Non-bee insects are important contributors to global crop pollination

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Abstract

Wild and managed bees are well-documented as effective pollinators of global crops of economic importance. However, the contributions by pollinators other than bees have been little explored despite their potential to contribute to crop production and stability in the face of environmental change. “Non-bee” pollinators include flies, beetles, moths, butterflies, wasps, ants, birds and bats among others. Here we focus on non-bee insects and synthesize 39 field studies from 5 continents that directly measured the crop pollination services provided by non-bees, honey bees and other bees, in order to compare the relative contributions of these taxa. Non-bees performed 25-50% of the total number of flower visits. Although non-bees were less effective pollinators than bees per flower visit, they provided slightly more visits; thus these two factors compensated for each other resulting in pollination services that were similar to bees. In the subset of studies that measured fruit set, fruit set increased with non-bee insect visits independently of bee visitation rates, indicating that non-bee insects provide a unique benefit that is not provided by bees. We also show that non-bee insects are not as reliant on the presence of remnant natural or semi-natural habitat in the surrounding landscape as bees. These results strongly suggest that non-bee insect pollinators play a significant role in global crop production and respond differently than bees to landscape structure, which should make crop pollination

services more robust to land use change. Non-bee insects provide a valuable service and are a potential insurance against bee population declines.

Significance statement

Many of the world's crops are pollinated by insects, and bees are often assumed to be the most important pollinators. Our study is the first quantitative evaluation of the relative contribution of non-bee pollinators to global pollinator-dependent crops. Across 39 studies we show that insects other than bees are efficient pollinators providing 39% of visits to crop flowers. Assessments of crop pollinator biodiversity and the economic value of pollination require a shift in perspective from a bee-only focus to also consider the services provided by other types of insects such as flies, wasps, beetles and butterflies; important pollinators which are currently overlooked.

Introduction

Pollinator-dependent crops are increasingly grown to provide food, fiber and fuel as well as micronutrients essential to human health (1-5). The yield and quality of these crops benefit to varying degrees from flower visitation by animals. The honey bee, *Apis mellifera* L. (Hymenoptera: Apidae) is the most versatile, ubiquitous and commonly used managed pollinator (6), yet the global reliance on this single pollinator species is a risky strategy, especially given major threats to the health of managed honey bee colonies due to the ectoparasitic mite *Varroa destructor* Anderson and Trueman (Mesostigmata: Varroidae), poor nutrition and a number of other pests and diseases (7-10).

Honey bees, however, are not the only insects that pollinate crops. Apart from a few managed bee taxa, the vast majority of other pollinators are free-living or ‘wild’, providing an ecosystem service to crops. Wild pollinators other than honey bees have recently been recognized for their role in increasing and stabilizing crop pollination services (11, 12). Wild bees are known to improve seed set, quality, shelf life and commercial value of a variety of crops (13-17). Increasingly, studies indicate that insect pollinators other than bees, such as flies, beetles, moths and butterflies, are equally if not more important for the production of some crops (18-23). Despite this, the contribution to crop pollination by non-bee insects has been largely unnoticed, with most global syntheses focusing on bees (24-27) or grouping all bee and non-bee wild insect pollinators (11).

Diverse pollinator assemblages have been shown to increase pollination services as a result of complementary resource use due to variations in morphology and behavior among pollinator taxa (28, 29). For example, pollinator species may visit different parts within a flower or inflorescence, or different flowers within a plant (high versus low flowers), improving the quality or quantity of pollination services overall (13, 30-32). Non-bee taxa, in particular, often have broader temporal activity ranges (33-35) and can provide pollination services at different times of the day compared with bees, and in weather conditions when bees are unable to forage (36-39). In addition, non-bee taxa may be more efficient at transferring pollen for some crops under certain conditions (18, 19, 37) and/or carry pollen further distances than some bees (40). It has been suggested that this long-distance pollen transfer could have important genetic consequences for wild plants (41, 42). There is little information, however, on the overall importance of the diverse group of non-bee wild pollinators (but see 38, 43) and their importance to global crop production.

Anthropogenic land use change and intensification are considered to be among the main drivers of bee declines (44, 45). One of the underlying mechanisms for observed declines is thought to be the loss of habitat that supports host plants (46) and nesting sites (47). However, different pollinator taxa respond differently to disturbances (48, 49). Natural habitat proximity and area are often associated with higher crop flower visitation and bee diversity (24, 45, 50). Yet, while several studies have investigated the habitat requirements of non-bee taxa (51-54), little is known about how habitat availability affects crop pollination services from non-bee taxa (but see 43). Thus, differential response to habitat proximity between bees and non-bees, if such exists, could provide an additional stabilizing effect on crop pollination services.

In sum, non-bees are often neglected as potential providers of crop ecosystem services by the scientific community and by growers. In the data collation for the present synthesis, for example, 36% of the original 58 pollination studies we obtained did not record or distinguish non-bee pollinators from bee pollinators and thus had to be excluded.

In this study we address the knowledge gap about non-bee crop pollination and ask:

1. How does the crop pollination provided by non-bee insects compare to that provided by honey bees and other bees?
2. How does the crop pollination provided by non-bees, honey bees and other bees translate into fruit/seed set?
3. Do non-bee crop pollinators respond similarly to bees with regard to isolation from natural and semi/natural habitats?

To answer these questions we compiled a data set comprising 39 studies from around the world of crop pollinators and the pollination services they provide (SI Appendix, Table S1).

Results

Pollination services provided by honey bees, other bees and non-bees

Flower visitor assemblages were diverse, with representatives from the orders Hymenoptera, Diptera, Lepidoptera, and Coleoptera. Non-bee taxa included flies (Diptera: mainly dominated by Syrphidae, Calliphoridae, Tachinidae, Empididae and Muscidae), butterflies and moths (Lepidoptera) and various beetle families (Coleoptera) and hymenopterans including ants (Formicidae) and wasps. Bees observed in the studies included Apidae (e.g. Meliponini, *Bombus* spp., Xylocopini, Ceratinini), Halictidae, Colletidae, Megachilidae and Andrenidae.

The total pollination services provided, which we calculated as the product of visitation frequency and pollen deposition per visit (n=9 studies; 55) did not differ significantly between honey bees, other bees and non-bees (Fig 1A). On average, non-bees accounted for 38% (CI: 29-49%), honey bees 38% (CI: 29-50%) and other bees 23% (CI: 15-33%) of the visits to crop flowers (N=37 studies; Fig 1B). Visitation rates of other bees and non-bees were very weakly correlated (Pearson's product-moment correlation: 0.22), while non-bees and honey bees, and other bees and honey bees, were not correlated (0.02 and 0.04 respectively). In contrast, the per-visit pollen deposition (N=11 studies) was significantly lower for non-bees than for either type of bee (Fig 1C). Thus, non-bees' higher visitation frequency and the lower per visit pollen deposition compensated for each other, resulting in levels of pollination service delivery similar to that of bees (Fig 1A).

Spatial variation in pollinator community composition

Observations of insect visitation rates revealed that assemblage composition varied across crop type and region (Fig 2A, 2B). Across the 37 crop studies, 31 recorded visits by all three groups of taxa, i.e. honey bees, other bees (i.e. all species other than *Apis mellifera*) and non-bees (Fig 2A). Two custard apple crops in Australia and Brazil (*Annona* sp.) were visited exclusively by non-bee taxa. Spatial variation in pollinator community composition resulted in some crops being visited by a more diverse group of insects than others, even within the same crop type. For example, pollinators of oilseed rape (*Brassica napus*) were surveyed in Sweden, Germany, United Kingdom, Netherlands, Ireland and Australia, and the contribution to visitation by non-bees differed markedly (5-80%) among these. Even within the three studies in Sweden, (oilseed rape A, G and M), visitation by non-bees ranged from 5-60%, demonstrating that location can have a strong influence, as can crop type, in determining assemblage composition (Fig 1C).

Fruit/seed set

Higher visitation rates by non-bees and other bees each enhanced crop fruit and seed set more so than similar increases in visitation by honey bees (N=15 studies; Fig. 3). In fact, honey bee visitation was not correlated with fruit set, with the average slope of this relationship centered on zero (Beta = -0.019, CI 2.5 % = -0.164, CI 97.5 % = 0.126), while non-bees show a positive slope (Beta = 0.12) minimally overlapping with zero (CI 2.5 % = -0.016, CI 97.5 % = 0.265). The strongest relationship was between other bee visitation and fruit set (beta = 0.187, CI 2.5 % = 0.044, CI 97.5 % = 0.330). Importantly, fruit set increased with non-bee visits independently of bee visitation rates, meaning that non-bee pollinators supplement rather than substitute for bee visitation. Both groups are therefore required for optimal pollination services.

Response to land use change

To test whether non-bees and bees respond differently to isolation from natural or semi-natural vegetation, we investigated the relationship between the proximity to these features and the visitation rate of honey bees, other bees and non-bee taxa across 23 studies. Other bee visits declined sharply with increasing isolation from natural/semi-natural vegetation, considering data from across all crop studies (Beta = -0.263, CI 2.5 % = -0.484, CI 97.5 % = -0.042 ; Fig. 4). In contrast, non-bee declines are moderate and the confidence intervals include zero (Beta -0.049, CI 2.5 % = -0.270, CI 97.5 % = 0.182) while honey bee visits show no response to proximity to natural/semi-natural vegetation (Beta = 0.070, CI 2.5 % = -0.161, CI 97.5 % = 0.301).

Discussion

The clear importance of non-bees as global crop pollinators, as shown in this study, illustrates how important the omission of non-bees from crop pollination studies is to our understanding of crop pollination services by wild insects. This is in addition to the well-established contributions that non-bees make to the reproduction of wild, native plant species (43, 56). Although the amount of pollen deposited per visit to crop flowers is, on average, lower for non-bees than bees, the high visitation frequency of non-bees to crop flowers compensates for this and results in high pollination services overall (Fig. 1A,B,C). Thus, our results are consistent with other studies which have found that visitation frequency drives the overall function provided by a species, because the variance across species in their flower visitation is much larger than the variance in per-visit function (27, 57). One outcome of this is that taxa with less efficient pollen deposition may be the most important pollinators in certain years or seasons when they are at high abundance relative to other taxa (27, 58, 59).

Increased visitation by other bees and non-bees each enhanced crop fruit and seed set more than increased visitation by honey bees (Fig. 3). Measuring this ‘downstream’ outcome variable is important because pollen deposition does not necessarily lead to fruit set (60), for example if pollinator visits are at saturating levels and result in flower damage or the transfer of poor quality/incompatible pollen (61, 62). For example, in our study, honey bees were good at depositing pollen in many crops, yet increased honey bee visitation did not increase fruit set, a result that has also been found by other researchers (11, 63). In contrast, increasing visits from other bees, like non-bees, were associated with increased fruit set. As argued by Garibaldi *et al.* (11), these patterns suggest that the effect of other bees and non-bees is additive to the effect of honey bees in the data sets examined.

A final benefit of non-bees documented here is that they respond less negatively to land use change than do bees (Fig. 4). Thus where non-bees and bees pollinate the same crop, the presence of non-bees could help stabilize crop pollination services against land use change, through a mechanism known as response diversity (48). Hence differences in responses among bee and non-bee taxa could potentially provide pollination “insurance” in the event of bee declines (32). While other bees responded positively to natural habitat, non-bees and honey bees did not show a clear pattern. This may be because most other bees are central place foragers, some of which require untilled ground and sparsely vegetated ground for nesting, and reliable, long-term pollen and nectar resources: these habitat features are associated with semi-natural or natural vegetation (45). In contrast, many non-bee taxa have diverse nesting habits, many flies lack central nest locations and others are only dependent on floral resources during adult life stages (64). As such, for this diverse group of insects, the agricultural matrix may be more permeable than for many bees (65).

The diversity of life history strategies exhibited by non-bees necessitates a different approach to habitat management compared to bees in order to ensure that a wide range of foraging and nesting resources are available. For example, within the hoverfly family (Diptera: Syrphidae) the larvae of some species feed on pollen (66), or aphids (64), or plant matter (67), or dung among other resources (68), while the adults are usually generalist flower visitors. Further, at least some hoverfly species appear to be less affected by land use change than bees in general as many are able to utilize resources from highly modified habitats, including agricultural fields (43, 45, 65). This may explain why some non-bee pollinator populations are known to benefit from the same pollinator enhancement practices as bees while others do not (53, 69, 70).

There are several reasons why non-bees have generally been overlooked in crop pollination studies until now. The diversity of families and the taxonomy of non-bee taxa are often poorly resolved (71, 72). Some non-bee taxa (such as flies and small wasps) move quickly and are difficult to follow in visual observations (e.g. transects). Further, many researchers have made the erroneous assumption that non-bee taxa are unimportant to pollination as demonstrated by the 36% of studies reviewed that did not collect data on non-bee taxa as an *a priori* decision.

With the growing economic importance of crops that require animal-mediated pollination (73), wild insect pollinators are increasingly being recognised for their role in improving and stabilizing crop pollination services (74). Here, we show that wild pollinators other than bees also make substantial contributions to global crop pollination services. This demonstrates the importance of including non-bee pollinators in future crop pollination surveys, pollination estimates and pollinator management practices to ensure that we ascertain the relative contributions from all crop pollinating taxa, over and above the well-known bee taxa.

Materials and Methods

We analysed data from 480 fields for 17 crops examined in 39 studies on 5 continents. Fields ranged from extensive monocultures to small, diversified systems (SI Appendix, Tables S1, S2). All crop studies that were included benefit in some way from insect pollination. The protocols and identity of studies used to investigate the visitation rate, efficiency, contribution to yield and response to natural or semi-natural vegetation in each study are provided in Tables S1 and S2. Across all the studies, 37 provided data on visitation frequency; 11 studies provided data on pollen transfer efficiency; 19 studies provided data on seed or fruit set and 23 provided data on distance to natural/semi-natural vegetation. Thirteen out of the 39 crop studies have not been included in any previous synthesis on wild pollinator contributions to crop pollination.

Flower visitation frequency

To investigate the frequency with which non-bees visit crop flowers in comparison to bees across our studies, we observed flower visitors within standardised quadrats and transects and measured flower visitation per unit of time for each insect species/group (37 studies). Pollinator observations were carried out during peak flowering. In several studies, visitation was standardized with respect to a unit area or branch. This was because some crops have hundreds of small flowers per plant, so visits per flower could not be accurately assessed. We analysed visitation by three different groups: honey bees, other bees and non-bees (i.e. all other insects). In this synthesis across all studies, we considered *Apis mellifera* to be the only species within the honey bee group for consistency across all datasets. Other Apis bees (e.g. *Apis cerana indica*) were pooled into the other bee category. We analyzed all feral and managed honey bees as a single group because they cannot be distinguished during field observations. Feral honey bees were uncommon in most studies with the exception of South Africa. The exact methods and numbers of sampling points surveyed in each study are published elsewhere or provided in the supporting information (SI Appendix, Table S1)

Pollen deposition per flower visit

To investigate differences in per visit efficiency among bee and non-bee taxa (11 studies, Table S2), pollen deposition on stigmatic surfaces or fruit set after a single visit was estimated in fine weather conditions from pollination efficiency experiments where virgin inflorescences were bagged with a fine mesh to exclude pollinators. When bagged flowers opened, the bag was removed and the flowers observed until an insect visited the flower and contacted the stigma. The stigma was then removed by carefully severing it from the style using finely pointed forceps and the number of pollen grains or pollen tubes were counted after one visit by each insect. A variation to this method was employed for several crops (i.e. radish, kiwi, avocado, carrot and watermelon), which involved removing the virgin flower and positioning it to allow visitation by particular taxa (SI Appendix, Tables S1 and S2). Single visit pollen deposition values were generally only available for the dominant taxa, hence this analysis does not necessarily represent the efficiency of entire communities.

Calculating total pollination per species

Total pollination is often considered to be a function of both visitation frequency and per visit efficiency (55). We estimated total pollination for the nine studies in which these data were available. We used species-level visitation records and multiplied total visitation of each group (i.e. Honey bee, other bees and non-bees) by the mean per visit pollen deposition of each group (Fig 1A).

Fruit/seed set

To investigate differences in fruit set or seed set in relation to bee and non-bee taxa visitation (19 studies; Table S2), we recorded the proportion of flowers that set fruit or the total number of fruits or seeds as a measure of pollination success.

Isolation from natural semi-natural habitat

Finally, to investigate the response of bees and non-bees to isolation from natural/semi-natural vegetation, we calculated the linear distance (km) from each field site to the nearest patch of natural or semi-natural vegetation (23 studies; Table S2). For two crops, almond and oilseed rape E, we transformed the percentage of semi-natural vegetation within a 1 km area to linear distances following (12).

Study Selection

We initially contacted 58 data holders with the following criteria for inclusion of datasets in the synthesis; (i) Field studies must have set out to record all groups of pollinators i.e. both bee and non-bee groups. Studies were excluded that did not set out to record non-bees (N=14) or that did not set out to record honey bees (N=1). If a researcher stated that they did do a systematic survey with the aim of sampling all pollinators (even though an entire group of pollinators was absent), we included that study. Finally, studies that included either bees or non-bees on an ad hoc basis (rather than a systematic survey), were excluded (N=4). Although the present study is limited to those crop studies in which data were available for non-bee taxa, we do include several crops for which bees are assumed to be the primary visitors, such as almond and watermelon (75, 76). Furthermore, the ratio of bee to non-bee visited crops in the FAOSTAT crop database (6) is comparable to the ratio investigated in this synthesis (SI Appendix, Table S3).

Data Analysis

Data on visitation rates, pollination efficiency, fruit or seed set and isolation from natural/semi-natural vegetation was standardized for cross-study analysis with the calculation of z-scores within each study. Z-scores do not modify the form (e.g. linear or non-linear) of the relationship between response and predictor variables and allow for direct comparison of the values collected in different studies (77).

We analyzed all data using general linear mixed-effects models using R software version 3.0.2, nlme package, lme function, with Gaussian error distribution (R Development Core Team 78). By including crop study as a random variable, our models estimated different intercepts (αj) for each study (j) which accounts for the hierarchical structure of the data, i.e. different fields are nested within each study (77, 79). The overall intercept ($\mu\alpha$) reflects a weighted average over crop studies (αj), where the relative influence of each crop study increases with the precision of its local model fit and its sample size (77, 80).

To answer the first question regarding differences in crop pollination services among non-bee and bee taxa to crop flowers, we ran a different model for each group (honey bees, wild bees and non-bees) with no predictor. This enabled calculation of the overall intercept (i.e. mean % visitation) and confidence intervals (CI) for each of the three groups taking into account the hierarchical structure of the data. Per capita efficiency values were regressed against pollinator group (categorical: honey bee, other bee, non-bee). Post hoc Tukey tests were used to disentangle the differences in efficiency between the three groups using the ‘multcomp’ package (81) with a Hochberg correction for multiple comparisons. To answer the second question, we built three sets of models to examine the relationship between fruit set and visitation rates of the different insect groups. In order to determine whether increased visitation rate by each of the three groups was associated with increased fruit set, the first model consisted of fruit set regressed against total visitation of honey bees, other bees and non-bees, with random intercepts for crop study. The second set of models included both random intercepts and random slopes. A third set of models was run including pairwise interactions among the three groups and only random intercepts. The three models were compared using AIC (82). The first model had the greatest support (AIC = 555) followed by both the interaction model (ΔAIC =5) and the random slopes model (ΔAIC =4), hence only the random intercept models are presented. Finally, to answer the third question, visitation rate by each group was regressed against isolation from natural habitats in a separate model with random intercepts as described above. We present estimated slopes and CI for all analyses. To meet the assumptions of homoscedasticity, we used a constant variance function when necessary. VIF (variance inflation factors) of the predictors was always below 1.5 indicating no multi-collinearity (83).

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Contributions by authors:

R.R. designed the study, collated datasets and wrote the first draft of the manuscript. I.B. conducted analyses with assistance from L.A.G; I.B, L.A.G., M.M.M, S.A.C., M.P.G., B.H., C.S.S., B.G.H and R.W. discussed and revised earlier versions of the project and manuscript. The remaining authors are listed alphabetically from A.D.A. to M.W, as they contributed equally to the manuscript by collecting and formatting field data, providing several important corrections to subsequent manuscript drafts and discussing ideas.

FIGURES

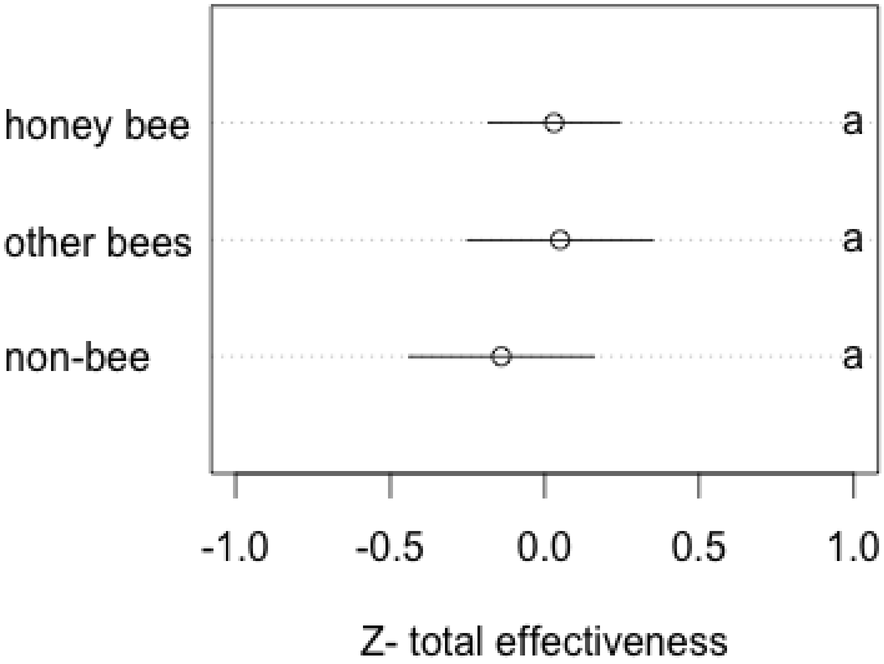


Figure 1A: Pollination considered as a function of visits*pollen deposition in a single visit among guilds for the nine studies with efficiency and visitation data. Note that per capita efficiency in each guild is measured only in a subset of dominant species in each study. Data from individual crop studies were standardized by z-scores prior to analysis permitting direct comparison of slopes.

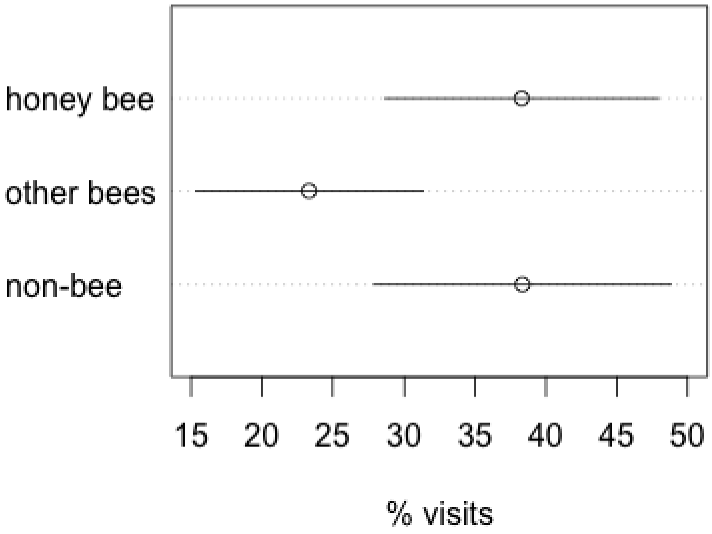


Figure 1B: The contribution by honey bees, other bees and non-bees to flower visitation across the 37 crop studies. To calculate the contributions of different insect groups to visitation (i.e. percentage of visits) we ran a different model for each group (honey bees, wild bees and non-bees). This enabled calculation of the overall intercept (i.e. mean % visitation) and confidence intervals (CI) from the partially pooled data. Data from individual crop studies were standardized by z-scores prior to analysis permitting direct comparison of intercepts.

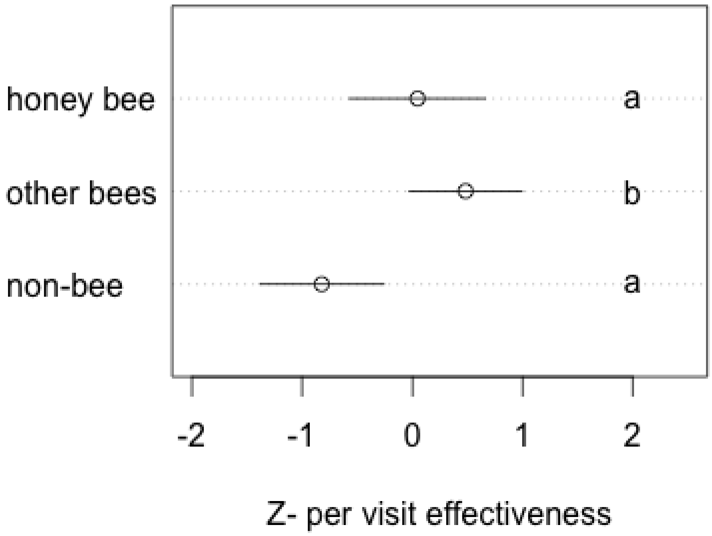


Figure 1C: The relative efficiency of honey bees, other bees and non-bees as measured by pollen deposition per visit, combined across the 11 crop studies for which pollen deposition data were available. Letters depict post-hoc test differences (at $P < 0.05$) among pollinator groups. Data from individual crop studies were standardized by z-scores prior to analysis permitting direct comparison of slopes.

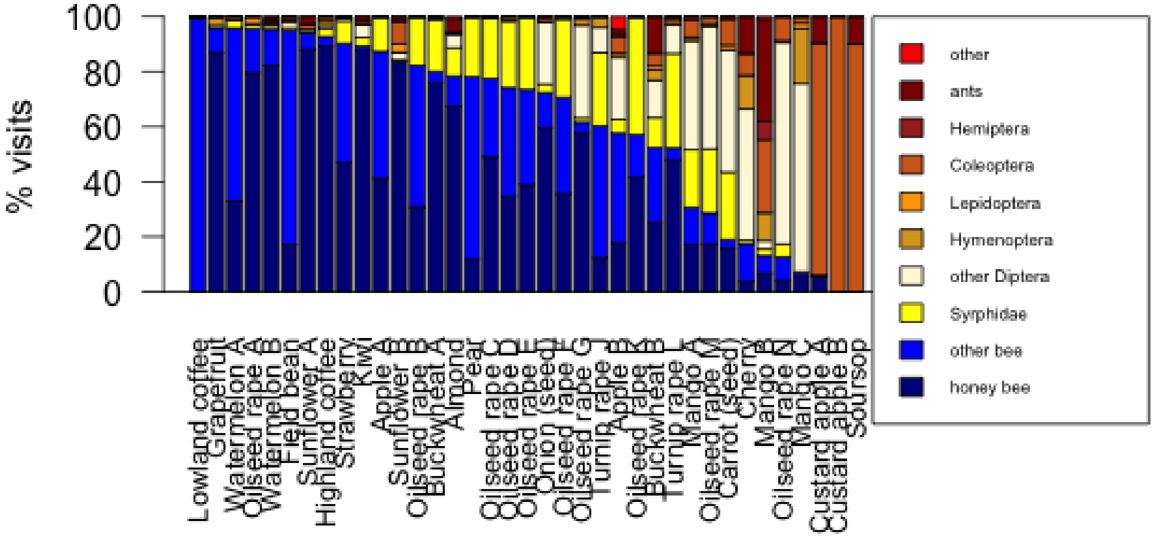
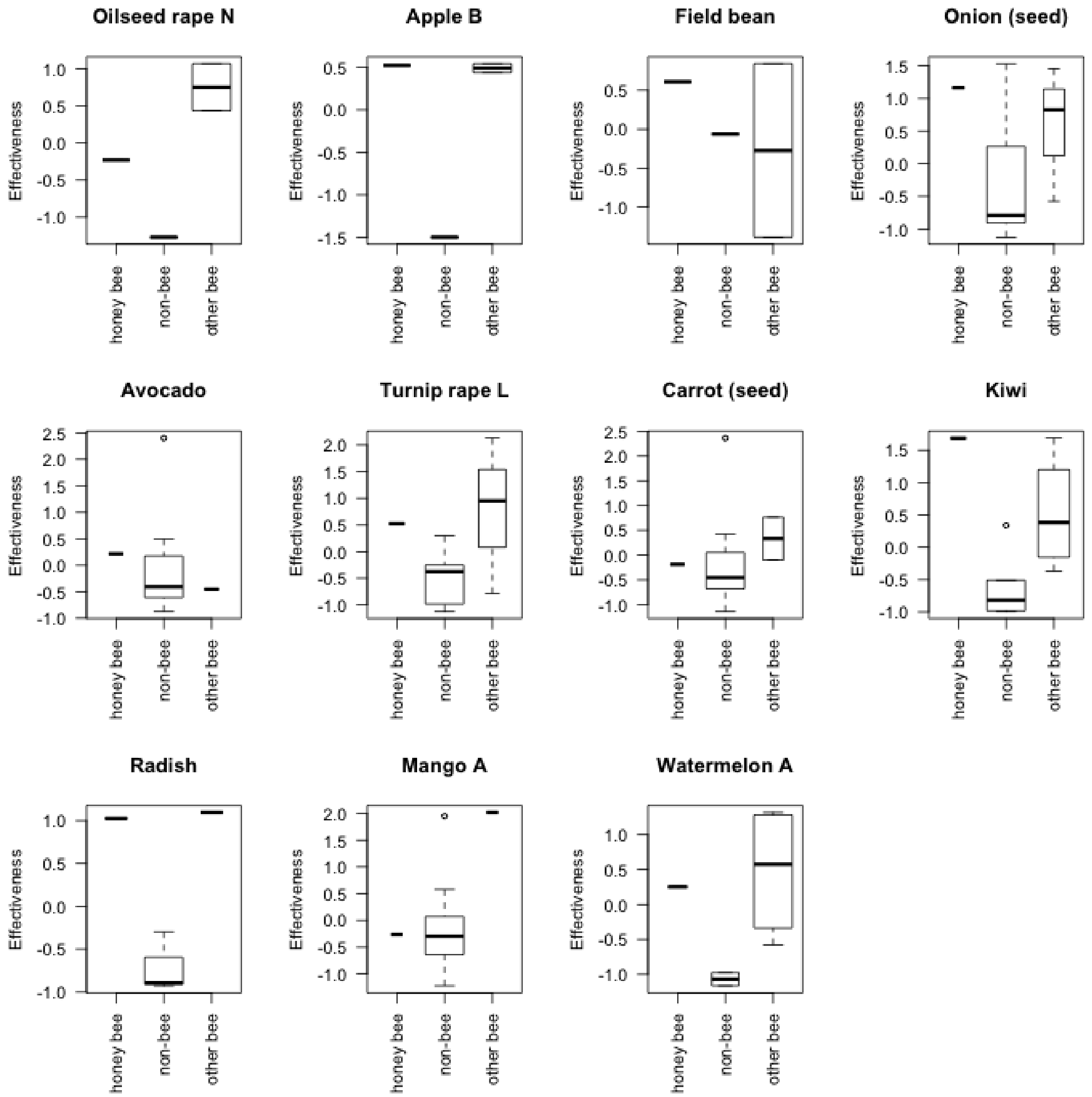


Figure 2A: The contribution of different insect groups to flower visitation across the 37 crop studies for which visitation data was available. Crops are ordered from mostly bee (left) to mostly non-bee dominated (right).



Oilseed rape N

Apple B

Field bean

Onion (seed)

Avocado

Turnip rape L

Carrot (seed)

Kiwi

Radish

Mango A

Watermelon A

Figure 2B: The relative differences in the efficiency of honey bees, other bees and non-bees across 11 crops as measured by pollen deposition per visit.

Figure 3: Regression coefficients (i.e. slopes $ß_i$ ± 95% CI) represent honey bee, other bees and non-bee contributions to overall fruit set as measured by seed set across 19 crop studies, estimated from the relationship between visitation and fruit set variation. Visitation by other bees increased fruit set (i.e., average slope is positive and confidence intervals for regression coefficients did not include zero). The average regression coefficients across crops for non-bees increased fruit set (i.e. positive mean), however confidence intervals minimally overlapped zero.

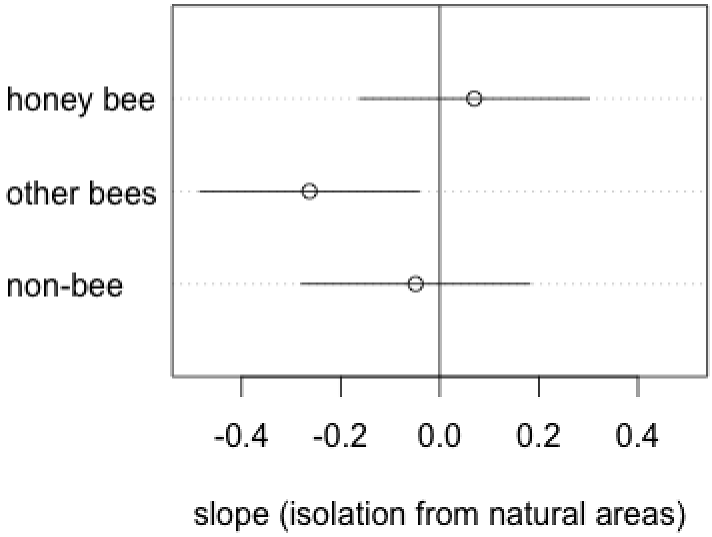


Fig 4: Regression coefficients (i.e. slopes $ß_i$ ± 95% CI) represent the relationship between honey bees, other bees and non-bee visitation and distance from natural / semi-natural habitat (23 studies). Visitation by other bees was negatively related to distance from natural / semi-natural habitat (i.e., average slope is negative and confidence intervals for regression coefficients did not include zero). Visitation by honey bees and non-bees was not related to distance from natural / semi-natural habitat (i.e., average slope is negative and yet confidence intervals overlapped zero for both taxa). Data from individual crop studies were standardized by z-scores prior to analysis permitting direct comparison of slopes.

SUPPORTING INFORMATION APPENDIX S1

Table S1: Datasets used in this study; *details of methodology for unpublished studies provided below.

Study Name	Crop common name	Data holder contact	Source of study methodology	Study location
Actinidia deliciosa	Kiwi	m.mayfield@uq.edu.au	(84)	New Zealand
Actinidia deliciosa A	Kiwi	brad.howlett@plantandfood.co.nz	*	New Zealand
Allium cepa	Onion	brad.howlett@plantandfood.co.nz	(85)	New Zealand
Annona muricata	Soursop	freitas@ufc.br	*	Brazil
Annona squamosa A	Custard apple	freitas@ufc.br	*	Brazil
Annona squamosa B	Custard apple	saul.cunningham@csiro.au	(20)	Australia
Brassica napus A	Oilseed rape	Riccardo.Bommarco@slu.se	*	Sweden
Brassica napus B	Oilseed rape	Frank.Jauker@allzool.bio.uni-giessen.de	(53)	Germany
Brassica napus C	Oilseed rape	jeroen.scheper@wur.nl	*	Netherlands
Brassica napus D	Oilseed rape	darastanley@gmail.com	(86, 87)	Ireland
Brassica napus E	Oilseed rape	Maj.Rundlof@biol.lu.se		Sweden
Brassica napus F	Oilseed rape	darastanley@gmail.com	(86, 88)	Ireland

Brassica napus G	Oilseed rape	Sandra.Lindstrom@hushallningssallskapet.se	*	Sweden
Brassica napus K	Oilseed rape	saul.cunningham@csiro.au	(89)	Australia
Brassica napus M	Oilseed rape	nacho.bartomeus@gmail.com	(90)	Sweden
Brassica napus N	Oilseed rape	m.p.garratt@reading.ac.uk	(91)	United Kingdom
Brassica rapa J	Turnip rape	Georg.Andersson@biol.lu.se	*	Sweden
Brassica rapa L	Turnip rape	brad.howlett@plantandfood.co.nz	(18)	New Zealand
Citrullus lanatus A	Watermelon	rwinfree@rutgers.edu	(92)	USA
Citrullus lanatus B	Watermelon	Yael.Mandelik@mail.huji.ac.il	*	Israel
Citrus paradisi	Grapefruit	nchacoff@gmail.com	(63)	Argentina
Coffea arabica	Highland coffee	carlosh.vergara@udlap.mx	(93)	Mexico
Coffea canephora	Lowland coffee	Smitha.krishnan@env.ethz.ch	(94) *	India
Daucus carota	Carrot	brad.howlett@plantandfood.co.nz	(37)	New Zealand
Fagopyrum esculentum A	Buckwheat	hajnalka.szentgyorgyi@gmail.com	(95)	Poland
Fagopyrum esculentum B	Buckwheat	htaki@affrc.go.jp	(96)	Japan
Fragaria vesca	Strawberry	m.p.garratt@reading.ac.uk	*	England
Helianthus annuus A	Sunflower	Yael.Mandelik@mail.huji.ac.il	(97)	Israel
Helianthus annuus B	Sunflower	lgcarvalheiro@gmail.com	(98)	South Africa
Malus domestica A	Apple	David.Kleijn@wur.nl	*	Netherlands
Malus domestica B	Apple	m.p.garratt@reading.ac.uk	(99)	United Kingdom
Mangifera indica A	Mango	rrader@une.edu.au	*	Australia
Mangifera indica B	Mango	lgcarvalheiro@gmail.com	(100)	South Africa
Mangifera indica C	Mango	jhdsousa@yahoo.com	(101)	Brazil
Persea americana	Avocado	brad.howlett@plantandfood.co.nz	*	New Zealand

Prunus avium	Cherry	entling@uni-landau.de	(102)	Switzerland
Prunus dulcis	Almond	alexandra.klein@nature.uni-freiburg.de	(32)	USA
Pyrus communis	Pear	David.Kleijn@wur.nl	*	Netherlands
Raphanus sativus	Radish	brad.howlett@plantandfood.co.nz	*	New Zealand
Vicia faba	Field bean	m.p.garratt@reading.ac.uk	(91)	United Kingdom

Table S2: The crops used to address the four research questions; 37 datasets were used to investigate differences in visitation rate; 11 datasets to investigate differences in pollen deposition; 19 datasets to investigate differences in fruit set and 23 datasets to investigate isolation from natural/semi-natural vegetation.

Study Name	Crop common name	Visitation	Pollen deposition	Seed / fruit set	Response to natural/semi-natural vegetation
Actinidia deliciosa	Kiwi	x		x	x
Actinidia deliciosa A	Kiwi		x		
Allium cepa	Onion	x	x		
Annona muricata	Soursop	x		X	
Annona squamosa A	Custard apple	x			
Annona squamosa B	Custard apple	x			x
Brassica napus A	Oilseed rape	x		x	
Brassica napus B	Oilseed rape	x			
Brassica napus C	Oilseed rape	x			x
Brassica napus D	Oilseed rape	x			
Brassica napus E	Oilseed rape	x		x	x
Brassica napus F	Oilseed rape	x		x	x
Brassica napus G	Oilseed rape	x			x
Brassica napus K	Oilseed rape	x			
Brassica napus M	Oilseed rape	x		x	x
Brassica napus N	Oilseed rape	x	x		x
Brassica rapa J	Turnip rape	x		x	x
Brassica rapa L	Turnip rape	x	x		x
Citrullus lanatus A	Watermelon	x	x		x
Citrullus lanatus B	Watermelon	x			x

Citrus paradisi	Grapefruit	x			
Coffea arabica	Highland coffee	x		x	x
Coffea canephora	Lowland coffee	x		x	x
Daucus carota	Carrot	x	x		
Fagopyrum esculentum A	Buckwheat	x		x	
Fagopyrum esculentum B	Buckwheat	x		x	x
Fragaria vesca	Strawberry	x		x	x
Helianthus annuus A	Sunflower	x			
Helianthus annuus B	Sunflower	x		x	x
Malus domestica A	Apple	x			
Malus domestica B	Apple	x	x	x	x
Mangifera indica A	Mango	x	x	x	x
Mangifera indica B	Mango	x		x	x
Persea americana	Avocado		x		
Prunus avium	Cherry	x		x	x
Prunus dulcis	Almond	x		x	x
Pyrus communis	Pear	x			
Raphanus sativus	Radish		x		
Vicia faba	Field bean	x	x	x	x

Table S3: Percentage of crops pollinated by bee and non-bee pollinators in FAO pollinator dependent crop database. [1] Composition of pollinator community based on Klein *et al.* (6). The Klein study demonstrated that of the top 208 global crops that are known to benefit from animal pollinators, 36% were visited mostly by bee pollinators, 23% were visited both by bee and non-bee pollinators (including birds and mammals), 11% were visited mostly by non-bees and the remaining 36% was unknown. Here we tallied the dominant pollinator taxa into four groups (i.e. bees only, bees and non-bees, honey bee and unknown) based on the FAO database data and present these values as a percentage of the total number of crops; [2] Composition of pollinator community expected for the crops selected in this synthesis based on (6). Here we performed the same tally for our crop species based on FAO database and present these values as a percentage of the total number of crop species in our study; [3]Actual pollinator composition based on empirical data collected for this synthesis. Here we compiled the actual tallies from the results of the empirical studies synthesized in this manuscript. We tallied data from individual studies (not crop species, hence the same crop type may have a different pollinator composition in a different region).

	Non bee only (%)	Bees plus non bees (%)	Bee only (%)	Unknown (%)
[1.]Composition of pollinators across all crop types worldwide	5	23	36	36

[2]Expected composition of pollinators across crop types selected in this study.	6	56	28	11
[3]Actual pollinator composition based on all studies in this synthesis	17	78	6	0

Table S4: Akaike's Information Criterion (AIC) for mixed effects models of the potential influences on fruit set, including visitation rate by other bees (ob), visitation rate by honey bees (hb) and visitation rate by non-bees (nb). The Δ column depicts the difference between a model's AIC and that of the best-fitting model. Different intercepts (αi) were estimated for each crop system in all models by including study system as a random factor (23). All variables were standardized using z-scores within each crop system prior to analyses. Model estimates presented in each variable and standard error in parentheses.

Model	**AIC**	**Δ**	***ob***	***hb***	***nb***	***ob*nb*hb***	***nb*ob***	***ob*hb***	***nb*hb***	***Random slope ob***	***Random slope hb***	***Random slope nb***
Null	591.28											
A:best	555.64		0.19 (0.07)	-0.02 (0.07)	0.12 (0.07)							
B	574.33	19	0.21 (0.08)	-0.04 (0.08)	0.12 (0.07)	0.17 (0.15)	0.02 (0.06)	0.05 (0.09)	-0.02 (0.09)			
C	561.47	6	0.19 (0.08)	-0.02 (0.07)	0.13 (0.07)		-0.007 (0.06)					
D	561.09	5	0.19 (0.07)	-0.02 (0.08)	0.12 (0.07)			-0.02 (0.07)				
E	560.52	5	0.19 (0.07)	-0.03 (0.08)	0.12 (0.07)				-0.03 (0.09)			
F	572.32	17	0.17 (0.08)	-0.014 (0.08)	0.14 (0.08)					X	X	X
G	559.37	4	0.17 (0.08)	-0.01 (0.08)	0.13 (0.07)					X		
H	559.27	4	0.20 (0.07)	-0.02 (0.09)	0.12 (0.07)						X	
I	559.63	4	0.19 (0.07)	-0.02 (0.07)	0.12 (0.07)							X

Methods S1- Additional information concerning unpublished studies

Methods for all the studies not described below are published elsewhere (see references in Table S1).

Research on the watermelon B system (Table S1) was carried out during 2009 in the Judean Foothills, a Mediterranean agro-natural ecosystem in central Israel (31.6–31.9ºN:34.7–35.0ºE, 60–280 m a.s.l.). All data were collected under standardized weather conditions (sunny days, wind velocity <6 m/s, temperature >18ºC). The Malali cultivar watermelon for seed production is commonly grown in the region under a crop rotation regime, either with drip irrigation or under dryland conditions. Fields are sown in March at a density of 3 plants/m^2, and reach bloom in mid-May; seeds are harvested from August to September. The majority of our research fields lacked honey bee hives, nevertheless honey bees from nearby hives were usually abundant. A survey of flower visitors to watermelon was conducted in 19 fields, all at a minimum distance of 1 km from each other. In each field, a 25x25 m plot was marked at the field edge; in eight fields that were sufficiently large to test for edge effects, an additional 25x25 m plot was marked at the interior of the field, 80−110 m from the edge. Edge plots were surrounded by 10−70% (median 25%) semi-natural habitat at 1000 m radius. Each plot was surveyed on one to two different dates, two times per day, between 7:00−9:00 and 9:00−11:00, with intervals of ≥60 min between successive rounds. Each sampling round included 10 min of slow walking along the rows of the plot and recording the number of honey bees, wild bees and other insect visitors to watermelon flowers.

In the soursop and custard apple A studies insect visitation was assessed for 20 minutes at four times during the day. For soursop these time intervals were: 8:00 -8:20h, 12:00 12:20h, 16:00 – 16:20h and 20:00 – 20:20h; for custard apple the time intervals were: 8:30 -8:50h, 12:30 12:50h, 16:30 – 16:50h and 20:30 – 20:50h. Insects were surveyed by walking along the tree rows and checking the interior of the flowers for visitors. The number of flowers sampled at each transect varied according to the blooming stage of the different plants. Each flower observed was marked individually and the number and identity of insects within that flower was recorded. Fruit set was recorded 15 days later as the proportion of marked flowers which have turned into fruitlets.

For avocado, observations were conducted around the circumference of each tree. A 1.5 m pole marked with coloured tape at both ends was held vertically 30-50 cm from the tree racemes so that the number of racemes observed were restricted within a marked area of the tree. Flower visitors were counted around the entire circumference of the tree at 9-10.30 am 12-1.30pm and 3-4.30 pm. Twenty -five flowering racemes of each raceme type (outside versus within) were counted to compare tallies of flower visiting insects.

In the oilseed rape J study in Sweden, data on insect visitation and seed set was collected in eleven landscapes during 2010. In each landscape, four phytometers were placed in a field edge to wheat. On sunny days during the flowering period in June and July insect visitation was observed four or five times during 45-60 minutes. The observations sessions were distributed evenly over the day and all flower visiting insects were noted. In August, five branches on each phytometer were harvested and all the pods, both developed and underdeveloped, were counted.

When the pods were dry, the seeds from ten pods from each plant were counted and the weight was measured.

In the strawberry study in Yorkshire, UK, eight fields were selected and 2*150m transects were walked between rows in each field in 2011. For recording purposes, the transects were sub divided into 3*50m transects each of which was walked in 10 minutes. Any pollinators observed carrying out floral visits were recorded. If the pollinator could not be identified on the wing it was caught in a hand net and identified back at the laboratory. Three rounds of strawberry surveys were carried out in each field between the 18th of May and the 14th of June. All surveys were conducted at temperatures in excess of 15 degrees with only light wind.

In the oilseed rape C study, flower visiting insects were surveyed in 14 oilseed rape fields in the eastern part of the Netherlands. Eight oilseed rape fields were surveyed in 2011; six other fields were surveyed in 2012. In each year, the distance between fields was at least 2 km. With the exception of one field, which was only sampled once on 30 April 2011, all fields were surveyed twice between 27 April and 30 May, once in the morning and once in the afternoon. In each field, flower visiting insects were surveyed in two 1 x 150 m transects located at the edge and in the interior of the field (>25 m from field edge). Transects were subdivided into three 1 m x 50 m plots. In each plot, insects visiting crop flowers were collected during a period of 5 minutes. Easily recognizable species were generally identified in the field; all other species were collected and identified in the lab. Surveys were carried out under dry weather conditions, with low to moderate wind speeds and temperatures above 15 °C. Landscape composition in a 1 km radius around the focal fields was determined using national topographical maps and field inspections and the nearest distance to semi-natural habitat (e.g. forest edges, semi-natural grasslands, hedges, heathlands, orchard meadows) was determined using ArcMap 10 (ESRI, Redlands, CA, USA).

In the oilseed rape A study, 10 autumn-sown oilseed rape fields located in the western part of Sweden (Västergötland; 58°21'41"N 13°9'59"E WGS84) were surveyed in 2009. Fields were separated by minimum 1.7 and maximum 38.3 km. Fields were surveyed for flowers visiting insects four times during the flowering 16 May- 1 June 2009. Insect surveys were conducted in three 200 x 2 m transects per field. Transects were located 100, 200 and 300 m from the field edge. Observed flower visiting insects were identified as honey bees, bumble bees, other wild bees and non-bee pollinators. Surveys were conducted in dry weather, with no to moderate winds and temperatures above 15ºC. Surrounding land use was extracted from a national database on agricultural land use (the Integrated Administration and Control System (IACS)), combined with a land use classifications based on satellite images and a variety of national maps (provided by the Swedish mapping, cadastral and land registration authority). Harvest and threshing to estimate seed yield was done by hand of ten plants per transect, and, in addition, with an experimental threshing machine harvesting an area of around 1.5 x 10 m areas near each transect.

In the oilseed rape E study, 32 autumn-sown oilseed rape fields located in the southernmost part of Sweden (Scania; N 55° 48' 15.31", E 13° 28' 4.12") were surveyed 2011-2012, with 16 fields surveyed each year. Fields within a year were separated by at least 2 km, to avoid regular exchange of insects. Fields were surveyed for flowers visiting insects twice in a year during 9 May-5 June 2011 and 7 May-7 June 2012. Insect surveys were conducted in two 150 x 1 m transects per field, one transect located 8 m from the edge of the field and the other 100 m from the field edge. Each transect was surveyed for insects visiting the crop flowers during 15 minutes. Insects that could not be identified to species in the field were collected, frozen and brought to the lab for species determination. Surveys were conducted during dry weather, with no to moderate winds and above 14ºC (except in one case where the temperature was 12ºC). Surrounding land use was extracted from a national database on agricultural land use (the Integrated Administration and Control System (IACS)), combined with a land use classifications based on satellite images and a variety of national maps (provided by the Swedish mapping, cadastral and land registration authority) and landscape mapping of the land use during the study years. Relative covers of different land uses were calculated using an automated procedure in MATLAB (MathWorks, Natick, MA, USA, version R2012b (8.0.0.783)) combined with a SAS (SAS Institute Inc., Cary, NC, USA, version 9.3) script.

Surveys on flower visiting insects in the apple A and pear studies were conducted in six apple and six pear orchards, respectively. Surveys were performed in 2010 and 2011, using the same apple and pear orchards in both years. Each orchard was surveyed twice per year, once in the morning and once in the afternoon with at least three and at most seven days separating surveys. Surveying was conducted between 23 April and 6 May, 2010 and between 8 and 20 April, 2011 under sunny conditions or scattered clouds. Temperatures ranged between 15 °C and 20 °C with calm wind to moderate breeze. Flower visitors were surveyed using a single transect between two rows of trees along the length of each orchard, with the transect subdivided into 25 m long plots (mean number of plots per orchard ± s.e.: 8.5±1.0 for apple and 9.7±0.5 for pear). In each plot all flower visitors observed on apple or pear flowers during a 10 minute period were identified to species. Easily recognizable species were generally identified in the field; all other species were collected and identified in the lab. All orchards were adjacent to semi-natural habitat (river levee).

In the *Coffea canephora* study, Google Earth Quickbird images of 0.6 meter resolution from the year 2009, in addition to topographic maps developed by the Survey of India (1:50,000 scale), the Forest Survey of India and LANDSAT satellite images were used to develop localised maps around our study sites. The landscape components were classified as forests, coffee plantations, rice paddies, water-bodies and human settlements. We were able to differentiate between forests and coffee plantations by the difference in canopy pattern using Google Earth. The shade trees in the coffee plantations are pruned extensively and hence have a much narrower crown than the forested areas. The sites were ground-truthed, and local farmers were consulted to confirm the presence of any forested regions around the study areas, thus reducing the possibility of errors. The area of each landscape component was calculated for three spatial scales (500, 1000 and 1500 m radius from the centre of the forest sampled), while water bodies within these areas were counted. Three sites had to be excluded from the spatial analysis due to cloud cover which obscured the determination of land cover types. All the GIS data was processed using the software ArcGIS version 9.3.

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