees and hoverflies, see Results) between consecutive inflorescence visits to unmanipulated inflorescences growing in situ. Due to the difficulty in tracking pollinators over distances greater than 5 m, the flight distance was categorised as a scale from 1 to 4 representing the following: (1) 0–0.30 m; (2) 0.31–1.0 m; (3) 1.01–5.0 m; and (4) more than 5.0 m. Because the two study sites (Quarry Field and Scrub Field) had different overall floral densities of *K. arvensis* (see above) we were able to test whether the results are a property of the flower visitors' behaviour, and not due to flower density, by collecting the same data in the two subpopulations.

2.5 | Pollinator effectiveness

Pollinator effectiveness (PE) was assessed as the product of pollinator abundance (I) and pollinator quality (E), following Freitas (2013 and references therein). To calculate pollinator quality (E), we measured pollen deposition on virgin stigmas of *Knautia arvensis* flowers. Virgin flowers were obtained by bringing cut inflorescences in bud to the laboratory, placing them into separate, water-filled conical flasks, and waiting for anthesis and the receptive female phase (Larsson, 2005) before taking them back into the field for the experiments. This was done rather than bagging inflorescences in situ because we had earlier discovered that bagged inflorescences tended to deform and go mouldy regardless of the fabric mesh size used.

Each inflorescence was exposed to a single visitation event by presenting to flower visitors using a 0.8-metre hand-held pole with a slotted T-piece to hold the flower head (see Appendix B). The mounted inflorescence was placed in the proximity of a flower visitor on an in situ *Knautia* inflorescence, in the expectation that such insects would be carrying *Knautia* pollen. As for the transect surveys, the identity of the flower visitor was recorded to species where this was possible in the field, otherwise to a broad taxonomic group. The duration of the inflorescence visit to the nearest second was measured with a stopwatch. The flowers were then immediately examined under a stereomicroscope in the field to count the number of stigmas and the number of *K. arvensis* pollen grains per stigma. This pollen is easily identifiable due to its relatively large size and distinctive pinkish colouration. Using this small bench microscope we found that in bright sunshine there was enough illumination to not require an artificial light source (see Appendix B). To act as a control for the possibility that moving and manipulating the flower heads could result in pollen transfer to stigmas, a proportion of each set of inflorescences that was transported into the field was treated

identically to the experimental inflorescences, except that we did not allow insects to visit them.

As each female flower contains only a single ovule, and presumably could be fertilised by a single pollen grain, we used the proportion of stigmas per inflorescence with pollen as a measure of pollen deposition. Flower visitors were categorised into the broad groups noted above to test their ability for pollen deposition, as the focus of much discussion about the effectiveness of visitors to generalist flowers has been on functional groups of pollinators (e.g. Armbruster, 2017; Brunet & Sweet, 2006; Fenster et al., 2004; Lamborn & Ollerton, 2000; Ollerton, Killick, et al., 2007,).

We used the abundance of the different groups of insects in each year (I) and the proportion of stigmas with pollen after a single visit to an inflorescence (E) as components of pollinator quantity and quality (Herrera, 1987; King et al., 2013; Ne'eman et al., 2010; Olsen, 1997; Stone, 1996). Considering these two parameters we calculated an index of pollinator effectiveness (PE) for each one of the groups of insects as follows:

$$PE = I * E$$

Where PE = Pollinator effectiveness, I = abundance of the flower visitor and E = the pollinator quality. Pollinator effectiveness results are shown as the proportional annual contribution of each group to *K. arvensis* pollination.

2.6 | Data analysis

We used generalised linear models (GLMs) for all analyses, adjusting the error probability distribution and link function according to which type of data, and model selection based on the corrected Akaike information criterion (AIC, Burnham & Anderson, 2002) using the R package bbmle (Bolker & Core Team, 2020). In all cases, we compared the set of all the possible candidate models considering the combinations of the predictors used, with an additional null model including only the intercept. To distinguish differences between levels of each categorical variable within the best model, we calculated marginal means and employed Tukey pairwise comparison tests using the emmeans package (Lenth, 2021).

To model time spent on flowers, we used a gaussian model with a log link, as this variable was highly skewed. As predictors, we used site and the functional group of pollinator. Similarly, for flight distance we had site and functional group as predictors, and in addition also the natural logarithm of the time spent on the flower. As flight distance was an ordinal variable with discrete values, we used a Poisson distribution to model it.

We also built models to test for differences in the effectiveness of single-visit pollen deposition. We used the proportion of stigmas per inflorescence with pollen as the response variable, using a binomial distribution. The predictors used were pollinator functional group, number of stigmas as a surrogate for flower size and time spent on the inflorescence (log-transformed). All means are presented as ± standard deviation, and sample sizes are shown in figure titles. All analyses were performed in R (R Development Core Team, 2008).

3 | RESULTS

3.1 | Floral biology and flower visitor observations and

In all years, *Knautia arvensis* flowered in the study area from July to October, with the peak of open flowers in the middle of this period. Inflorescences have a mean (± SD) diameter of 43.4 ± 3.8 mm and contain an average of 23.7 ± 5.7 ray florets and 58.9 ± 13.6 disc florets. Over the course of flower development, nectar production rose from a mean (± SD) of 0.29 ± 0.07 μL ($n = 10$) on day one of anthesis (male phase) to 0.46 ± 0.32 μL ($n = 17$) by the third day (female phase). Sugar concentration during the male phase of anthesis was consistently greater than 50%, falling to 44.0 ± 13.5% by the third day (female phase). Inflorescence density was approximately 1.5 ± 2.1 inflorescences per m^2 within the low floral density site (Quarry Field) and 4.7 ± 4.4 inflorescences per m^2 within the high floral density site (Scrub Field). The three-fold average difference in floral density was significantly different (t-test for independent samples: $t = 5.68$, $df = 47$, $p < 0.001$) and we used this natural variation in inflorescence density as the basis for our observations of pollinator movements (see below).

More than 35 species of flower visitors were classified as potential pollinators and they represented six different insect orders: Hymenoptera (8 species), Lepidoptera (11 species), Diptera (8 species), Coleoptera (2 species), Hemiptera (1 species) and Mecoptera (1 species) [Appendix C]. Bumblebees (*Bombus* spp.–Apidae: Hymenoptera), hoverflies (Diptera: Syrphidae), and day-flying Lepidoptera (hereafter "butterflies", including some day-flying moths) had the greatest visitation frequency, although their relative proportions varied considerably between years (Figure 1). The large proportion of "Other" visitors in 2007 was due to an increase in numbers of soldier beetles (*Rhagonycha fulva* Coleoptera: Cantharidae).

3.2 | Pollinator effectiveness

The model including pollinator group, number of stigmas and residence time on the inflorescence, without interactions, best explained the variation in the proportion of stigmas with pollen after a single visit (Table 1 and Figure 2). Butterflies, for example, on average deposited pollen on about 10% of the stigmas in an inflorescence, bumblebees and hoverflies on about 6%, and the others on just 1% of stigmas (Figure 2).

Although flower visitor was one factor in the best model, the three main groups of pollinators (butterflies, hoverflies and bumblebees) had similar efficacies in delivering pollen, all different only from "Others" ($p < 0.004$). The number of stigmas alone performed almost equal to the null model suggesting that this variable had a

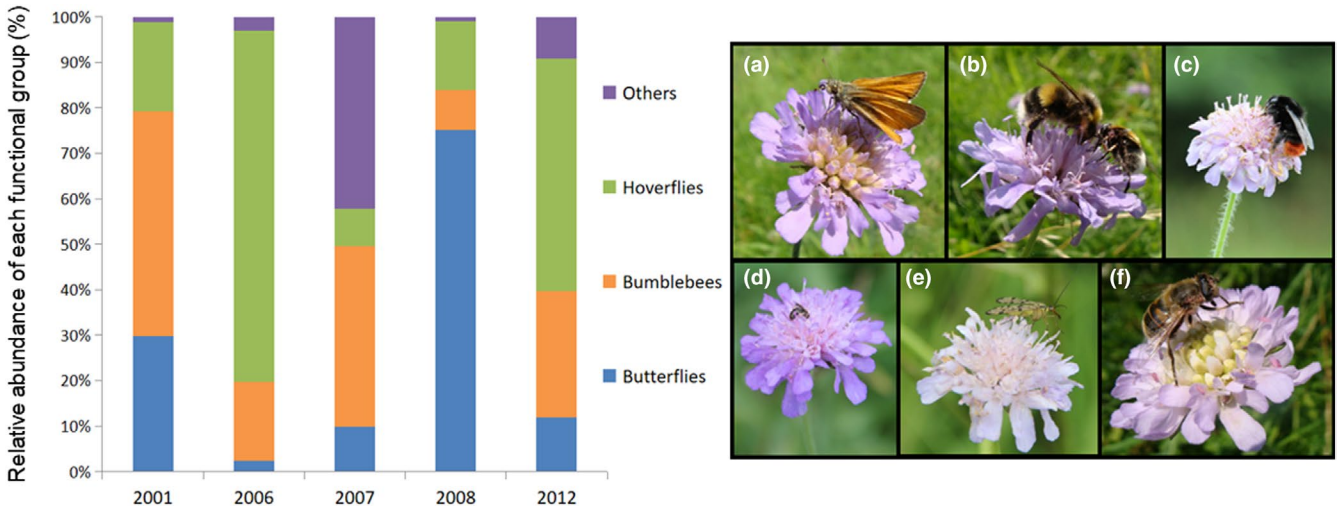


FIGURE 1 Variation in frequency of the most common flower-visiting groups to *Knautia arvensis* over the 5 years of sampling in Northampton, UK. Samples sizes are 2001 $n=488$ insects; 2006 $n=133$; 2007 $n=675$; 2008 $n=111$; 2012 $n=469$. Also shown are some examples of flower visitors: (a) *Thymelicus sylvestris* (Lepidoptera); (b) *Bombus* sp. (Hymenoptera-left) and *Volucella bombylans* (Diptera-right); (c) *Bombus lapidarius*. (Hymenoptera); (d) *Andrena* sp. (Hymenoptera); (e) *Panorpa* sp. (Mecoptera); (f) *Eristalis tenax* (Diptera). [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Results of the model selection for factors determining pollen deposition on stigmas of *Knautia arvensis*.

Model	dAIC	Degrees of freedom
Visitor + Stigmas + Time	0.0	6
Visitor + Stigmas	2.7	5
Full Model (Visitor, Stigmas, Time and Interaction)	6.0	9
Visitor + Time	8.6	5
Only Time	13.0	2
Only Visitor	17.0	4
Only Stigmas	20.8	2
Null Model	23.8	1

Note: Visitor are grouped as bumblebees, hoverflies, butterflies, and others; time is log transformed and number of stigmas per inflorescence is used as a control for different-sized inflorescences. The full model included the fixed factors: Visitor group, time spent on flowers, number of stigmas and the possible interaction between time and visitor group. The null model is only the intercept.

lower contribution to explain the amount of pollen on inflorescences after a single visit. Combining pollinator quality (E) with the relative abundance of each pollinator group (I) to give pollinator effectiveness (PE) by year, it is clear that the relative importance of the main groups of flower visitors as pollinators varied between years (Figure 3). In 2001 bumblebees were the most important pollinators, followed by butterflies, then hoverflies. In 2006 this had changed such that hoverflies were the most important, with bumblebees and butterflies much less so. The following year (2007) was more similar to 2001, except that "Others" were of greater importance, while 2008 saw butterflies dominating. The situation in 2012 was more similar to 2006, with hoverflies ranking as the most important pollinators.

3.3 | Residence times and flight distances of insects

The best predictors of residence time on inflorescences were pollinator group and floral density without interaction between factors (Table 2). Residence time was highly variable between groups and subpopulations. Butterflies spent 50–80 s on an inflorescence, bumblebees and hoverflies anywhere from 10 to 20 s on average (Figure 4).

Floral density provided the greatest predictive power for the variation in flight distance between inflorescence visits (Table 3, Figure 5). This result shows that all groups of flower visitors fly larger distances between inflorescences in areas of lower floral density. Two other models including the flower visitor group and the time spent on the inflorescence before departure were as likely as the one including only flower density. Thus, we considered the single factor, most parsimonious model, as the best one to explain flight distance after a flower visit to an inflorescence. In the high-density, Scrub Field site, a smaller proportion of short-distance (<30 cm), and a larger proportion of longer-distance (101 cm–500 cm), butterfly flights were observed compared to the bumblebees and hoverflies, plus butterflies were the only group observed to fly >500 cm (Figure 5a). Similar results were seen in the low-density, Quarry Field sites, though bumblebees were also observed making some flights >500 cm (Figure 5b).

4 | DISCUSSION

Contrary to the assumption that large bees are usually the most effective pollinators of generalist plants, a key finding of this study has been establishing the effectiveness of Lepidoptera as pollinators for *K. arvensis*. Butterflies and day-flying moths are traditionally

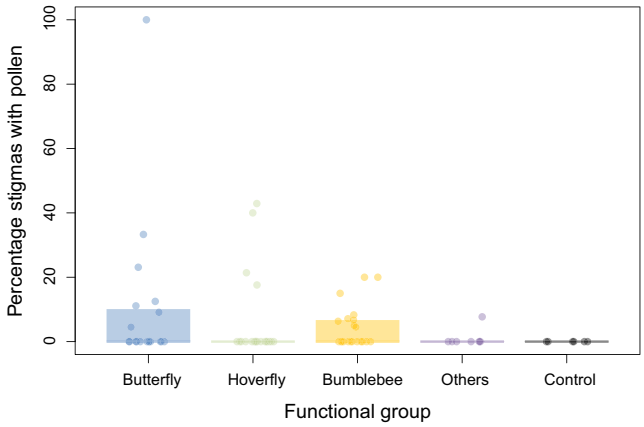


FIGURE 2 The average proportion of stigmas with pollen grains after a single visit to an inflorescence of *Knautia arvensis* in Northampton, United Kingdom. Sample sizes are Lepidoptera = 20 inflorescences; Hoverflies = 20 inflorescences; Bumblebees = 21 inflorescences; Others = 7 inflorescences. At every field work day, we counted the last inflorescence without visitation as a control and no pollen was ever found on virgin flowers. [Colour figure can be viewed at wileyonlinelibrary.com]

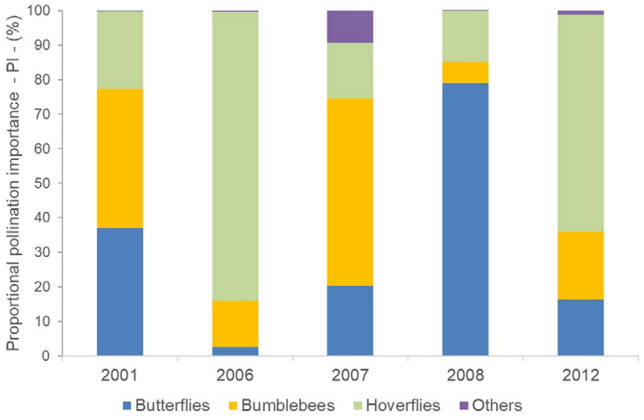


FIGURE 3 Relative annual importance of each pollinator group to the pollination of *Knautia arvensis* in Northampton, United Kingdom. Importance is given by pollinator abundance and effectiveness (number of stigmas with pollen after a single visit). [Colour figure can be viewed at wileyonlinelibrary.com]

regarded as poor pollinators (Morse, 1982; Percival, 1965; Wiklund et al., 1979). However, our results show them to be at least as important as bumblebees in the pollination services that they provide to *K. arvensis*. In 2008, Lepidoptera were the most frequent visitors to *K. arvensis* in our sites, corroborating observations by Jennersten (1984) in Sweden in 1980–81 and Lack (1982a) in the UK in 1979. Although the differences between groups in flight distance were not statistically significant due to the coarse scale at which they were measured, there was a clear pattern of butterflies travelling the greatest distance between inflorescence visits, leading to high potential pollen dispersal. This is a feature of butterfly behaviour that has also been found in other studies (Herrera, 1987; Larsson, 2005; Murawski & Gilbert, 1986). Importantly, butterflies were found to be the highest quality pollinators in terms of the proportion of stigmas with pollen grains deposited after a single visit.

TABLE 2 Results of the model selection for residence time on inflorescences of *Knautia arvensis*.

Model	dAIC	Degrees of freedom
Only visitor	0.0	4
Visitor and site plus interaction	0.5	7
Visitor and site without interaction	0.6	5
Only site	85.6	3
Null	85.6	2

Note: Visitors are grouped as bumblebees, hoverflies and butterflies, and the site refers to two sites with low and high flower densities.

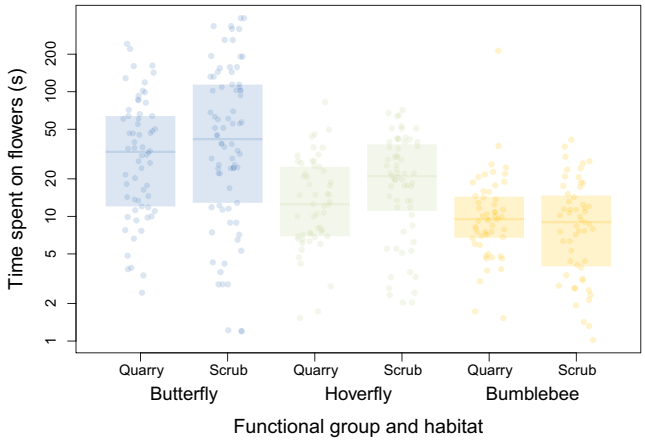


FIGURE 4 Average time spent on flowers by the functional groups of pollinators of *Knautia arvensis* in two sites with different inflorescence densities in Northampton, United Kingdom. Quarry Field is a site with low flower density in contrast to the Scrub Field. Images were obtained from www.divulgare.net. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 Results of the model selection for pollinator flight distance after visiting inflorescences of *Knautia arvensis*.

Model	dAIC	Degrees of freedom
Floral density and visitor without interaction	0.0	4
Floral density, visitor and residence time	0.8	5
Floral density	1.3	2
Visitor	3.7	3
Floral density and visitor interaction	4.0	6
Null	4.6	1
Distance and residence time	6.5	2

Note: Visitors are grouped as bumblebees, hoverflies and butterflies; floral density and residence time refers to the time spent on flowers before flight departure.

Conversely, bumblebees had the shortest flight distances between inflorescence visits, often moving to the closest flowers, mirroring studies by others, e.g., Zimmerman (1979) and Collevatti

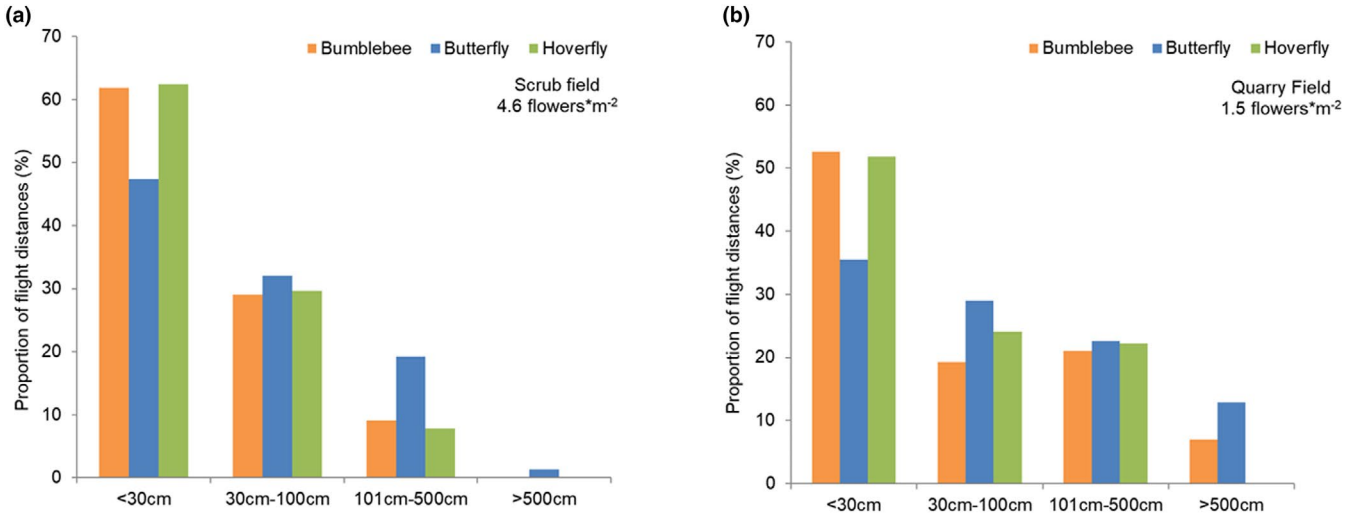


FIGURE 5 The proportion of the average flight distances of the three major groups of pollinators in an area with (a) high and (b) low density of inflorescences of *Knautia arvensis*. [Colour figure can be viewed at wileyonlinelibrary.com]

et al. (2000). The result is a probable increase in geitonogamous fertilisation events, which could reduce the effectiveness of bumblebees as pollinators in a species with high inbreeding depression (Larsson, 2005). Moreover, of the three main pollinator groups we identified for *K. arvensis*, bumblebees were the lowest quality. The natural histories of the different pollinator groups thus explain much of the variation between and within groups. Bees are central place foragers and therefore optimal foraging behaviour generally involves utilising all the inflorescences in a given area. Lepidoptera and hoverflies are nomadic and use nectar to fuel travelling to find mates and egg laying sites. Bumblebees collect nectar and pollen to provision their nests for both offspring and workers, and adult hoverflies consume both products. For this reason, they are equally likely to visit male and female flowers. Solitary bees, on the other hand, primarily forage for pollen to provision their offspring and thus favour male flowers. Their overall foraging requirements are also lower, and thus visitation rates are lower (Larsson, 2005).

The abundance of the different groups has a clear effect on their relative importance as pollinators. Across the 5 years of study, there were only 2 years where the most important pollinator group was the same. Dramatic fluctuations in pollinator groups have also been observed by Howard and Barrows (2014) and Lack (1982a).

Knautia arvensis has a long flowering period (3 months), and nectar-rich inflorescences composed of multiple flowers that are easily accessible to pollinators with extensible mouthparts. These characteristics make *K. arvensis* very attractive to a wide range of pollinator groups (Biella et al., 2019; Ebeling et al., 2008; Knuth, 1898a, 1898b, 1898c; Lack, 1982a; Larsson, 2005). Under the classification of pollination systems proposed by Ollerton, Killick, et al. (2007), *K. arvensis* would be considered a generalist in all parameters: although tubular, the flower morphology allows all visitors to access nectar, making it phenotypically generalised; the number of pollinator species is high, making it ecologically generalised; and the pollinator species belong to several groups of unrelated taxa, making it functionally generalised. All of the main groups of flower visitors effectively pollinate the flowers of *K. arvensis*; thus, it can be considered to have a highly generalised pollination system.

The flowers of *K. arvensis* are protandrous and as inflorescences age, there is a shift from predominantly male flowers, which provide pollen and nectar, to female flowers, which provide only nectar. The increase in nectar volume as the pollen reward is lost allows female flowers to maintain visitation rates by specialist bees that would normally visit to collect pollen (Larsson, 2005). By providing nectar at both the male and female stage, nectar-collecting flower visitors are more likely to act as effective pollinators as they will visit more equally male and female phase flowers than exclusively pollen-eating flower visitors (Jennersten, 1984; Larsson, 2005).

While protandry reduces the probability of self-pollination by flowers on the same inflorescence, there remains the possibility of geitonogamy via pollination from inflorescences in a different sexual phase on the same plant (Eckert, 2000; Vange, 2002). Vange (2002) calculated the mean inbreeding depression for *K. arvensis* at 58% in offspring produced by self-pollination. Such high inbreeding depression shows the importance of effective outcrossing, as mediated by pollinators and their flight distances (Larsson, 2005). It is essential, therefore, to interpret pollinator importance as a product of flight distance between flower visits, in addition to conventional measures of visitation frequency, and pollen deposition (Howard & Barrows, 2014; Ivey et al., 2003; Larsson, 2005).

Relatively few studies have experimentally compared pollinator effectiveness among flower visitors in generalised pollination systems. Previous research by King et al. (2013) defined a bee/hoverfly pollination "syndrome" for *K. arvensis*; however, this syndrome (in a strict sense) has never been formally described (Faegri & van der Pijl, 1979; Ollerton et al., 2009) and is better termed a pollination system sensu Ollerton (2021). Whilst we agree with King et al. (2013) that effective pollinator identity must be determined in order to understand floral evolution, we believe that they underestimate the

difficulty of assessing every species of pollinator for highly generalised plants, especially if time and space are taken into account. For example, for *K. arvensis* King et al. (2013) included only eight species of flower visitors from two groups (bees and hoverflies), whereas, for our study and the limited published results, we know that the flower visitors to *K. arvensis* include at least 30 species from six functional groups, and that butterflies are the most effective pollinators. The species is native across a large swathe of Eurasia and Scandinavia and no doubt interacts with a huge number of different pollinators across its range. In contrast to King et al. (2013), we consider *K. arvensis* to be a species with a highly generalised pollination system that does not fit neatly into a formal pollination syndrome, and is certainly not a bee/hoverfly 'specialist'. Acknowledging this diversity of pollinators across time and space, and the consequent variation in selection on floral phenotype that will result is important if we are to fully understand how generalist pollination systems evolve (Ollerton, 2021).

Our study adds to a growing literature showing that different proxies of pollinator effectiveness must be used for different plant species. For example, while time spent on inflorescences may be a good predictor of pollinator effectiveness in *Asclepias incarnata* (Ivey et al., 2003), it is not for *K. arvensis* and other species (King et al., 2013). Flower visitor frequency correlated with effectiveness in *Raphanus raphanistrum* while it is a poor predictor in many other species (Johnson & Steiner, 2000; Sahli & Conner, 2007). Nonetheless, the amount of pollen deposited on stigmas (normally measured as single-visit pollen deposition) will only be useful for plants with more than one ovule, otherwise, the number of stigmas with pollen (as we measured here) will be more informative.

5 | CONCLUSION

Understanding the pollination ecology of highly generalised and ecologically important species such as *K. arvensis* requires careful study over multiple populations and years using adequate proxies for pollinator effectiveness and frequency. The results of our study corroborate the adaptive value of generalised pollination systems. Specifically, our findings support the notion that plants should generalise on a diversity of pollinators that are equally effective, but vary in identity between years, therefore buffering plants against reproductive failure during periods of environmental flux that affect the abundance of particular pollinators (Waser et al., 1996; Wolowski et al., 2014). Importantly, our findings show that butterflies may be more effective pollinators than is widely assumed. In the future, climate change, along with other fluctuations in the environment, may have less of an impact on the reproduction of such generalist plant species than they will on plants with more specialised pollination systems. These plants in turn can support a wide range of different types of pollinators, many of which are neglected in studies of plant-pollinator interactions, as contributions to this Special Issue of the *Journal of Applied Entomology* have demonstrated. Thus the conservation of "core generalist" (sensu Ollerton, 2021), abundant species such as *Knautia arvensis* should be also a priority (Biella et al., 2017, 2019).

AUTHOR CONTRIBUTIONS

Jeff Ollerton: Conceptualisation; data collection; funding acquisition; writing; initial analysis; data curation. **Emma Coulthard**: Data collection; writing; **Sam Tarrant**: Data collection; writing. **James Woolford**: Data collection; writing. **Leonardo Ré Jorge**: Data analysis; writing. **André Rodrigo Rech**: Conceptualisation; data collection; funding acquisition; writing; initial analysis; visualisation.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw data from this study are/is available on Figshare: https://doi.org/10.6084/m9.figshare.26502400.v1

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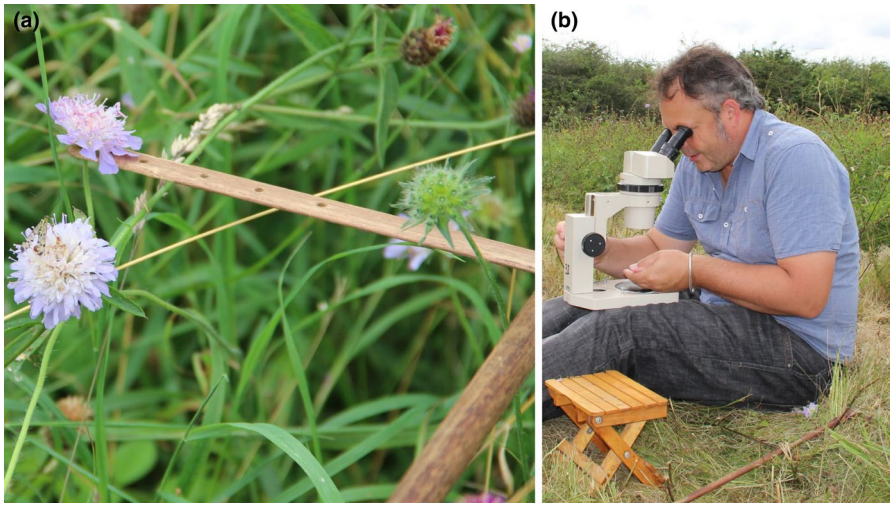
APPENDIX A

Photographs to illustrate the different densities of flower heads of *Knautia arvensis* at the two subpopulations. Note the many brown post-anthesis flower heads in the higher-density site. Tape measure = 50 cm. Photographs by André Rodrigo Rech. [Colour figure can be viewed at wileyonlinelibrary.com]



APPENDIX B

(a) The T-piece end of the 0.8 m pole used to present virgin inflorescences to potential pollinators. (b) The first author examined a recently visited inflorescence in the field using a small bench Olympus stereomicroscope. Note the 0.8 m pole at the bottom of the image. Photographs taken in 2012 by André Rodrigo Rech. [Colour figure can be viewed at wileyonlinelibrary.com]



APPENDIX C

Visitors to the flower heads of *Knautia arvensis* during the survey periods.

Hymenoptera
Bombus pascuorum
Bombus terrestris
Bombus lucorum
Bombus lapidarius
Bombus hortorum
Apis mellifera
Megachile sp.
Andrena sp.
Solitary wasp sp.
Symphyta sp.
Diptera
Syrphus ribesii
Episyrphus balteatus
Volucella bombylans
Eristalis tenax
Sphaerophoria scripta
Hoverfly spp.
Calliphora sp.
Asilidae sp.
Lepidoptera
Polyommatus icarus
Maniola jurtina
Pyronia tithonus
Pieris brassicae
Pieris napi
Aglais io
Aglais urticae
Thymelicus sylvestris
Zygaena filipendulae
Noctuidae sp.
Incurvariidae sp.
Coleoptera
Rhagonycha fulva
Coleoptera sp.
Hemiptera
Hemiptera sp.
Mecoptera
Panorpa sp.