

# Larger pollinators deposit more pollen on stigmas across multiple plant species—A meta-analysis

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## Abstract

1. Many insect species provide essential pollination services. However, the amount of pollen deposited onto a stigma when visiting a flower ('single visit pollen deposition', SVD) can vary greatly among taxa depending on morphological traits of pollinators. Further, SVD is commonly measured using one of two methods ('static': waiting for an insect to visit a flower present on plant, and 'active': removing the flower and presenting it to a flower visitor) that may also differ in their effectiveness.
2. To gain a more comprehensive understanding of how SVD compares among pollinators, we conducted a hierarchical meta-analysis using data from 28 studies identified by a systematic review. These contained SVD data for 94 bee and 33 fly taxa (hereafter 'wild pollinators'), across 30 plant species from which we included 127 observations. In the analysis of each study, we used the western honey bee *Apis mellifera* as a comparator species.
3. Wild pollinators deposited more pollen onto stigmas per single visit than honeybees, and those with larger body deposited significantly more pollen than smaller ones. Of the two methodological approaches to assess SVD, 'static' versus 'active', we found no significant difference regarding the amount of deposited pollen.
4. *Synthesis and applications.* Our meta-analysis highlights the breadth of wild pollinators that contribute to pollination effectiveness via their delivery of pollen to many crop and non-crop plant species. However, just 25% of the observations assessed the amount of pollen deposited by fly species. Our findings point to the need to further quantify the pollination effectiveness of non-bee pollinators as studies have largely focused on managed and wild bee species.

## KEYWORDS

bees, body size, flies, honey bee, intertegular distance, pollen deposition, pollination effectiveness, wild pollinators

## 1 | INTRODUCTION

There is an increasing recognition of the contribution to pollination made by wild bees and other insect groups (e.g. flies, beetles, butterflies)

as pollinators within natural and agro-ecosystems (Garibaldi et al., 2013; Ollerton et al., 2011; Rader et al., 2016). However, effectiveness of pollinators in pollination differs and the ability to compare this effectiveness can be complicated through the inconsistency of

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methodology used between studies (Ne'eman et al., 2010). Regarding methodology, studies have used one or a combination of parameters to assess the effectiveness of various insect species as pollinators of various plant species. These may include information on visit frequency, duration or amount of pollen grains attached to the body of pollinators as a proxy of pollination effectiveness of insect species (Garibaldi et al., 2013; Howlett et al., 2018). Single visit pollen deposition (King et al., 2013), the number of developed pollen tubes within styles (Zhang et al., 2015) and/or fruit or seed set (Garratt et al., 2014), are other parameters often used in order to gain further information on pollinator effectiveness. Single visit pollen deposition (SVD) measures the amount of conspecific pollen deposited on a stigma per one (single) visit by a pollinator (King et al., 2013). This variable has often been used as a practical and reliable measure of a pollinators' contribution to pollination (Ballantyne et al., 2015); however, it also has limitations (quantity and quality of pollen, and stigma receptivity) which have to be taken account. For instance, it may not be possible to accurately identify pollen to species level. Moreover, deposited pollen has to be conspecific, compatible and viable on the receptive target stigma (Ne'eman et al., 2010).

In practice, the measurement of the single visit pollen deposition resulting from an insect visit necessitates the monitoring of virgin flowers until an insect completes a visit (King et al., 2013; Rader et al., 2009). Two approaches are commonly used to monitor the flower visitation, these being known as 'static' and 'active' approaches (Howlett et al., 2017). In the static approach, a virgin flower (often initially bagged to prevent unobserved insect visitations) is left attached to the plant and the observer waits until an insect visits the flower. In the active approach, a flower is removed from the plant and presented near to the target pollinator species in a process referred to as 'interviewing' (Natalis & Wesselingh, 2012; Thomson, 1981). In both methods, the stigma is removed from a flower following the single visit, placed into a drop of melted glycerin jelly with basic fuchsin on a micro slide, pressed with cover slip, then number of conspecific pollen is assessed or counted under a compound microscope (Dafni et al., 2005; Kearns & Inouye, 1994). The static approach is more frequently used (Howlett et al., 2017), however, it is time-consuming and only practical for very common flower visitors that have high probability of contacting the observed flower. In contrast, the active approach may need less time until a pollinator visits a flower, but the presentation of flower may potentially alter the behaviour of insect resulting in an unrealistic measure (Howlett et al., 2017). Moreover, the approach is less suitable for insects that are easily disturbed through the process of presenting a flower (Howlett et al., 2017). Although several studies have already measured the SVD for a wide variety of plant-pollinator interactions (King et al., 2013; Phillips et al., 2018; Rader et al., 2009), the effect of static and active approaches on SVD were compared just in one study—this being for onion *Allium cepa* L. (Howlett et al., 2017).

Flowers of many plant species are visited by a diverse range of insect visitors that can vary widely in their ability to deposit pollen (Ballantyne et al., 2015) depending on behavioural and morphological traits of the visitors (Ivey et al., 2003; King et al., 2013). For example,

some flower visitors may be partly or entirely nectar thieves according to their behaviour without making contact with the floral reproductive structures, and therefore avoid depositing pollen grains on stigmas (Maloof & Inouye, 2000; Junker et al., 2010). Otherwise, pollinators' body size such as body length, or intertegular distance (hereafter ITD), and/or hairiness may also influence the amount of deposited pollen (Goulson et al., 2002; Stavert et al., 2016). However, the number of studies that have been examined the effect of these parameters on SVD simultaneously on a wide range of plant species remains limited. Floral traits may also influence the amount of deposited pollen by a pollinator, however these are rarely measured in studies (Solís-Montero & Vallejo-Marin, 2017).

In this study, we conducted a meta-analysis to examine: (a) how SVD varies with body length and intertegular distance of pollinators; (b) how SVD differs across bee (Apoidea), and fly species from a broad range of insect ( $n = 77$ ) and plant species ( $n = 30$ ) in order to gain a broader perspective of the comparative SVD; and (c) whether the two commonly used methodological approaches (static and active) provides consistent data on SDV. In our meta-analysis we used the western honey bee *Apis mellifera* L. as a comparator ('control') species, to compare to the other flower visiting taxa because it is the most intensively studied managed pollinator species globally (Hung et al., 2018; Morse, 1991). Moreover, it was the only consistent species across the analysed datasets.

## 2 | MATERIALS AND METHODS

### 2.1 | Search strategy and inclusion criteria

We searched the Web of Science Core Collection database using the following terms: TOPIC: bee OR bees OR Hymenoptera OR fly OR flies OR Diptera AND TOPIC: 'pollen deposition' AND 'single-visit deposition' OR 'single visit deposition' AND 'single-visit' OR 'single visit' OR 'pollin\* effectiveness' OR 'pollin\* efficiency'. Refined By: DOCUMENT TYPES: ARTICLE OR PROCEEDINGS ARTICLE AND Year Published = 1945–2019. The latest search was conducted in November 2019 and resulted in 637 potential articles.

Each study was vetted by title and abstract according to inclusion/exclusion criteria as described below, then we reviewed the full text of articles for potential inclusion. We included studies containing the following data: (a) the mean number of deposited pollen grains per stigma following a single visit by honeybees along with similar data for other bee (Apoidea) or non-bee pollinators (fly species); (b) the standard deviation (SD) or standard error of the mean (SEM); and (c) sample size (N). To sum up, we used only flower-visiting observations to species ( $n = 97$ ) or genus level ( $n = 30$ ; e.g. '*Lasioglossum* spp.', '*Bombus* spp.') in the analysis because ITD would not have been assessed reliably at higher taxonomical categories due to size variability of species between genera. An observation is a bee or fly taxon (species or genus) where the mean number of deposited pollen grains per stigma following the single visit was recorded. Moreover, the standard deviation or standard error of the

mean, and sample size (number of stigma, where conspecific pollen was assessed) were also given.

Studies were excluded if (a) the number of deposited pollen grains was divided or multiplied with other metrics (e.g. seed set, number of pollen grains of flowers), so that the original value could not be calculated; (b) multiple genera were grouped into broader categories (e.g. 'small syrphids', 'small Muscidae'), or (c) did not contain the data above. We included only observations, where sample size ( $N$ ) of control (honey bee) or experimental group (given wild pollinator species or genus) was equal to or more than three. We did not include studies with other taxa, for example, butterfly species, because these studies mostly did not contain honey bee, moreover ITD data for butterfly species were not available within datasets used.

We checked the references of a qualitative review of Howlett et al. (2017) in our topic in order to complete the main search with further potential studies. The study included a list of relevant articles focusing on SVD by insects and also contained new data on pollen deposition. Twelve articles were relevant from the list and eight of them were also available in the Web of Science Core Collection database. Additionally, we completed the meta-analysis with unpublished data from two studies (see the PRISMA flow diagram Figure S1).

Altogether, we found 28 studies with 16 focusing on crop and 14 on non-crop plant species (Table S1). Eighteen studies examined the 'honey bee + other bees' group, and 10 studies the 'honey bee + flies' or 'honey bee + other bees + flies' group. We found 94 observations on bee and 33 observations on fly taxa in the studies. Twenty-one studies applied the static approach (with 95 observations) and eight studies the active approach (with 32 observations; one study used both approaches). Plant species investigated in studies were either self-incompatible or anthers were carefully removed to avoid self-pollination. Each flower was covered by a net to avoid being pollinated before observation.

Single visit pollen deposition values were extracted from text, bar/box plots or tables within the studies. In two studies (Park et al., 2016; Phillips et al., 2018) with eight observations median values were reported instead of mean values, therefore, we applied formulas according to Hozo et al. (2005) to calculate mean values. Mean values were included in the case of 26 studies with 119 observations.

Body size has often been measured as the body length (distance from the front of the eyes to the tip of the abdomen) and/or the intertegular distance (the width of pollinator's thorax, hereafter 'ITD'; Cane, 1987) of an insect. To compare body size, we applied body length and intertegular distance in cm for bee and fly species from a dataset of POLLIMETRY R package (Kendall et al., 2019). This dataset contains body length (as dried material) and ITD data of almost 400 bee and more than 100 fly species. If the given dataset contained multiple measurements of body length or ITD (e.g. for some common species such as *Bombus terrestris*), we calculated the arithmetic mean of the respective values. If the exact name of species was not addressed in the study (e.g. '*Melissodes* spp.'), we used the arithmetic mean of body length and ITD of species in the genus given in the dataset. Body length and ITD data of bee and fly species were averaged among sexes. One study reported the mean values of body length of the examined species, and here we used these data (Sun et al., 2013).

The difference between body length and ITD values of different species within a genus and also the intraspecific body size difference—particularly in the case of bumblebee species—can vary widely. Therefore, we conducted a sensitivity analysis excluding genus-level observations ( $n = 30$ ) from the analysis. For particular bee, bumblebee and fly species from South America and New Zealand no reliable ITD measurements were available, therefore, we omitted them from ITD subset analysis. For species in the given dataset without body length values, body length data were obtained from the literature (Scheuchl & Willner, 2016; van Veen, 2004) and online databases (Ratnasingham & Hebert, 2007; Roskov et al., 2018).

In summary, we obtained body length data to all of the species and genus observations ( $n = 127$ ) while ITD data were available for 106 taxa (of 127), therefore, we conducted a subset analysis with these 106 ITD data to species or genus observations.

We used the honey bee as control species from each study comparing the SVD value of honey bee to SVD values of other bee and fly species. Finally, the body length ratio and ITD ratio between given pollinator and honey bee was calculated and used in the meta-analysis models (see Section 2.2).

## 2.2 | Statistical analysis

We calculated effect sizes and their variances per observation (each species or genus) by using the log response ratio ( $\ln R$ ) based on the mean and standard deviation of stigmatic pollen deposition, and sample size (number of stigma; Borenstein et al., 2009). Then we corrected this with a small-sample bias estimator using the Delta method (Lajeunesse, 2015) to minimize the inaccuracies caused by small sample size ( $N$ ) present within studies (see Appendix S1 for equations).

In the meta-analysis models described below, we weighted the effect sizes by their inverse variances. To examine the heterogeneity of effect sizes, we performed hierarchical meta-analyses using mixed-effects models with moderators as predictor variables. These were body length and ITD ratio (between a pollinator and honey bee), taxonomic order of pollinators (Hymenoptera vs. Diptera), and approach (active vs. static). Since effect sizes were often taken for different pollinator species, but the same plant species from the same study, we used study ID as a nested factor in the models. Additionally, data within a study were also non-independent since we used the same comparator (honey bee), thus using study ID as a nested factor is necessary. Furthermore, often the same plant and pollinator species were studied in different studies, therefore, we used plant and pollinator species also as nested factors in a crossed-nested way. Finally, we assumed that phylogenetic relatedness might also have an effect on the heterogeneity of effect sizes as species of pollinators and plants with high taxonomic variability, but often with related species, were included in the meta-analyses (Chamberlain et al., 2012). To assess whether different ecological traits of pollinator species result in taxonomic differences in effect

sizes, we added taxonomic rank (such as taxonomic order and family of pollinators except when taxonomic order was involved as a moderator in the model) to the meta-analysis as nested random factors (Chamberlain et al., 2012; Marczak et al., 2007). For model structure, see Appendix S2. Additionally, we tested the interaction between the taxonomic order of pollinators (Hymenoptera vs. Diptera) and ITD ratio, as well as between the taxonomic order and approach (active vs. static) to assess whether pollen deposition of different pollinators at this broader taxonomic grouping depended on approach. Finally, all effect sizes and CI (confidence interval) values were back-transformed [from lnR to R(=response ratio)] for data visualisation.

### 2.3 | Analysis of publication bias

Publication bias may result from an overrepresentation of published studies with significant and novel findings whereas studies with non-significant findings could potentially remain in the grey literature, and therefore difficult to identify and access (Lortie et al., 2007). To test for this potential bias we checked funnel plots (a graphical test) and performed a regression test (a statistical test) in which a significant *p* value may indicate publication bias. We calculated Rosenthal's fail-safe number to estimate the number of unpublished studies, which would erase the significant effect measured by the meta-analysis (Rosenberg, 2005).

All statistical analyses and graphical presentations were carried out in R (R Development Core Team, 2020) by using R-packages META-FOR (Viechtbauer, 2010), GGPLOT2 (Wickham, 2016) and POLLIMETRY (Kendall et al., 2019).

## 3 | RESULTS

### 3.1 | SVD, body length and ITD

Altogether, we included 127 observations from 28 studies in our hierarchical meta-analyses. Based on the summary meta-analysis of all observations we found that the SVD made by wild pollinators (bee and fly species together) was significantly higher compared to the SVD of honey bees (Table 1; Figure 1).

We found that body length and also ITD ratio had a significantly positive effect on the amount of pollen deposited, that is, a larger pollinator had a larger SVD on stigmas (Table 1; Figure 2; Figure S2). Furthermore, body length had basically a similar, but a slightly stronger effect on SVD than ITD (Table 1; Figure 1). Performing sensitivity analysis by excluding genus-level observations and using only SVD of species level the results remained the same (Table 1). According to the interaction model there was no significant interaction between taxonomic order and body length or the ITD ratio of pollinators, indicating that an increasing body size corresponded with increasing SVD independently of whether bees or flies were tested in the meta-analysis.

**TABLE 1** Summary table of meta-analyses showing total heterogeneity ('All' is single visit pollen deposition of all of pollinators compared to the honey bee without moderators), and heterogeneities explained by moderators [body length and ITD ratio in cm, taxonomic order (Diptera vs. Hymenoptera), and approaches (active vs. static)] with corresponding residual heterogeneities for all models with intercept. Results of three interaction models are also shown (body length ratio × taxonomic order of pollinators, ITD ratio × taxonomic order of pollinators, and taxonomic order of pollinators × approach)

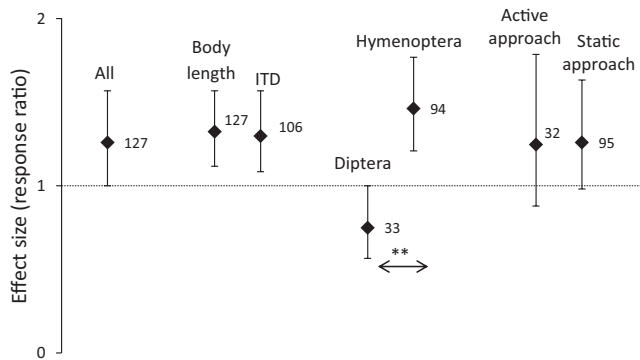
	<i>df</i>	<i>Q</i>	<i>p</i>
All	126	376.93	<0.000
Body length ratio	1	8.73	0.003
Residual	125	359.01	<0.000
Body length ratio without genera obs.	1	6.86	0.008
Residual	95	266.19	<0.000
ITD ratio	1	4.04	0.044
Residual	105	319.28	<0.000
ITD ratio without genera obs.	1	4.95	0.026
Residual	78	227.21	<0.000
Pollinator order	1	27.02	<0.000
Residual	125	310.06	<0.000
Approach	1	0.002	0.965
Residual	125	376.5	<0.000
Body length ratio × Pollinator order	3	35.38	<0.000
Residual	123	304.11	<0.000
ITD ratio × Pollinator order	3	28.66	<0.000
Residual	103	254.4	<0.000
Pollinator order × Approach	3	26.8	<0.000
Residual	123	303.38	<0.000

### 3.2 | Taxonomical order

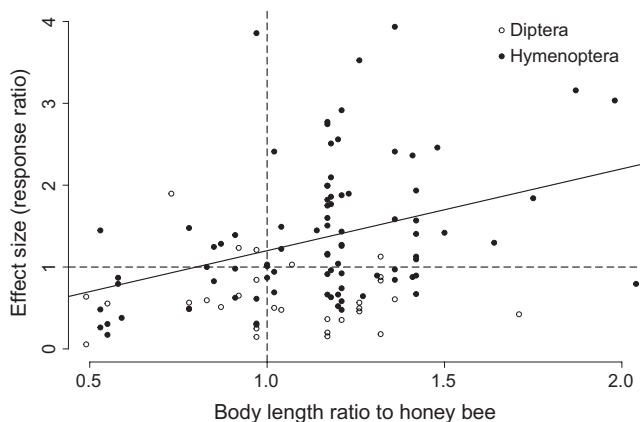
When taxonomic order of pollinators was used as a moderator, we found that non-honey bee Hymenoptera species (94 bee taxa of Apoidea) deposited significantly more pollen onto stigmas than honey bees whereas Diptera species (33 fly taxa) deposited fewer pollen grains onto stigmas than honeybees (Figure 1). When comparing Hymenoptera with Diptera (test of between-group heterogeneity), we found that bees transfer significantly more pollen to a stigma than flies (Figure 1).

### 3.3 | Methodological approaches

The between-group heterogeneity in the case of survey methods (i.e. comparing the active approach with static) was not significant (Table 1). The interaction model between pollinator taxonomic order



**FIGURE 1** The effect size related to single visit pollen deposition (SVD) depending on body length ratio and intertegular distance (ITD) ratio to honey bee, taxonomic order of pollinators (Diptera vs. Hymenoptera), and approach (active vs. static). Horizontal dashed line means that SVD of wild pollinator species is the same as for honey bee. Symbols are above dashed line mean higher SVD than honey bee. 95% CIs (confidence intervals) are shown. If they do not contain the dashed line, the significance level at  $p = 0.05$ . Numbers in parentheses next to symbols show sample sizes. The horizontal arrow indicates a significant difference between groups.  $**p < 0.01$



**FIGURE 2** Effect of body length ratio on single visit pollen deposition. The x-axis shows the ratio between the body length of wild pollinators and of honey bee. Vertical long-dashed line means that wild pollinators have the same body length as honey bee, whereas the horizontal long-dashed line indicates that wild pollinators deposited the same amount of pollen as honey bee. Black solid line shows the regression values

and the methodological approach did not reveal evidence for a significant difference in SVD showing that both survey methods can be used effectively for both groups.

### 3.4 | Publication bias

The funnel plot of effect size versus standard error of mean was not strongly skewed (Figure S4), indicating no evidence of publication bias in our dataset. The fail-safe number of 999 using the Rosenthal's approach was also robust. This number shows the number of studies

which would need to erase the significant effect measured by the meta-analysis (for the  $N = 127$  observations that were included, the benchmark value of Rosenthal is  $5N + 10 = 645$ , and this was smaller than the fail-safe number of 999). However, the regression test showed a significant difference from a symmetric funnel ( $z = -2.68$ ,  $p = 0.0072$ ), which among others can be caused by a potential publication bias (Sterne et al., 2011). Therefore, we applied the trim and fill method as a form of sensitivity analysis (Peters et al., 2007). This is an iterative nonparametric method to correct the asymmetry by removing the most extreme small studies from the positive side, and recalculating the estimated mean effect size at each iteration until symmetry is reached (trimming). Although this trimming yields an adjusted mean effect size, it reduces variances of effect sizes, therefore an algorithm adds the original studies back and imputes a mirror image for each one (filling). The trim and fill method did not change the outcome of the summary meta-analysis (Table 1; Figure 1), and showed that no studies were missing on the left side of the plot (Figure S3). Thus based on all these diagnostic methods, we think that publication bias did not affect our results.

## 4 | DISCUSSION

### 4.1 | Effect of body length and ITD on SVD

This study demonstrates that larger pollinators tended to deposit more pollen on stigmas than smaller as both pollinator body length and also intertegular distance of the different pollinator species had a positive effect on SVD across a broad range of plant species ( $n = 30$ ). This result is in accordance with previous studies which have also shown that larger pollinator species can deposit more pollen onto stigmas than smaller pollinators hence they were found to be more likely to contact the sexual organs of flowers (Ramalho et al., 1998; Willmer & Finlayson, 2014).

The interpretation of the relationship between pollen deposition and body size can depend on the influence of other morphological traits of pollinators such as hairiness (Phillips et al., 2018; Stavert et al., 2016) and proboscis length (Sun et al., 2013), particularly in circumstances where a specific floral morphology is better suited for pollination by a specific flower-visiting taxon (Stout, 2000). Moreover, this relationship may not be apparent due to a limited breadth of available data (e.g. low numbers of flower-visiting species assessed and low sample size). For instance, there are just a few studies that use consistent methodology to compare SVD in relation to other morphological parameters such as hairiness or proboscis length. Therefore, we used the more straightforward measures of body size and ITD and their relationship with SVD.

### 4.2 | SVD of wild pollinators

In this meta-analysis, we included observations on wild pollinators from almost all continents across a wide range of plant species from different ecosystems such as agricultural fields or urban areas.

Despite heterogeneity of the data origin, findings showed that wild pollinators, especially wild bee species, deposited significantly more pollen grains on a stigma per single visit to a flower than did honey bee. The number of observations on bumblebee species was high ( $n = 45$ ), as they were a focus of many studies (e.g. King et al., 2013; Potts et al., 2001). Bumblebees often collect significantly more pollen from anthers, and deposit more pollen on stigmas than honey bees (Thomson & Goodell, 2001; Willmer & Finlayson, 2014). This is not only because of body size, but also the hairiness of body and their adaptation to morphological traits of flowers they visit (Goulson et al., 2002). From studies involved in the analysis just a few non-Apidae bee families (e.g. Halictidae and Megachilidae) could be incorporated in our dataset. This reflects a general taxonomic bias in pollination studies towards particular bees (De Palma et al., 2016). Alike we strongly advocate the need for studies towards understanding these relationships across broader taxonomic groups for both bee and non-bee pollinators.

We found that flies produced a smaller SVD than honey bees (within-group analysis) and wild bees (between-group analysis), a finding that agrees with Willmer et al. (2017) who found bee species deposited more pollen than fly species. However, we found fewer assessments of fly species than of bee species, and further data are required to be confident that this pattern is broadly consistent across many plant species. On the other hand, some studies have demonstrated that flies can be more effective pollinators of certain crop species than honey bees (Orford et al., 2015; Rader et al., 2016, 2020; Smith & Saunders, 2016). Currently hoverflies (Syrphidae) have received the greatest attention (Jauker et al., 2012; Rader et al., 2020), however the effectiveness of other fly groups as pollinators can be also important, for example, Calliphoridae species in carrot pollination (Howlett, 2012), or Anthomyiidae in pollination of *Brassica rapa* L. (Stavert et al., 2018). Yet, knowledge on the efficiency of most fly species has been largely ignored (Orford et al., 2015; Szymank et al., 2008). It is possible that a bias against the study of particular fly species as pollinators may reflect negative knowledge or perceptions by researchers or the community. For example, the fly families Sarcophagidae and Calliphoridae contain many species with larvae that consume decaying organic matter, including excrement, fluids from animal bodies, and are associated with human diseases or myiasis (Pape, 1996), livestock fly strike (Heath & Bishop, 1995) and contamination of drying stockfish (Aak et al., 2011). Despite such species are often flower visitors (Grass et al., 2016) and verified pollinators (Rader et al., 2012, 2016), their importance in the pollination of a broad range of crops has largely been overlooked (Inouye et al., 2015; Larson et al., 2001; Woodcock et al., 2014).

### 4.3 | Effect of approaches on SVD

From a methodological point of view, we found no significant difference between obtained values of SVD using either the active

approach of interviewing pollinators using detached flowers or the static approach of waiting for pollinators to visit flowers still attached to the plant. Both approaches were found to be equally suitable to measure SVD even though the number of observations using the static approach was three times that of the number of observations carried out by the active approach. Analysing the interaction between the orders and approaches, we found no interaction, that is, both survey methods were effective for both bees and flies. Howlett et al. (2017) also reported no differences in SVD of different flower visitors using both static and active approaches, however, only one plant species was studied (*Allium cepa* L.).

Additionally, we do not assume that we can generalise that both approaches are equally applicable irrespective of plant and/or insect species, but in our analysis no differences were detected between them. However, we propose that both approaches should be ideally applied within studies, if possible, and additional plant and/or insect species should be studied for future comparisons.

## 5 | CONCLUSIONS

In summary, our results show that body length and ITD had positive effects on SVD, indicating that larger pollinators deposit more pollen per single visit. Notwithstanding, other morphological and behavioural traits of pollinators may also play a role in pollen deposition which should be taken account. We also found that bees deposited more pollen than fly species moreover, that SVD of wild pollinators is often higher than SVD of honeybee. Wild pollinator species are therefore likely to play a key role in providing complementary pollination services to managed honeybees (Stavert et al., 2018; Woodcock et al., 2019). This corresponds to Rader et al. (2016) who demonstrated that many fly and wild bee species not only contribute to the pollination of a wide range of crops but also non-crop plant species.

Interestingly, we found no significant difference in the effectiveness of the active approach (presenting a detached virgin flower to a flower visiting insect) and the static approach (waiting for a flower visiting insect to visit a virgin flower on a plant) as related to subsequent SVD, despite the methodological differences between these approaches.

Our meta-analysis shows that despite the increasing awareness of the importance of pollinator diversity for increasing crop yields (Garibaldi et al., 2016), the stigmatic pollen deposition of non-bee species remains understudied, calling for further research to bridge this knowledge gap.

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## AUTHORS' CONTRIBUTIONS

R.F. and P.B. conceived the ideas and designed methodology with support from B.G.H. and I.G.; R.F. collected the data; R.F. and P.B. analysed the data with the support from I.G.; R.F., P.B., B.G.H. and I.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via Dryad Digital Repository <https://doi.org/10.5061/dryad.05qfttf1n> (Földesi et al., 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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