Received: 3 January 2023 | Accepted: 26 May 2023

DOI: 10.1002/2688-8319.12253

Ecological Solutions and Evidence | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

What makes a good pollinator? Abundant and specialised insects with long flight periods transport the most strawberry pollen

Edith Villa-Galaviz[1] | Alyssa R. Cirtwill[1] | Rachel Gibson[2] | Thomas Timberlake[2] | Tomas Roslin[1,3] | Jane Memmott[2]

[1]Faculty of Agriculture and Forestry, University of Helsinki, Helsinki, Finland

[2]Faculty of Life Sciences, University of Bristol, Bristol, UK

[3]Department of Ecology, Swedish Agricultural University (SLU), Uppsala, Sweden

Correspondence
Edith Villa-Galaviz
Email: edith.villagalaviz@helsinki.fi

Present address
Edith Villa-Galaviz, Technical University of Darmstadt, Darmstadt, Germany

Funding information
Academy of Finland, Grant/Award Number: 334787, 322266 and 1332999; Belmont Forum, Grant/Award Number: proposal 1550; Bristol Centre for Agricultural Innovation; Natural Environment Research Council, Grant/Award Number: NE/T013621/1; National Science Foundation (NSF); European Research Council Synergy, Grant/Award Number: 856506 (LIFEPLAN); Swedish University of Agricultural Sciences

Handling Editor: Molly Mitchell

Abstract

1. Despite the importance of insect pollination to produce marketable fruits, insect pollination management is limited by insufficient knowledge about key crop pollinator species. This lack of knowledge is due in part to (1) the extensive labour involved in collecting direct observations of pollen transport, (2) the variability of insect assemblages over space and time and (3) the possibility that pollinators may need access to wild plants as well as crop floral resources.
2. We address these problems using strawberry in the United Kingdom as a case study. First, we compare two proxies for estimating pollinator importance: flower visits and pollen transport. Pollen-transport data might provide a closer approximation of pollination service, but visitation data are less time-consuming to collect. Second, we identify insect *parameters* that are associated with high importance as pollinators, estimated using each of the proxies above. Third, we estimated insects' use of wild plants as well as the strawberry crop.
3. Overall, pollinator importances estimated based on easier-to-collect visitation data were strongly correlated with importances estimated based on pollen loads. Both frameworks suggest that bees (*Apis* and *Bombus*) and hoverflies (*Eristalis*) are likely to be key pollinators of strawberries, although visitation data underestimate the importance of bees.
4. Moving beyond species identities, abundant, relatively specialised insects with long active periods are likely to provide more pollination services.
5. Most insects visiting strawberry plants also carried pollen from wild plants, suggesting that pollinators need diverse floral resources.
6. Identifying essential pollinators or pollinator parameters based on visitation data will reach the same general conclusions as those using pollen transport data, at least in monoculture crop systems. Managers may be able to enhance pollination service by preserving habitats surrounding crop fields to complement pollinators' diets and provide habitats for diverse life stages of wild pollinators.

Edith Villa-Galaviz and Alyssa R. Cirtwill are joint first-authors.

KEYWORDS
crop pollination, insect, key species, monitoring, parameters, pollen, strawberry, visitation

1 | INTRODUCTION

Animal pollination of crops, especially by insects, is critical for many crops and can be valued at US$195–$387 billion annually (Porto et al., 2020). Preserving or enhancing this pollination service, especially in the face of ongoing climate change, is, therefore, an important consideration for farm managers. An important first step towards promoting pollination service for a crop is understanding which are the most important pollinators for that crop. However, while the effectiveness and value of bees (especially domesticated honeybees) is well understood for some crops (Eeraerts et al., 2019; MacInnis & Forrest, 2019), other wild pollinators have not been as frequently studied. Nevertheless, wild pollinators in general have been shown to substantially improve yield quantity and quality in many fruit crops in the family Rosaceae (e.g. strawberries and apples; Abrol et al., 2019; MacLeod et al., 2020). Identifying and protecting important wild pollinators, in tandem with appropriate management of domesticated bees, is, therefore, a sensible strategy for farm managers.

Identifying key wild pollinators is, however, not straightforward for plants with open, cup-shaped flower morphologies such as the Rosaceae (Kalkman, 2004). These flowers can be visited by insects in several orders (Kalkman, 2004), not all of which contribute significantly to pollination (Cirtwill et al., 2022). The most effective pollinators will combine frequent visits to crop flowers with large numbers of pollen grains deposited per visit. However, single-visit deposition data are resource-intensive to collect and, therefore, remain rare (see Page et al., 2021 for a meta-analysis of available studies).

The amount of crop pollen carried on an insect's body offers a proxy for different pollinators' potential effectiveness and are easier to collect than deposition data (although more difficult than visitation data alone, the most common source of information about which insects pollinate which plants). For example, insects that carry more crop pollen grains because they are large or hairy (Stavert et al., 2016) will, on average, have a higher chance of depositing sufficient pollen on the plants that they visit (Cullen et al., 2021; Földesi et al., 2021). Abundant pollen deposition is especially important for plants with composite fruits such as strawberries, where at least 70%–80% of the carpels must be pollinated to avoid malformations (Carew et al., 2003). Combining the amount of crop pollen carried by an individual with the frequency of its visits to the crop, we can estimate the total quantity of crop pollen moved by each species (Gibson, 2012).

An insect's pollen load also reveals how much *non-crop* pollen it carries. Since heterospecific pollen deposition can reduce pollination success (Arceo-Gómez & Ashman, 2011), a load with more conspecific pollen will be higher quality from the plant's perspective (Ashman & Arceo-Gómez, 2013). Resolving the makeup of individual pollen loads may also reveal individual-level specialisation within generalist species (Lucas et al., 2018; Somme et al., 2015). Where individuals are much more specialised than species, an apparently low-quality species may actually provide high-quality pollen transport.

Another difficulty in managing wild pollinators is that the insect community is likely to differ between farms. The insects that are expected to be the best pollinators based on data from one site may not even be present at another site, reducing farm managers' ability to apply recommendations to their local context. Instead of identifying specific taxa as key pollinators, it may be more helpful to identify parameters that are strongly related to pollinator quality and quantity so that farm managers can promote the local pollinator taxa that best match those parameters. This is also likely to be a cheaper management strategy than buying commercial bee colonies in many cases. For example, larger insects are likely to carry larger pollen loads (Cullen et al., 2021) and, hence, transport more pollen than small insects. Larger insects also tend to fly longer distances (Greenleaf et al., 2007), potentially allowing individuals to specialise on spatially dispersed preferred plant species. Similarly, more abundant insects and those with longer active periods tend to make more visits in total than rare or briefly active insects, such that both groups generally carry more pollen. Conversely, generalist insect species may carry more mixed (lower-quality) pollen loads, unless generalist species are more specialised at the individual level or during shorter time periods.

In this study, we use strawberry—an economically important Rosaceae crop with generalist flower morphology—as a model system to answer the following three questions: (1) Does estimated pollinator importance differ when estimated from flower visitation or pollen-load data? As strawberries had a long flowering season at our study sites, we estimate pollinator importance per fortnight and over the whole season and test whether both approaches highlight congruent sets of important insects. (2) Are there general insect parameters that can predict importance? Again, we consider both pollen-based and visit-based metrics and short-term and long-term estimates. (3) How frequently do crop pollinators visit and collect pollen from non-crop plants? This indicates whether the strawberry crop alone can sustain populations of key pollinators.

2 | MATERIALS AND METHODS

2.1 | Study sites and data collection

We sampled three commercial strawberry farms (8–19 ha in size, cultivar: Elsanta) in Somerset County, South-West England (hereafter farms A, B and C). Strawberries were grown in open fields and open-sided polytunnels with rotation of new plants into the fields as ripe berries were harvested (Gibson, 2012). On each farm, we established 5 (farms B, C) or 10 (farm A) randomly positioned 25 × 2 m transects in the crop field (including open-sided tunnels) and the same number of transects in the field margins (natural and semi-natural grasses, wildflowers, and hedgerows). This means that farm A was sampled twice as intensively as the other two farms. All insects observed visiting any flower were collected during transect walks conducted on fine days every ~7–10 days March 16–September 29, 2009. The flower (strawberry or non-strawberry) and habitat (field or margin) where each insect was collected was recorded. Insects were identified and swabbed for pollen, which was identified as strawberry or non-strawberry by comparison to a reference library. For further site and sampling details, see Supplementary information S2.1. Commercial hives of *Bombus terrestris* were placed at farm B to supplement pollination; this species is native to the area and locally common, and *B. terrestris* was observed at all three farms (Martin et al., 2019). Samplings were done with approval of the land owners (see "Acknowledgements" section) no permits are required for invertebrate collecting in the area. We did not collect any listed species.

2.2 | Estimating pollinator importance

For each type of data (pollen-transport and flower visitation), we estimated the importance of each insect species as a pollinator (henceforth referred to as its 'importance', for brevity) based upon separate, but related, metrics of quantity and quality:

$$pI = pQ \times pF. \quad (1)$$

For the pollen-based estimated importance (pI), our quantity estimate is the proportion of the total strawberry pollen pool at each farm carried by each species (pollen quantity; pQ). Our quality estimate is the proportion of strawberry pollen in pollinator loads at each farm (pollinator fidelity; pF). Both proportions and their product range between 0 and 1.

When estimating pollinator importance based on visitation data, we only have information about one visit per individual (i.e. the plant where the insect was captured). We, therefore, estimate visit quantity (vQ) for each insect as the proportion of all observed visits to strawberries at a farm made by the focal pollinator. Similarly, we estimate visitation fidelity (vF) as the proportion of individuals of the focal species at each farm that were captured on strawberries rather than any other plant. As with pollen-based importance, visit-based importance is the product of these components:

$$vI = vQ \times vF. \quad (2)$$

We estimated pollinator importance for each farm separately. We calculated each species' overall importance, based on the full sampling season, and its short-term importance during each week (defined as a rolling average of approximately fortnightly pairs of consecutive samples at each farm). These short-term estimates highlight species that may fill gaps in pollination service (demonstrated by a high short-term importance despite having lower importance over the whole year). Pairs of consecutive samples separated by more than 14 days (Figure 1) were not pooled as the insect community is less likely to remain constant over longer time periods. After estimating pollinator importance based on each approach, we then tested whether these estimates were related. To do this, we fitted a series of linear models that also included a fixed effect of farm (see Supplementary information S2.2 for details).

2.3 | Relating insect parameters to estimated importance

2.3.1 | Defining parameters

We extracted morphological traits of insects (assumed to be constant across farms) from the literature and estimated abundance and active period from our data (separately for each farm). All parameters (morphological and community-based) are briefly defined below. For details on inter-tegument distance (ITD) and active period, see Supplementary information S2.2. As an exploratory tool, we calculated the correlations between each of the parameters below. We also tested whether each parameter was related to each component of pollinator importance using a series of Kendall's rank correlation tests (Supplementary information S3.1).

Inter-tegument distance

To approximate insect size and movement range, we used the ITD: the distance between the wing bases. We obtained mean ITD values for British pollinators from Baldock et al. (2019) and Hackett et al. (2019). As ITD values could not be measured for Coleoptera, we removed these species from our main analyses. Repeating our analyses using the length and width of elytra for Coleoptera (taken from Baldock et al., 2019) as substitutes for ITD did not qualitatively affect our conclusions (Supplementary information S3.2).

Degree

We define each species' annual degree as the number of plant species visited over the whole year, at the focal farm. Species with long flight periods might be generalist over the course of the year but specialist at any point within the year. We, therefore, also calculated the average weekly degree (number of plant species visited per farm per sampling event) for each species.

Abundance

We used the total number of visits observed for each insect, at the focal farm, as a proxy for abundance. Insects observed in flight (not visiting a flower) were not included.

Active period

We define active period as the number of sampling events in which the insect was observed at the focal farm. Insects might be important pollinators if they are active during a period when few other pollinators are available, regardless of the total length of the active season. We, therefore, also estimated the uniqueness of each pollinator's active period, defined as the average Bray–Curtis dissimilarity between the vector of proportions of a focal insect's total visits made in each fortnight at each farm and the vectors for all other species.

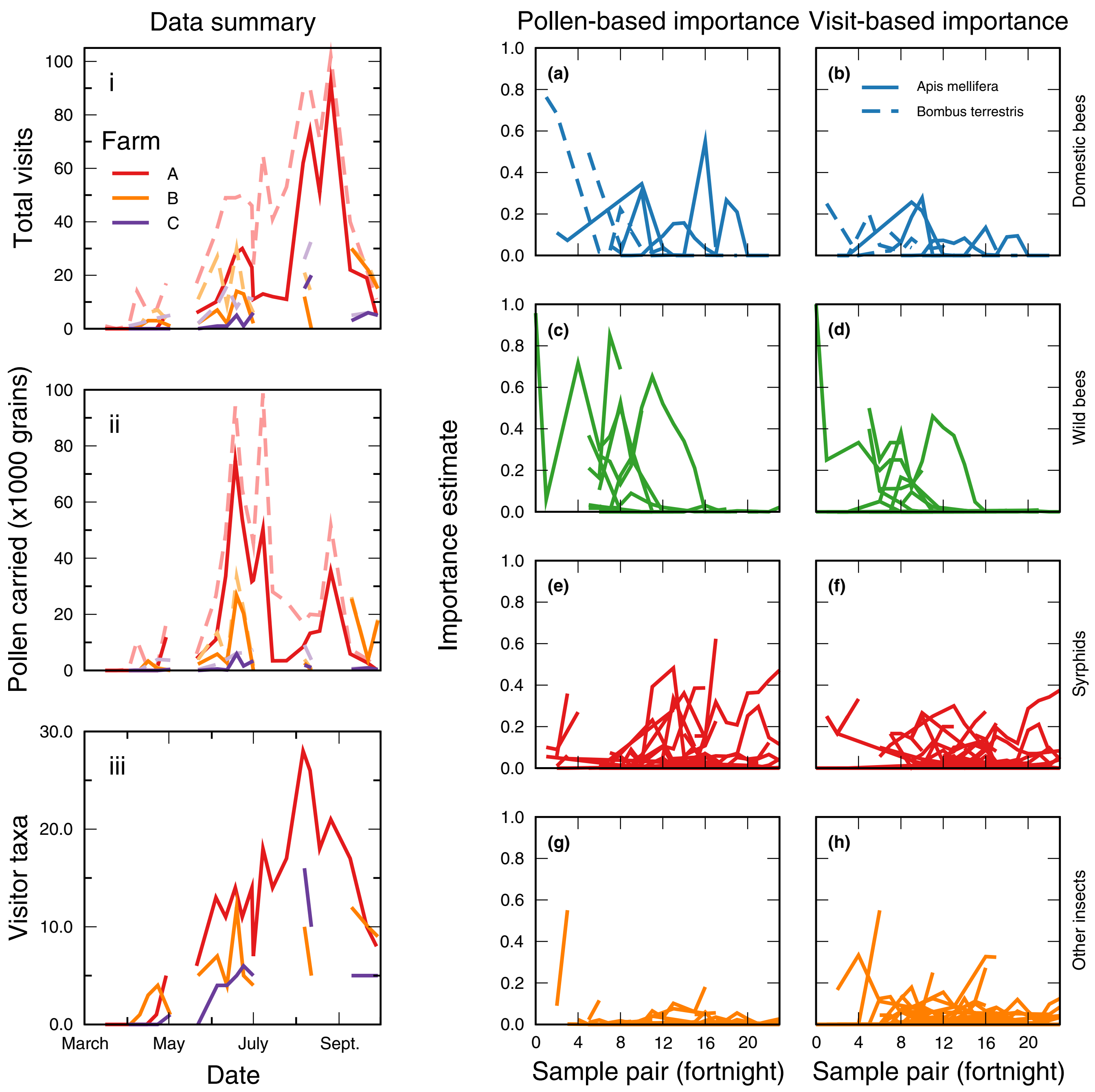

FIGURE 1 (i–iii) Transport of strawberry pollen peaked earlier than the number of visits and number of visitor taxa to strawberry plants. We show visits and pollen transport for strawberry plants alone (solid lines) and all plants (faded, dashed lines). For visitors, we show only those where at least one individual carried at least one strawberry pollen grain. Gaps indicate instances where the time between samples was longer than 14 days. Note: ten transects were sampled at farm A and five at farms B and C. (a–h) Short-term importance estimates were quite variable between species and farms whether they were estimated based on pollen transport (left) or visitation (right). (a, b) Domesticated honeybees *Apis mellifera* (solid lines) and bumblebees *Bombus terrestris* (dashed lines) did not have especially high short-term importance, despite the high overall importance of honeybees. (c, d) Wild bees had high estimated importance in the beginning of the season. (e, f) Syrphids had lower, but steady, estimated short-term importance throughout the season. (g, h) Insects that were neither bees nor syrphids generally had lower estimated importance. Each line indicates a single species at a single farm.

2.3.2 | Relating parameters to estimated importance of pollinators

To test whether importance was related to the insect parameters above, we fit two structural equation models (SEMs; one for PI and one for VI). In each model, we related parameters to pollinator quantity and fidelity (pQ and pF or vQ and vF), and quantity and fidelity, in turn, affected pollinator importance (PI or VI). We did not include any direct paths from parameters to importance as pollinator importance is explicitly defined in terms of fidelity and quantity (see Equations 1 and 2). This multi-step pathway allows us to test how insect parameters could affect importance through fidelity, quantity, or both, and overall test how parameters ultimately define importance.

To test the paths linking parameters to fidelity and quantity, we used generalised multilevel path models Shipley (2009), fitting separate models for each of the paths in the SEM. This means that each SEM included three sub-models, that is, (1) each individual parameter effect on fidelity, (2) each individual parameters effect on quantity and (3) fidelity and quantity affecting importance. Model fitting was implemented in the R (R Core Team, 2016) packages PIECEWISESEM (Lefcheck, 2016) and LME4 (Bates et al., 2015). We tested for the model fit of each SEM using a d-separation test estimate. This test estimates a Fisher's *C* statistic and performs a χ^2 test on it Shipley (2009). Note that, for this test, a *p*-value of the χ^2 test greater than 0.05 indicates that the model is an acceptable fit to the data. After fitting these models for annual or whole-season estimates of importance, we repeated the procedure for short-term estimates of importance. See Supplementary information S3.3 for full details.

2.4 | Evaluating strawberry pollinator use of wild plants

Insects are unlikely to meet their nutritional needs from a single source of nectar and pollen, and frequent use of wild plants may indicate that these resources fill a temporal or nutritional gap in the resources provided by the crop (Filipiak, 2019). To establish whether insect taxa depend on different resources beyond the crop plant and infer how movement between crop and non-crop flowers might affect pollen transport within the crop, we assessed the extent to which crop pollinators also visit non-crop flowers and how pollen loads differ depending on where insects were captured. More specifically, we calculate (a) the number of non-crop plant species at each farm, which share flower visitors with the strawberry crop, (b) the percentage of individuals carrying both strawberry and non-strawberry pollen (indicating that these individuals visit both habitats) and (c) the percentages of insects caught in one habitat (strawberry crop or margin) carrying pollen from the other habitat. To provide an individual-level perspective on cross-habitat pollen transport, we calculate the mean and standard error of the proportion of an insect's pollen load made up of strawberry pollen. We calculate this measure separately for insects caught on strawberry plants and insects caught on margin plants.

3 | RESULTS

3.1 | Bees and flies are important pollinators of strawberry in the United Kingdom

Across the whole year, both bees and flies were among the insects with the highest estimated importance (based on pollen transport; Table 1). Although the ranks of estimated importance varied between farms, the hoverfly *Eristalis arbustorum*, the honeybee *Apis mellifera*, and one of two wild bumblebees (*Bombus lapidarius* or *B. pratorum*) had the three highest estimated importances at each site. Notably, *B. terrestris* was not the most-important pollinator on any farm—not even on farm B where managed *B. terrestris* were present. Visit-based estimated importance for these species was generally lower than pollen-based importance, and differences were especially large for the bees (Table 1). For example, *A. mellifera* had the 10th highest and *Bombus terresstris* had the 19th highest visit-based estimated importance at farm A despite both species being among the species with the highest estimated importance based on pollen loads.

3.1.1 | Pollen-based and visit-based estimated importance are correlated

Annual pollen-based and visit-based estimated importance values were strongly, significantly, and positively correlated (Figure 2c; $\beta=0.772$, $p<0.001$; only insects with non-zero visit-based importance included to avoid model singularity). Rank of visit-based estimated importance was also strongly, significantly, and positively correlated with rank of pollen-based estimated importance ($\tau=0.533$, $z=8.42$, $p<0.001$). Short-term pollen-based importance was even more strongly and positively associated with visit-based importance (Figure 2d; $\beta=0.978$, $p<0.001$ for a linear model relating PI to VI; $\tau=0.446$, $z=13.7$, $p<0.001$ for a test of rank correlation Supplementary information S3). Finally, short-term and annual or whole season estimated importance were also significantly and positively correlated, but the association was stronger for pollen-based than visit-based estimated importance (Supplementary information S3; Figure 2a,b).

3.2 | Insect activity and degree predict estimated importance

In all models, we observed significant effects of quantity and fidelity on importance. This confirms that parameters related to quantity and fidelity ultimately affect estimated importance (Supplementary information S3.4). All SEM were a good fit ($p>0.5$).

3.2.1 | Annual or whole-season importance

Both pollen and visit quantity increased with longer active periods and higher abundance but decreased with active period uniqueness (Figure 3a,c; $\beta=0.4$, $p<0.001$, $R^2=0.45$; $\beta=0.3$, $p<0.001$, $R^2=0.45$ and $\beta=-0.1$, $p=0.03$, $R^2=0.45$ for pQ; $\beta=0.5$, $p<0.001$, $R^2=0.64$; $\beta=0.8$, $p<0.001$, $R^2=0.64$ and $\beta=-0.2$, $p=0.002$, $R^2=0.64$ for vQ). Both pollen and visit fidelity, conversely, decreased for insects with higher annual degrees and more unique active periods ($\beta=-0.5$, $p<0.02$, $R^2=0.29$ and $\beta=-0.1$, $p=0.03$, $R^2=0.45$ for

TABLE 1 Importance estimates for the five most important strawberry pollinators (ranked by pollen-based importance; pI) at each of the three farms. For each species, we give the pollen-based importance estimate (pI), pollinator fidelity (pF), pollen quantity (pQ), visit-based importance estimate (vI), visitation fidelity (vF), visit quantity (vQ), and rank of visit-based and pollen-based importance estimates. We also give values for key parameters at each farm: length of active period (AP), annual degree (Deg), and abundance (Abun). Domesticated *Bombus terrestris* were placed at farm B but did not have especially high estimated importance (estimated based on pollen loads). Farms A and C relied on wild pollination although domesticated *Apis mellifera* were observed at all farms.

Farm	Order	Species	pI	pF	pQ	vI	vF	vQ	R_{vI}	R_{pI}	AP	Deg	Abun
A	Apidae	*Bombus lapidarius*	0.27	0.53	0.50	0.07	0.54	0.13	2	1	15	9	7.87
A	Diptera	*Eristalis arbustorum*	0.06	0.79	0.08	0.15	0.93	0.16	1	2	11	4	7.91
A	Apidae	*Apis mellifera*	0.06	0.39	0.16	0.02	0.36	0.07	10	3	14	9	6.57
A	Diptera	*Eristalis abusivus*	0.04	0.81	0.05	0.07	0.95	0.07	3	4	7	3	5.43
A	Apidae	*Bombus terrestris*	0.02	0.35	0.06	0.01	0.38	0.02	19	5	10	6	2.60
B	Diptera	*Eristalis arbustorum*	0.16	0.90	0.18	0.12	0.95	0.12	2	1	5	2	4.00
B	Apidae	*Apis mellifera*	0.15	0.74	0.20	0.06	0.72	0.08	5	2	8	3	2.25
B	Apidae	*Bombus lapidarius*	0.12	0.74	0.16	0.03	0.78	0.04	8	3	4	3	2.25
B	Apidae	*Bombus lucorum*	0.11	0.66	0.17	0.04	0.69	0.06	6	4	7	5	1.86
B	Diptera	*Eristalis tenax*	0.08	0.84	0.10	0.10	0.94	0.10	3	5	7	2	2.43
C	Diptera	*Eristalis arbustorum*	0.15	0.95	0.16	0.07	1.0	0.07	3	1	3	1	2.33
C	Apidae	*Apis mellifera*	0.09	0.29	0.31	0.02	0.28	0.08	11	2	5	3	5.80
C	Apidae	*Bombus pratorum*	0.07	0.70	0.11	0.02	0.75	0.03	10	3	2	2	2.00
C	Diptera	*Eristalis tenax*	0.07	0.73	0.09	0.06	0.88	0.07	4	4	5	2	1.60
C	Diptera	*Morellia aenescens*	0.06	1.0	0.06	0.06	1.0	0.06	6	5	1	1	6.00

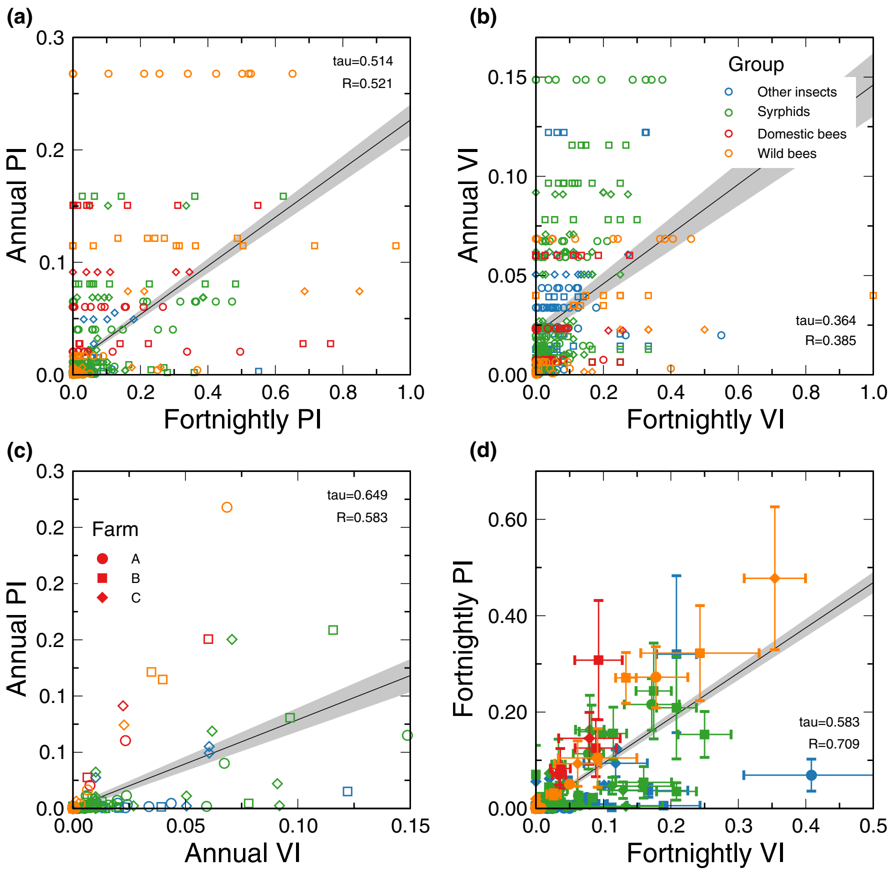

FIGURE 2 Estimated pollinator importance was congruent across different calculation methods. (a, b) Annual and short-term estimates were weakly and positively correlated. (c, d) Importance estimated based on visits and pollen loads were more strongly correlated. We show importance values for each species at each farm (indicated by colour) with fit lines for linear models relating estimates of importance (shaded areas represent ±SE). In (d), we show the mean ± SE of short-term importance across the year. In each panel we give Kendall's τ and the R statistic for the corresponding Pearson's product–moment correlation.

pF; $\beta=-0.8$, $p=0.005$, $R^2=0.51$ and $\beta=-0.2$, $p=0.002$, $R^2=0.64$ for vF). ITD was also significantly related to pollen quantity, while annual degree was related to visit quantity (Supplementary information S3.4); the remaining parameters considered were not significantly related to any component of estimated importance.

3.2.2 | Short-term importance

Both pollen and visit quantity were higher for insects with greater abundance (Figure 3b,d; $\beta=0.4$, $p<0.001$, $R^2=0.26$ for pQ and $\beta=0.2$, $p=0.02$, $R^2=0.03$). Likewise, both pollen and visit fidelity were higher for insects with longer active period and lower for insects with higher annual degrees and more unique active periods ($\beta=0.3$, $p<0.001$, $R^2=0.19$; $\beta=-0.6$, $p<0.001$, $R^2=0.19$ and $\beta=-0.1$, $p<0.001$, $R^2=0.19$ for pF; $\beta=0.5$, $p<0.001$, $R^2=0.26$; $\beta=-0.8$, $p<0.001$, $R^2=0.26$ and $\beta=-0.2$, $p<0.001$, $R^2=0.26$ for vF). Pollen quantity was also significantly related to ITD while no other parameters were related to pollen or visit fidelity or visit quantity (Supplementary information S3.4).

3.3 | Strawberry pollinators also make use of wild plants

Strawberry pollinators made extensive use of wild plants to meet their nutritional needs. This was demonstrated by strong links between crop and margin habitats on all farms, even while strawberry flowers were continually available. Most of the wild plants (65%–86%) shared pollinators with strawberries (Figure 4a), and most individual pollinators (62%–71% across the three farms) carried both crop and non-crop pollen (Figure 4b; Table S8, Supplementary information S3.5). Pollinators captured in a strawberry field were especially likely to carry at least some non-strawberry pollen (75%–85% of insects) while pollinators captured in the margins were somewhat less likely to carry both strawberry and non-strawberry pollen (54%–57% of insects). However, by quantity, the pollen loads of individual insects were generally dominated by pollen from the plant group on which they were captured (Figure 4c). This was true for all but the least-important strawberry pollinators, where individuals caught on strawberry might have high or low proportions of strawberry pollen in their pollen loads.

4 | DISCUSSION

Strawberries are a strongly pollinator-dependent fruit crop. In examining the roles of different pollinator species, we find that metrics of pollinator importance tend to agree between measures based on visits and pollen transport. Although the precise importance order varied between farms, both bee (*Apis* and *Bombus*) and hoverfly (*Eristalis*) species emerged as key pollinators. A single hoverfly species (*E. arbustorum*) is likely to be the most important pollinator on two of the three farms sampled, providing further evidence that hoverflies can be effective pollinators (Rader et al., 2020; Tiusanen

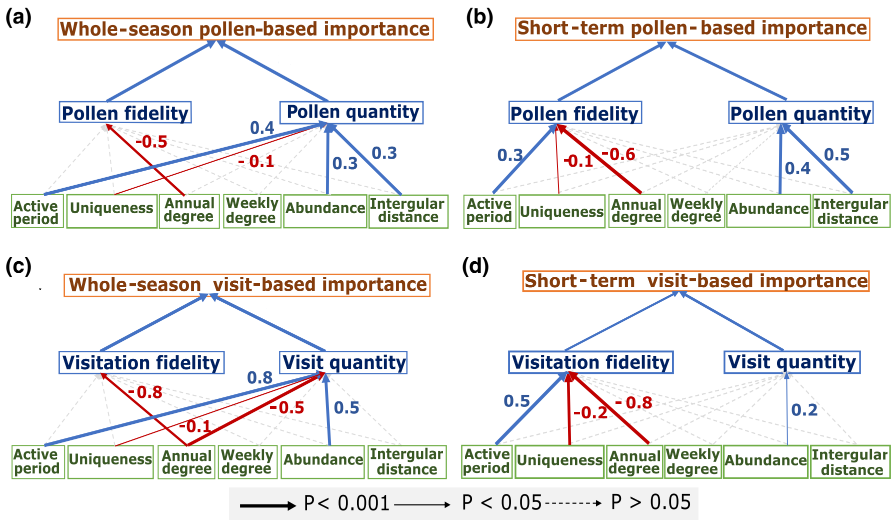

FIGURE 3 Structural equation models for estimated importance of pollinators based on pollen loads (a, b) or flower visits (c, d) and calculated over the whole-season (a and c) or on a short-term (fortnightly) basis (b and d). Most of the parameters we considered were related to a component of whole-season importance (quality or quantity). Fewer parameters were related to short-term estimated importance. Significant paths are indicated with coloured lines. Line weight indicates significance and effect sizes are given beside each path. Values correspond to standardised coefficients (β).

et al., 2016). Although commercial hives of *B. terrestris* were placed at farm B, this species was estimated to be less important than hoverflies and wild *Bombus*. Moving beyond species identities, we found that pollinator degree, abundance, and active period (among other parameters) were strongly associated with estimated importance. This suggests that these parameters hold the most promise as 'rule-of-thumb' indicators of key pollinators. Finally, we found that most pollinators also visited non-crop flowers, emphasising the need for management to consider areas beyond the crop field.

4.1 | Visits and pollen loads give similar information

There is currently a debate over the extent to which flower-visitor data can be used to estimate the provision of pollination service (Kortsch et al., 2023; Rader et al., 2016). In our dataset, importance estimates based on visits to strawberry flowers and based on the transport of strawberry pollen were strongly (τ=0.649) and significantly correlated. This result suggests that, at least in strawberry farms in the UK, visitation data offer reasonable proxies for pollen transport. Other studies have come to similar conclusions based on the large contribution of visitor frequency to the total pollination service provided by a species (Rader et al., 2016). Nevertheless, we note that visit-based metrics generally ranked the importance of bees much lower than did pollen-based metrics. Since visitation fidelity and pollen fidelity values were generally similar, this discrepancy is due to the total amount of pollen carried: large, hairy bees can collect larger amounts of pollen per visit than other insects (Stavert et al., 2016).

In making this comparison between inferences based on flower visits and pollen transport, we note that both metrics represent proxies of the currency of interest: realised pollination of the crop plant. From this perspective, both visitation and pollen transport neglect other components of pollination, such as pollen deposition (Popic et al., 2013). For an ideal measure of the full chain of events resulting in pollination, we should be measuring the full sequence from visitation to seed set (Cirtwill et al., 2022; Corbet, 1998; Naeem, 1998; Rodger et al., 2021; Stavert et al., 2016). We, therefore, agree with previous recommendations to include information about multiple components of pollination service whenever feasible (Cirtwill et al., 2022; Rader et al., 2016). Encouragingly, our measures of two different steps in this sequence (flower visit and transport of pollen between flowers) offered a coherent ranking of species' importance.

Visitation data may be particularly useful where sampling resources are limited. We found much stronger correlations between visit-based and pollen-based estimated importance than between fortnightly and annual pollen-based estimated importance. This suggests that an arbitrary short snapshot of pollen transport is unlikely to identify the most important pollinators for a long-flowering crop like strawberries in the UK. Although short-term sampling targeting the peak of activity can accurately identify key species (Hegland et al., 2010), where this peak is unknown, or when dealing with a long-flowering crop, we suggest that longer-term sampling of flower visitors will be more accurate than short-term sampling of pollen loads.

4.2 | Abundant specialists with long flight periods are likely to be key pollinators

Similar to previous studies, more abundant pollinators tended to have higher estimated importance because they generally make

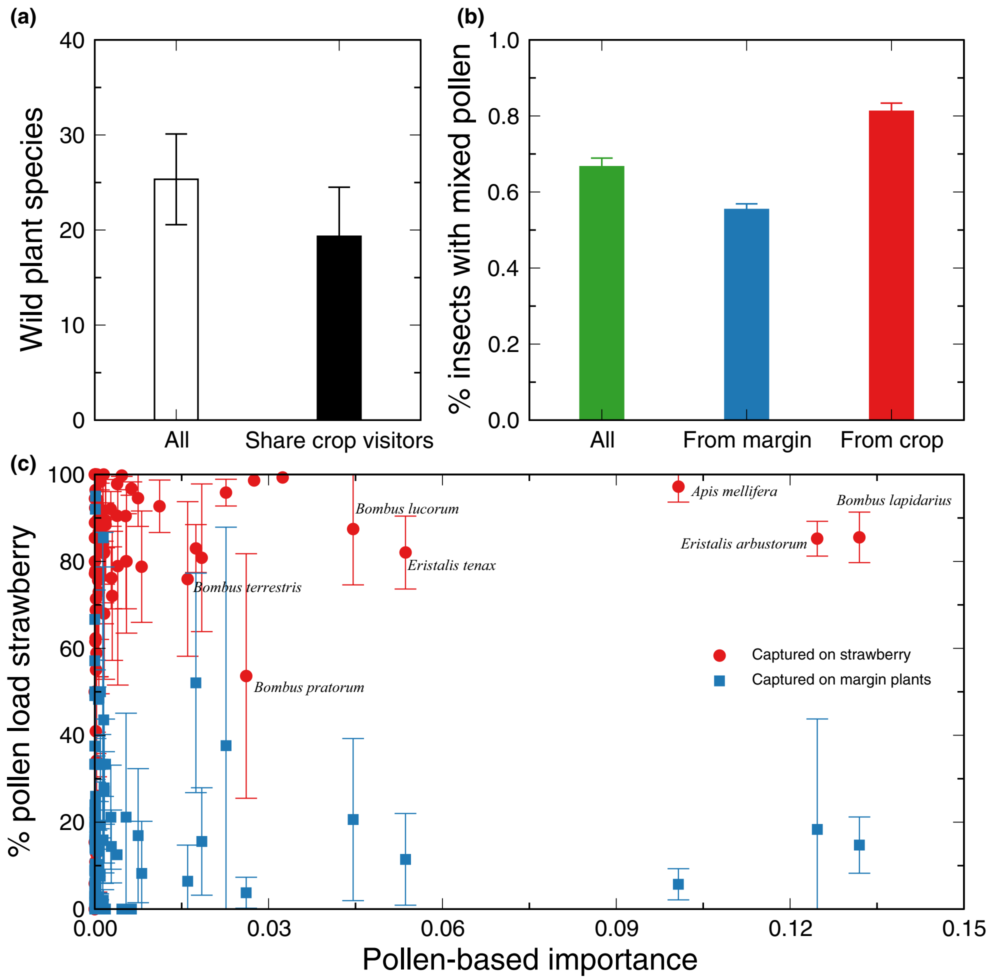

FIGURE 4 Strawberry visitors also used wild plants in the field margins. (a) Most of wild plants shared visitors with the strawberry crop). (b) Moreover, most individual insects carried both strawberry and non-strawberry pollen. In (a and b), error bars represent ±SE across the three farms. (c) Although individuals usually carried mixed pollen loads regardless of where they were caught, individuals caught on strawberry flowers (red) often carried mostly strawberry pollen while individuals caught on margin plants (blue) usually carried mostly non-strawberry pollen. This separation was especially clear for insects with high pollen-based estimated importance. Error bars represent ±SE across all individuals caught in the focal habitat.

more visits (Ellis et al., 2017). Long active periods (which likely imply non-unique active periods) were also associated with pollinators making many visits and moving large amounts of pollen (although active period may be less important for crops with brief flowering periods). However, species with longer active periods also tended to be more generalist. This generalism is likely due to a requirement for a variety of resources over the course of the season (Cirtwill et al., 2022), but higher generalism was also associated with lower pollen and visit fidelity. Despite the possibility that insects may learn to visit an abundant, long-lasting resource more consistently (Amaya-Márquez, 2009), these correlations between some beneficial and detrimental parameters may mean that there is no single 'ideal' pollinator for a crop. This result partly explains why commercial bees were not among the most important pollinators despite parameters predicting high importance. In this context, management to promote multiple pollinators with several beneficial parameters may be more effective than targeting a single species.

4.2.1 | Pollen-based and visit-based estimated importance are related to similar sets of parameters

In general, the same parameters predicted pollen-based and visit-based estimated importance over the short-term and throughout the whole season. One exception to the consistency of associations between parameters and importance was ITD. Larger insects carried larger pollen loads (as expected, Cullen et al., 2021) but did not make more visits. Instead, there was a negative effect of annual degree (number of different plants visited) on visit quantity without a corresponding association with pollen quantity (since generalist bees can collect large amounts of pollen with few visits). The lack of relationship between ITD and visit quantity may be due to the specific spatial context we examined. Flight distance may not be a limiting factor in crop fields where crop flowers are likely to be close together. In more mixed systems, however, flight ability is related to insects' ability to seek out preferred flowers and may influence their de facto specialisation (Kortsch et al., 2023).

4.3 | Wild plants are often used by key pollinators

Although strawberry flowers were highly abundant throughout our sampling period, most pollinator individuals visited wild plants as well as strawberry. This suggests that strawberries alone cannot meet pollinators' nutritional needs, which is consistent with the low sucrose and protein content in the nectar and pollen of Elsanta strawberries (Ahrenfeldt et al., 2019). A potential dependency on wild supplemental resources is also consistent with several studies showing that pollinators need access to multiple nectar and pollen sources to meet their nutritional needs (Filipiak, 2019) as well as a consistent supply of floral resources over time (Timberlake et al., 2021).

4.3.1 | Applications and limitations

The most important strawberry pollinators varied between farms, included insects from different orders, and did not include commercially added native bumblebees at the one farm where they were placed (although the same species was highly important elsewhere). Given this variability in pollinator importance across only three farms, it may be wise for farm managers to promote a diverse set of pollinators including bumblebees, hoverflies, and domesticated honeybees, rather than focus on a single species. A diversity of pollinators with different foraging behaviours can provide more reliable pollen deposition than a single species (Abrol et al., 2019), prevent fruit malformation (Chagnon et al., 1993), and increase yields (Stewart et al., 2017) as well as providing ‘insurance’ against losses of any one pollinator taxon. Although our study uses data from a small number of farms in one county of the UK, a diversity-focused approach to improving pollination service should be reasonable for many insect-pollinated crops with generalist morphology. While the specific taxa we highlight have also been identified as key pollinators elsewhere (Abrol et al., 2019), we note that these rankings are based on a small sample of farms from one county in the UK, and the set of most-important pollinators is highly likely to differ at other sites. Indeed, that is the main reason we explore traits related to pollinator importance: while *B. lapidarius* (for example) is unlikely to be the key pollinator everywhere, it is much more likely that large, abundant insects with long active periods will generally be good strawberry pollinators.

Preserving a diverse set of pollinators, however, requires maintaining a variety of habitats near crop fields to support different insect life stages and fill gaps in crop floral resources. For example, wild bee populations benefit from the preservation of nesting sites such as tussocks or steep banks (Kells & Goulson, 2003) while some hoverflies require ponds as larvae (Rader et al., 2020). Providing a variety of floral resources, including plants used by relatively specialised pollinators and plants flowering when crop flowers are rare, ensures that pollinators will have sufficient food throughout the year (Baldock et al., 2019). This is especially important for insects with long active periods, which were also expected to be more important pollinators.

While the presence of wild plants can sometimes decrease visits to crops or increase the mixing of pollen (Ye et al., 2014), in our study individual pollinators tended to carry mostly crop *or* mostly wild plant pollen. This suggests that important pollinators use wild plants to supplement their diets while still providing high-quality pollination service to the crop and that increasing the abundance of pollinators with ample food resources is likely to compensate for any loss of visits per individual. Providing additional resources for wild pollinators may be even more effective than directly adding additional insects, as the bumblebee *B. terrestris* was not among the most important pollinators at the single farm in our sample where commercial hives were placed. Note, however, that this inference is based on a single farm and so we can draw no conclusions about the general effectiveness of adding bumblebee hives.

5 | CONCLUSIONS

Our case study of strawberry pollination at three British farms has important implications for estimating pollination service. First, we found that flower visits provide good proxies of pollinator importance. A strawberry farmer seeking to identify key pollinators in their fields or to test the effect of an intervention (e.g. increasing margin flowers) can thus use visitation data to draw rule-of-thumb conclusions. Such data can be obtained without collecting resource-intensive pollen-transport data (especially if the generally larger pollen loads of bees are accounted for).

Second, we found that a pollinator's parameters provide good indications of its importance. Rather than exploring the specific contribution of each taxon in each strawberry-farming region, we may infer that abundant and long-flying insects with relatively high specialisation are likely to be important strawberry pollinators in similar cultivation systems elsewhere (i.e. in systems where strawberry cropping uses varieties or methods that produce a long flowering period). Managers can, therefore, target these parameters (e.g. by ensuring floral resources through the whole flight season of long-flying insects, Timberlake et al., 2019) as an alternative to species-specific measures.

Third, our findings highlight the importance of considering the crop in a landscape context when making management decisions. Diverse habitat requirements of pollinator taxa and life stages and the frequent use of wild plants by strawberry pollinators underline the difficulties for insects in living in crop fields alone. Overall, we hope our study may contribute to an improved understanding of what good pollinators are made of, and improved guidelines for conserving and managing these valuable species.

AUTHOR CONTRIBUTIONS

Alyssa R. Cirtwill, Edith Villa-Galaviz, Rachel Gibson, Thomas Timberlake, Tomas Roslin and Jane Memmott conceived the ideas; Rachel Gibson collected the data; Edith Villa-Galaviz and Alyssa R. Cirtwill analysed the data; Edith Villa-Galaviz and Alyssa R. Cirtwill led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We would like to thank the owners of the field sites: Richard, Philip and Adrian Winter at Team Green Growers, and Jan Butterley at Nynehead Fruit. We are grateful to Mark Pavett, John Deeming, Brian Levey and Mike Wilson at the National Museum of Wales, Cardiff for insect identifications. We would like to thank the members of the Spatial Foodweb Ecology Group for their useful comments on this manuscript. This work was supported by the Natural Environment Research Council (NERC) (NE/T013621/1), the National Science Foundation (NSF) and the Academy of Finland (AKA) (grant 334787), coordinated through the Belmont Forum Climate, Environment and Health Collaborative Research Action (proposal 1550). Further support was provided by the Bristol Centre for Agricultural Innovation. T.R. was funded by the European Research Council Synergy Grant 856506 (LIFEPLAN), by the Academy of Finland (grant 322266), and by a Career Support grant from the Swedish University of Agricultural Sciences. A.C. was supported by a postdoctoral fellowship from the Academy of Finland (1332999).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12253.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2rbnzs7t2 (Villa-Galaviz et al., 2023).

ORCID

Edith Villa-Galaviz https://orcid.org/0000-0002-2783-7877
Alyssa R. Cirtwill https://orcid.org/0000-0002-1772-3868
Thomas Timberlake https://orcid.org/0000-0001-8166-0825
Tomas Roslin https://orcid.org/0000-0002-2957-4791

REFERENCES

Abrol, D. P., Gorka, A. K., Ansari, M. J., Al-Ghamdi, A., & Al-Kahtani, S. (2019). Impact of insect pollinators on yield and fruit quality of strawberry. *Saudi Journal of Biological Sciences*, *26*, 524–530. https://doi.org/10.1016/j.sjbs.2017.08.003

Ahrenfeldt, E. J., Sigsgaard, L., Hansted, L., Jensen, A. C., & Toldam-Andersen, T. B. (2019). Forage quality and quantity affect red mason bees and honeybees differently in flowers of strawberry varieties. *Entomologia Experimentalis et Applicata*, *167*, 763–773. https://doi.org/10.1111/eea.12820

Amaya-Márquez, M. (2009). Floral constancy in bees: A revision of theories and a comparison with other pollinators. *Revista Colombiana de Entomologia*, *35*, 206–216. https://doi.org/10.25100/socolen.v35i2.9221

Arceo-Gómez, G., & Ashman, T. L. (2011). Heterospecific pollen deposition: Does diversity alter the consequences? *New Phytologist*, *192*, 738–746. https://doi.org/10.1111/j.1469-8137.2011.03831.x

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

Baldock, K. C., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Staniczenko, P. P., Stone, G. N., Vaughan, I. P., & Memmott, J. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology and Evolution*, *3*, 363–373. https://doi.org/10.1038/s41559-018-0769-y

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

Carew, J. G., Morretini, M., & Battey, N. H. (2003). Misshapen fruits in strawberry. *Small Fruits Review*, *2*, 37–50. https://doi.org/10.1300/J301v02n02_03

Chagnon, M., Gingras, J., & DeOliveira, D. (1993). Complementary aspects of strawberry pollination by honey and indigenous bees (hymenoptera). *Journal of Economic Entomology*, *86*, 416–420. https://doi.org/10.1093/jee/86.2.416

Cirtwill, A. R., Kaartinen, R., Rasmussen, C., Redr, D., Wirta, H., Olesen, J. M., Tiusanen, M., Ballantyne, G., Cunnold, H., Stone, G. M., Schmidt, N. M., & Roslin, T. (2022). Stable pollination service in a generalist high arctic community despite the warming climate. *Ecological Monographs*, *93*, e1551. https://doi.org/10.1002/ecm.1551

Corbet, S. A. (1998). Fruit and seed production in relation to pollination and resources in bluebell, *Hyacinthoides non-scripta*. *Oecologia*, *114*, 349–360.

Cullen, N., Xia, J., Wei, N., Kaczorowski, R., Arceo-Gómez, G., O'Neill, E., Hayes, R., & Ashman, T. L. (2021). Diversity and composition of pollen loads carried by pollinators are primarily driven by insect traits, not floral community characteristics. *Oecologia*, *196*, 131–143. https://doi.org/10.1007/s00442-021-04911-0

Eeraerts, M., Vanderhaegen, R., Smagghe, G., & Meeus, I. (2019). Pollination efficiency and foraging behaviour of honey bees and non-*Apis* bees to sweet cherry. *Agricultural and Forest Entomology*, *22*, 75–82. https://doi.org/10.1111/afe.12363

Ellis, C. R., Feltham, H., Park, K., Hanley, N., & Goulson, D. (2017). Seasonal complementary in pollinators of soft-fruit crops. *Basic and Applied Ecology*, *19*, 45–55. https://doi.org/10.1016/j.baae.2016.11.007

Filipiak, M. (2019). Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. *Journal of Applied Ecology*, *56*, 1410–1418. https://doi.org/10.1111/1365-2664.13383

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

Gibson, R. (2012). *Pollination networks and services in agro-ecosystems* (Ph.D. thesis). University of Bristol.

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*, 589–596. https://doi.org/10.1007/s00442-007-0752-9

Hackett, T. D., Sauve, A. M. C., Davies, N., Montoya, D., Tylianakis, J. M., & Memmott, J. (2019). Reshaping our understanding of species' roles in landscape-scale networks. *Ecology Letters*, *22*, 1367–1377. https://doi.org/10.1111/ele.13292

Hegland, S. J., Dunne, J., Nielsen, A., & Memmott, J. (2010). How to monitor ecological communities cost-efficiently: The example of plant–pollinator networks. *Biological Conservation*, *143*, 2092–2101. https://doi.org/10.1016/j.biocon.2010.05.018

Kalkman, C. (2004). Rosaceae. In K. Kubitzki (Ed.), *Flowering plants. Dicotyledons: Celastrales, oxalidales, rosales, cornales, ericales* (pp. 343–386). Springer. https://doi.org/10.1007/978-3-662-07257-8_39

Kells, A. R., & Goulson, D. (2003). Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK.

Biological Conservation, *109*, 165–174. https://doi.org/10.1016/S0006-3207(02)00131-3

Kortsch, S., Saravia, L., Cirtwill, A. R., Timberlake, T., Memmott, J., Kendall, L., Roslin, T., & Strona, G. (2023). Landscape composition and plant-pollinator network structure interact to influence pollination success in an individual-based model. *Functional Ecology*, 1–16. https://doi.org/10.1111/1365-2435.14353

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*, 573–579. https://doi.org/10.1111/2041-210X.12512

Lucas, A., Bodger, O., Brosi, B. J., Ford, C. R., Forman, D. W., Greig, C., Hegarty, M., Neyland, P. J., & de Vere, N. (2018). Generalisation and specialisation in hoverfly (Syrphidae) grassland pollen transport networks revealed by DNA metabarcoding. *Journal of Animal Ecology*, *87*, 1008–1021. https://doi.org/10.1111/1365-2656.12828

MacInnis, G., & Forrest, J. R. K. (2019). Pollination by wild bees yields larger strawberries than pollination by honey bees. *Journal of Applied Ecology*, *56*, 824–832. https://doi.org/10.1111/1365-2664.13344

MacLeod, M., Reilly, J., Cariveau, D. P., Genung, M. A., Roswell, M., Gibbs, J., & Winfree, R. (2020). How much do rare and crop-pollinating bees overlap in identity and flower preferences? *Journal of Applied Ecology*, *57*, 413–423. https://doi.org/10.1111/1365-2664.13543

Martin, C. D., Fountain, M. T., & Brown, M. J. (2019). Varietal and seasonal differences in the effects of commercial bumblebees on fruit quality in strawberry crops. *Agriculture, Ecosystems & Environment*, *281*, 124–133. https://doi.org/10.1016/j.agee.2019.04.007

Naeem, S. (1998). Species redundancy and ecosystem reliability. *Conservation Biology*, *12*, 39–45. https://doi.org/10.1046/j.1523-1739.1998.96379.x

Page, M. L., Nicholson, C. C., Brennan, R. M., Britzman, A. T., Greer, J., Hemberger, J., Kahl, H., Müller, U., Peng, Y., Rosenberger, N. M., Stuligross, C., Wang, L., Yang, L. H., & Williams, N. M. (2021). A meta-analysis of single visit pollination effectiveness comparing honeybees and other floral visitors. *American Journal of Botany*, *108*, 2196–2207. https://doi.org/10.1002/ajb2.1764

Popic, T. J., Wardle, G. M., & Davila, Y. C. (2013). Flower-visitor networks only partially predict the function of pollen transport by bees. *Austral Ecology*, *38*, 76–86. https://doi.org/10.1111/j.1442-9993.2012.02377.x

Porto, R. G., de Almeida, R. F., Cruz-Neto, O., Tabarelli, M., Viana, B. F., Peres, C. A., & Lopes, A. V. (2020). Pollination ecosystem services: A comprehensive review of economic values, research funding and policy actions. *Food Security*, *12*, 1425–1442. https://doi.org/10.1007/s12571-020-01043-w

R Core Team. (2016). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://doi.org/10.1017/CBO9781107415324.004

Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P., Howlett, B. G., Winfree, R., Cunningham, S. A., Mayfield, M. M., Arthur, A. D., Andersson, G. K., Bommarco, R., Brittain, C., Carvalheiro, L. G., Chacoff, N. P., Entling, M. H., Foully, B., Freitas, B. M., Gemmill-Herren, B., Ghazoul, J., … Viana, B. F. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 146–151. https://doi.org/10.1073/pnas.1517092112

Rader, R., Cunningham, S. A., Howlett, B. G., & Inouye, D. W. (2020). Non-bee insects as visitors and pollinators of crops: Biology, ecology, and management. *Annual Review of Entomology*, *65*, 391–407. https://doi.org/10.1146/annurev-ento-011019-025055

Rodger, J. G., Bennett, J. M., Razanajatovo, M., Knight, T. M., van Kleunen, M., Ashman, T. L., Steets, J. A., Hui, C., Arceo-Gómez, G., Burd, M., Burkle, L. A., Burns, J. H., Durka, W., Freitas, L., Kemp, J. E., Li, J., Pauw, A., Vamosi, J. C., Wolowski, M., … Ellis, A. G. (2021). Widespread vulnerability of flowering plant seed production to pollinator declines. *Science Advances*, *7*, 1–11. https://doi.org/10.1126/sciadv.abd3524

Shipley, B. (2009). Confirmatory path analysis in a generalized multilevel context. *Ecology*, *90*, 363–368. https://doi.org/10.1890/08-1034.1

Somme, L., Vanderplanck, M., Michez, D., Lombaerde, I., Moerman, R., Wathelet, B., Wattiez, R., Lognay, G., & Jacquemart, A. L. (2015). Pollen and nectar quality drive the major and minor floral choices of bumble bees. *Apidologie*, *46*, 92–106. https://doi.org/10.1007/s13592-014-0307-0

Stavert, J. R., Liñán-Cembrano, G., Beggs, J. R., Howlett, B. G., Pattemore, D. E., & Bartomeus, I. (2016). Hairiness: The missing link between pollinators and pollination. *PeerJ*, *2016*, 1–18. https://doi.org/10.7717/peerj.2779

Stewart, R. I. A., Andersson, G. K. S., Brönmark, C., Klatt, B. K., Hansson, L. A., Zülsdorff, V., & Smith, H. G. (2017). Ecosystem services across the aquatic–terrestrial boundary: Linking ponds to pollination. *Basic and Applied Ecology*, *18*, 13–20. https://doi.org/10.1016/j.baae.2016.09.006

Timberlake, T. P., Vaughan, I. P., Baude, M., & Memmott, J. (2021). Bumblebee colony density on farmland is influenced by late-summer nectar supply and garden cover. *Journal of Applied Ecology*, *58*, 1006–1016. https://doi.org/10.1111/1365-2664.13826

Timberlake, T. P., Vaughan, I. P., & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, *56*, 1585–1596. https://doi.org/10.1111/1365-2664.13403

Tiusanen, M., Hebert, P. D., Schmidt, N. M., & Roslin, T. (2016). One fly to rule them all—Muscid flies are the key pollinators in the arctic. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20161271. https://doi.org/10.1098/rspb.2016.1271

Villa-Galaviz, E., Cirtwill, A. R., Gibson, R., Timberlake, T., Roslin, T., & Memmott, J. (2023). Data from: What makes a good pollinator? Abundant and specialized insects with long flight periods transport the most strawberry pollen. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.2rbnzs7t2

Ye, Z. M., Dai, W. K., Jin, X. F., Gituru, R. W., Wang, Q. F., & Yang, C. F. (2014). Competition and facilitation among plants for pollination: Can pollinator abundance shift the plant-plant interactions? *Plant Ecology*, *215*, 3–13. https://doi.org/10.1007/s11258-013-0274-y

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. We investigate the relationship between several components of pollinator importance (top) and species parameters (bottom). Pollinator fidelity is calculated per individual (based on individual pollen loads) and then averaged within a species. All other measures are calculated per species.

Table S2. Kendall's τ (above the diagonal) and *p*-values (below the diagonal) for correlations between insect parameters. We did not have ITD values for the eight species of Coleoptera; these species were removed before calculating correlations. ITD was not strongly correlated with the other parameters we consider while most other parameters were moderately to strongly correlated. Note that no correction for multiple testing has been performed; *p*-values are therefore for illustration only.

Table S3. Kendall correlations and *p*-values for relationships between insect parameters and components of annual pollen-based (p) and visit-based (v) importance. We considered both the quantity (Q) and fidelity (F) of an insect's visits or pollen transport.

Table S4. Kendall correlations and *p*-values for relationships between insect parameters and components of short-term pollen-based (p) and visit-based (v) importance. We considered both the quantity (Q) and fidelity (F) of an insect's visits or pollen transport.

Table S5. Coefficients of the SEM of the whole-season incorporating the elytra measures of Coleoptera. Width: width of elytra and Length: length of elytra.

Table S6. Coefficients of the short-term SEM incorporating the elytra measures of Coleoptera. Width: width of elytra and Length: length of elytra.

Table S7. We tested if parameters affect pollinator's important through changes in quantity and fidelity. For this we included a last path in the SEM in which we assessed the effect of quantity and fidelity on importance. We tested the fit of each SEM to the data.

Table S8. We quantify several measures of the links between wild plants and strawberry crops. These include: the number and proportion of wild plants sharing pollinators with strawberries, the proportion of individual pollinators carrying both crop and non-crop pollen, and the proportion of pollinators captured in one habitat (crop or margin) carrying pollen from the other.

Table S9. List of Coleoptera, Hymenoptera, and Lepidoptera pollinator species recorded across the three farms.

Table S10. List of Diptera pollinator species recorded across the three farms.

How to cite this article: Villa-Galaviz, E., Cirtwill, A. R., Gibson, R., Timberlake, T., Roslin, T., & Memmott, J. (2023). What makes a good pollinator? Abundant and specialised insects with long flight periods transport the most strawberry pollen. *Ecological Solutions and Evidence*, *4*, e12253. https://doi.org/10.1002/2688-8319.12253