Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance

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The diversity and abundance of wild insect pollinators have declined in many agricultural landscapes. Whether such declines reduce crop yields, or are mitigated by managed pollinators such as honey bees, is unclear. We found universally positive associations of fruit set with flower visitation by wild insects in 41 crop systems worldwide. In contrast, fruit set increased significantly with flower visitation by honey bees in only 14% of the systems surveyed. Overall, wild insects pollinated crops more effectively; an increase in wild insect visitation enhanced fruit set by twice as much as an equivalent increase in honey bee visitation. Visitation by wild insects and honey bees promoted fruit set independently, so pollination by managed honey bees supplemented, rather than substituted for, pollination by wild insects. Our results suggest that new practices for integrated management of both honey bees and diverse wild insect assemblages will enhance global crop yields.

Human persistence depends on many natural processes, termed ecosystem services, which are usually not accounted for in market valuations. The global degradation of such services can undermine the ability of agriculture to meet the demands of the growing, increasingly affluent, human population (*1*, *2*). Pollination of crop flowers by wild insects is one such vulnerable ecosystem service (*3*), as the abundance and diversity of these insects are declining in many agricultural landscapes (*4*, *5*). Globally, yields of insect-pollinated crops are often managed for greater pollination through the addition of honey bees (*Apis mellifera* L.) as an agricultural input (Fig. 1) (*6*–*8*). Therefore, the potential impact of wild pollinator decline on crop yields is largely unknown. Nor is it known whether increasing application of honey bees (*9*) compensates for losses of wild pollinators, or even promotes these losses.

Fruit set, the proportion of a plant's flowers that develop into mature fruits or seeds, is a key component of crop yield (fig. S1). Wild insects may increase fruit set by contributing to pollinator abundance, species number (richness), equity in relative species abundance (evenness), or some combination of these factors. Increased pollinator abundance, and therefore the rate of visitation to crop flowers, should augment fruit set at a decelerating rate until additional individuals do not further increase fruit set (e.g., pollen saturation) or even decrease fruit set (e.g., pollen excess) (*10*–*12*). Richness of pollinator species should increase the mean, and reduce the variance, of fruit set (*13*) because of complementary pollination among species (*14*, *15*), facilitation (*16*, *17*), or "sampling effects" (*18*), among other mechanisms (*19*, *20*). Pollinator evenness may enhance fruit set via complementarity, or diminish it if a dominant species (e.g., honey bee) is the most effective pollinator (*21*). To date, the few studies on the importance of pollinator richness for crop pollination have revealed mixed results (*22*), the effects of evenness on pollination services remain largely unknown, and the impact of wild insect loss on fruit set has not been evaluated globally for animal-pollinated crops.

We tested four predictions arising from the assumptions that wild insects effectively pollinate a broad range of crops, and that their role can be replaced by increasing the abundance of honey bees in agricultural fields: (i) For most crops, both wild insect and honey bee visitation enhance pollen deposition on stigmas of flowers; (ii) consequently, for most crops, wild insect and honey bee visitation both improve fruit set; (iii) visitation by wild insects promotes fruit set only when honey bees visit infrequently (i.e., there is a negative interaction effect between wild insect visitation and honey bee visitation); and (iv) pollinator assemblages with more species benefit fruit set only when honey bees visit infrequently (i.e., there is a negative interaction effect between richness and honey bee visitation).

To test these predictions, we collected data at 600 fields on all continents, except Antarctica, for 41 crop systems (Fig. 1). Crops included a

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wide array of animal-pollinated, annual and perennial fruit, seed, nut, and stimulant crops; predominantly wind-pollinated crops were not considered (fig. S2 and table S1). The sampled fields were subject to a diversity of agricultural practices, including extensive monocultures and small or diversified systems (fig. S2 and table S1), fields stocked with low to high density of honey bees (Fig. 1 and table S2), and fields with low to high abundance and diversity of wild insects (fig. S3 and table S2). For each field, we measured flower visitation per unit of time (hereafter "visitation") for each insect species, from which we estimated species richness and evenness (*23*). We quantified pollen deposition for 14 systems as the number of pollen grains per stigma, and fruit set (fig. S1) for 32 systems as the percentage of flowers setting mature fruits or seeds. Spatial or temporal variation of pollen deposition and fruit set were measured as the coefficient of variation (CV) over sample points or days within each field (*10*). The multilevel data provided by fields within systems were analyzed with general linear mixed-effects models that included crop system as a random effect, and wild insect visitation, honey bee visitation, evenness, richness, and all their interactions as fixed effects. Best-fitting models were selected on the basis of the Akaike information criterion (AIC) (*23*).

In agreement with the first prediction, crops in fields with more flower visits received more pollen on stigmas, with an overall 74% stronger influence of visitation by honey bees than by wild insects (Fig. 2A and table S3). Honey bee visitation significantly increased pollen deposition (i.e., confidence intervals for individual regression coefficients, β_i, did not include zero) in 7 of 10 crop systems, and wild insects in 10 of 13 systems (fig. S4). Correspondingly, increased wild insect and honey bee visitation reduced variation in pollen deposition among samples (fig. S5).

Contrary to the second prediction, fruit set increased significantly with wild insect visitation in all crop systems, but with honey bee visitation in only 14% of the systems (Fig. 2B). In addition, fruit set increased twice as strongly with visitation by wild insects as with visitation by honey bees (Fig. 2A). These partial regression coefficients did not differ simply because of unequal abundance, nor because of disparate variation in visitation between wild insects and honey bees. In crop systems visited by both honey bees and wild insects, honey bees accounted for half of the visits to crop flowers [mean = 51%; 95% confidence interval (CI) = 40 to 62%], and among-field CVs for visitation by honey bees (mean = 73%; 95% CI = 57 to 88%) and by wild insects (mean = 79%; 95% CI = 62 to 96%) were equivalent. Furthermore, wild insect visitation had stronger effects than honey bee visitation, regardless of whether honey bees were managed or feral (fig. S6) and, comparing across systems, even where only wild insects or honey bees occurred (Fig. 2B). Wild insect visitation alone predicted fruit set better than did honey bee visitation alone ($\Delta_{\mathrm{AIC}} = 16$; table S4, model F versus model M). Correspondingly, the CV of fruit set decreased with wild insect visitation but varied independently of honey bee visitation (fig. S5).

Pollinator visitation affected fruit set less strongly than did pollen deposition on stigmas (compare regression coefficients in Fig. 2A). This contrast likely arose from pollen excess, filtering of pollen tubes by post pollination processes, and/or seed abortion (*11*, *24*), and so reflects pollination quality, in part. Intriguingly, the difference in coefficients between pollen deposition and fruit set for honey bees greatly exceeded that for wild insects (Fig. 2A); this finding indicates that wild insects provide better-quality pollination, such as greater cross-pollination (*14*, *16*, *17*, *19*). These results occurred regardless of which crop systems were selected (fig. S7), sample size (fig. S8), the relative frequency of honey bees in the pollinator assemblage (dominance) among systems, the pollinator dependence of crops, or whether the crop species were herbaceous or woody, or native or exotic (fig. S9). Poor-quality pollination could arise if foraging behavior on focal resources typical of honey bees (*16*, *17*) causes pollen transfer between flowers of the same plant individual or the same cultivar within a field, thereby limiting cross-pollination and increasing the incidence of self-pollen interference and inbreeding depression (*24*). The smaller difference in coefficients between pollen deposition and fruit set for wild insects, and the stronger effect of wild insect visitation on fruit set, suggest that management to promote diverse wild insects has great potential to improve the global yield of animal-pollinated crops.

The third prediction was also not supported. Fruit set consistently increased with visitation by wild insects, even where honey bees visited frequently (i.e., no statistical interaction; Fig. 2, A and C). In particular, the best-fitting model (lowest AIC) for fruit set included additive effects of visitation by both wild insects and honey bees (table S4, model P), which suggests that managed honey bees supplement the pollination service of wild insects but cannot replace it. Overall, visitations by wild insects and honey bees were not correlated among fields (fig. S10), providing no evidence either for

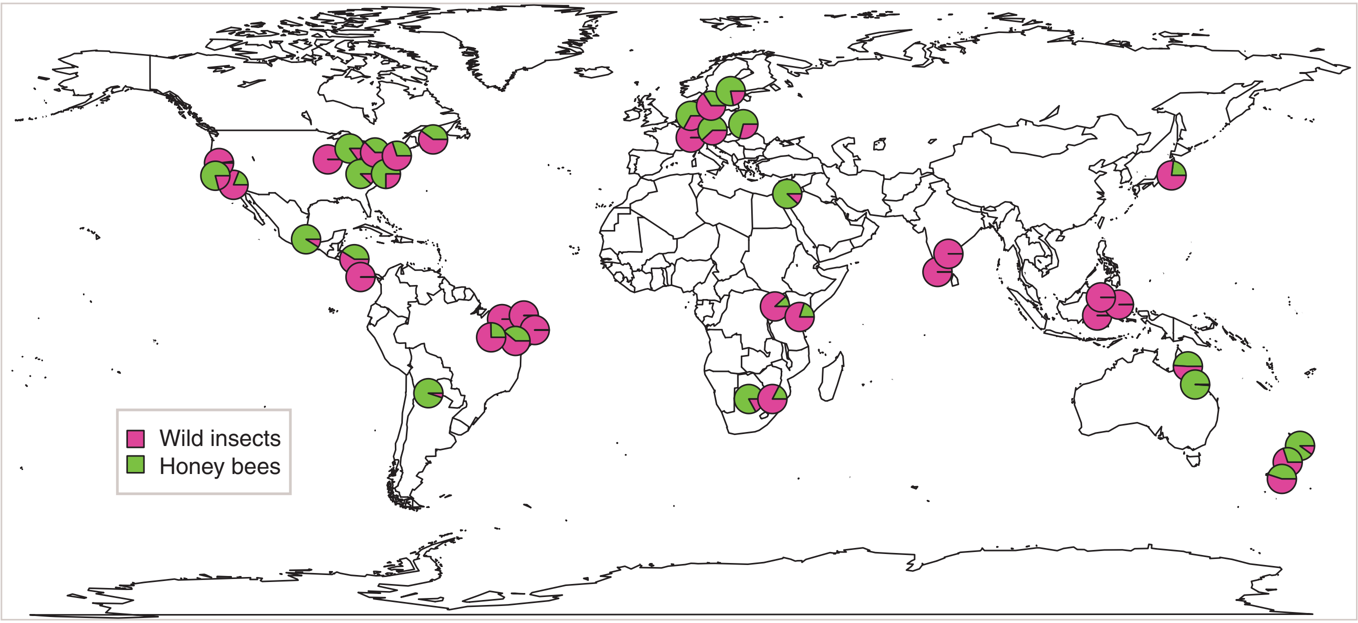


Fig. 1. Relative visitation by honey bees and wild insects to flowers of 41 crop systems on six continents. Honey bees occur as domesticated colonies in transportable hives worldwide, as a native species in Europe (rarely) and Africa, or as feral populations in all other continents except Antarctica.

competition for the resources obtained from crop flowers (pollen, nectar) or for density compensation (*13*) between wild insects and honey bees at the field scale. Even if honey bees displace wild insects (or vice versa) at the flower scale (*16*, *17*), this is unlikely to scale up to the field, as indicated by our data, if mass-flowering crops provide floral resources in excess of what can be exploited by local pollinator populations. Therefore, insect pollinators appear not to be limited by crop floral resources, but crop yield was commonly pollen-limited, as crops set more fruit in fields with more visitation by pollinators (Fig. 2).

Contrary to the fourth prediction, fruit set increased with flower-visitor richness independently of honey bee visitation (fig. S11). Correspondingly, the CVs of fruit set decreased with richness; in contrast, evenness did not affect the mean or CV of fruit set (figs. S12 and S13). Visitation by wild insects increased strongly with richness (Fig. 3) and improved model fit (lower AIC), even when richness was included in the model (table S4, model B versus model G). However, richness did not enhance model fit when added to a model with wild insect visitation (table S4, model F versus model G), which suggests that the effects of richness on fruit set reflect increased wild insect visitation (i.e., colinear effects; fig. S13). Like wild insect visitation (fig. S10), richness did not correlate with honey bee visitation (table S5). Previous studies have shown that agricultural intensification reduces both species richness of pollinator assemblages and wild insect visitation (*4*, *5*, *13*, *19*). Our results for multiple crop systems further demonstrate that fields with fewer pollinator species experience less visitation by wild insects and reduced fruit set, independent of species evenness or honey bee visitation. Globally, wild insect visitation is an indicator of both species richness and pollination services, and its measurement can be standardized easily and inexpensively among observers in field samples (*25*).

Large, active colonies of honey bees provide abundant pollinators that can be moved as needed, hence their appeal for pollination management in most animal-pollinated crops (*6*–*8*, *26*). By

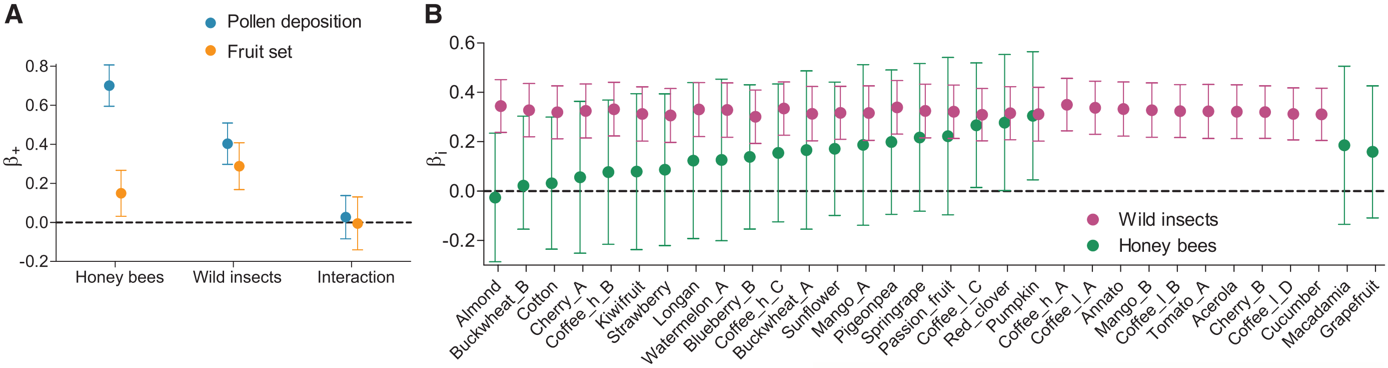
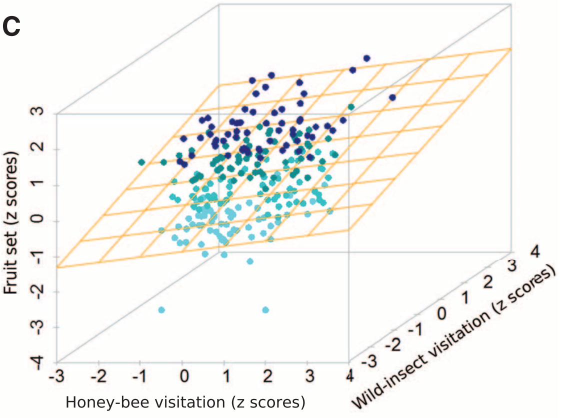


Fig. 2. Wild insect visitation to crop flowers enhances reproduction in all crops examined (regression coefficient $\beta_i > 0$), whereas honey bee visitation has weaker effects overall. (**A**) Overall partial regression coefficients ($\beta_+ \pm$ 95% CI) for the direct and interacting effects of visitation by wild insects and honey bees on pollen deposition or fruit set (models R and Q in tables S3 and S4, respectively). (**B**) Slopes ($\beta_i \pm$ 95% CI) represent the effects of visitation by wild insects or honey bees on fruit set for individual crop systems. Cases at the right are systems in which only wild insects or only honey bees were present. Data from individual crop systems were standardized by *z* scores prior to analysis, permitting comparison of regression coefficients in all panels. Letters after crop names indicate different regions (table S1); for example, Mango_A and Mango_B are located in South Africa and Brazil, respectively. (**C**) Given the absence of interaction between the effects of visitation by wild insects and honey bees, maximum fruit set is achieved with high visitation by both wild insects and honey bees (upper right area of graph). The plane in orange is the overall regression (model P in table S4; the inclination of the surface in the *y* and *x* directions reflects the β_+ for visitation of wild insects and honey bees, respectively), and each point is a field in a crop system (fruit set increases from cyan to dark blue).



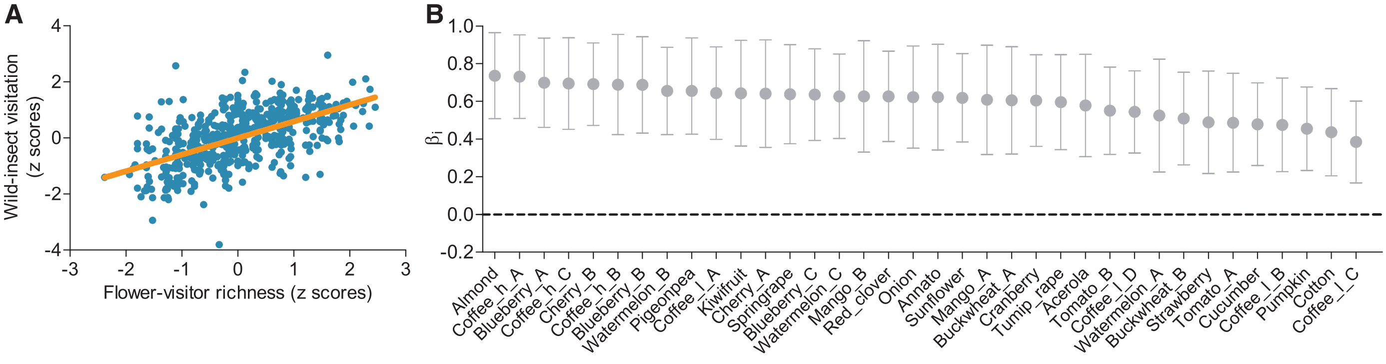


Fig. 3. Globally, rate of visitation to crop flowers by wild insects increases with flower-visitor richness. (**A**) The line is the overall regression, and each point is a field in a crop system. (**B**) Slopes ($\beta_i \pm$ 95% CI) represent the effect of richness on wild insect visitation for individual crop systems. Data from individual crop systems were standardized by *z* scores prior to analysis (after log-transformation for visitation), permitting direct comparison of regression coefficients.

comparison, methods for maintaining diverse wild insects for crop pollination are less developed, and research on such pollination services is more recent (*3*, *16*, *17*, *20*, *26*, *27*) (table S1). Although honey bees are generally viewed as a substitute for wild pollinators (*3*, *6*–*8*), our results show that they neither maximize pollination nor fully replace the contributions of diverse wild insect assemblages to fruit set for a broad range of crops and agricultural practices on all continents with farmland. These conclusions hold even for crops stocked routinely with high densities of honey bees for pollination, such as almond, blueberry, and watermelon (Fig. 2 and table S2). Dependence on a single species for crop pollination also carries the risks associated with predator, parasite, and pathogen development (*4*, *20*, *28*).

Our results support integrated management policies (*29*) that include pollination by wild insects as ecosystem service providers, along with managed species—such as honey bees, bumble bees (*Bombus* spp.), leafcutter bees (*Megachile* spp.), mason bees (*Osmia* spp.), and stingless bees (Meliponini)—as agricultural inputs, where they are not invasive species. Such policies should include conservation or restoration of natural or seminatural areas within croplands, promotion of land-use heterogeneity (patchiness), addition of diverse floral and nesting resources, and consideration of pollinator safety as it relates to pesticide application (*3*, *16*, *17*, *20*, *27*). Some of these recommendations entail financial and opportunity costs, but the benefits of implementing them include mitigation against soil erosion as well as improvements in pest control, nutrient cycling, and water-use efficiency (*30*). Without such changes, the ongoing loss of wild insects (*4*, *5*) is destined to compromise agricultural yields worldwide.

References and Notes

1. L. Roberts, *Science* **333**, 540 (2011).
2. D. Tilman *et al.*, *Science* **292**, 281 (2001).
3. A.-M. Klein *et al.*, *Proc. R. Soc. London Ser. B* **274**, 303 (2007).
4. S. G. Potts *et al.*, *Trends Ecol. Evol.* **25**, 345 (2010).
5. L. A. Garibaldi *et al.*, *Ecol. Lett.* **14**, 1062 (2011).
6. R. A. Morse, *Trends Ecol. Evol.* **6**, 337 (1991).
7. R. M. Goodwin, H. M. Cox, M. A. Taylor, L. J. Evans, H. M. McBrydie, *New Zeal. J. Crop Hort.* **39**, 7 (2011).
8. R. R. Rucker, W. N. Thurman, M. Burgett, *Am. J. Agric. Econ.* **94**, 956 (2012).
9. M. A. Aizen, L. D. Harder, *Curr. Biol.* **19**, 915 (2009).
10. L. A. Garibaldi, M. A. Aizen, A.-M. Klein, S. A. Cunningham, L. D. Harder, *Proc. Natl. Acad. Sci. U.S.A.* **108**, 5909 (2011).
11. N. P. Chacoff, M. A. Aizen, V. Aschero, *Proc. R. Soc. London Ser. B* **275**, 907 (2008).
12. W. F. Morris, D. P. Vázquez, N. P. Chacoff, *Ecology* **91**, 1276 (2010).
13. R. Winfree, C. Kremen, *Proc. R. Soc. London Ser. B* **276**, 229 (2009).
14. P. Hoehn, T. Tscharntke, J. M. Tylianakis, I. Steffan-Dewenter, *Proc. R. Soc. London Ser. B* **275**, 2283 (2008).
15. N. Blüthgen, A.-M. Klein, *Basic Appl. Ecol.* **12**, 282 (2011).
16. L. G. Carvalheiro *et al.*, *Ecol. Lett.* **14**, 251 (2011).
17. S. S. Greenleaf, C. Kremen, *Proc. Natl. Acad. Sci. U.S.A.* **103**, 13890 (2006).
18. B. J. Cardinale *et al.*, *Nature* **443**, 989 (2006).
19. A.-M. Klein, C. Müller, P. Hoehn, C. Kremen, in *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective*, D. E. Bunker, A. Hector, M. Loreau, C. Perrings, S. Naeem, Eds. (Oxford Univ. Press, Oxford, 2009), pp. 195–208.
20. T. Tscharntke, A.-M. Klein, A. Kruess, I. Steffan-Dewenter, C. Thies, *Ecol. Lett.* **8**, 857 (2005).
21. H. Hillebrand, D. M. Bennett, M. W. Cadotte, *Ecology* **89**, 1510 (2008).
22. B. J. Cardinale *et al.*, *Nature* **486**, 59 (2012).
23. See supplementary materials on *Science* Online.
24. M. A. Aizen, L. D. Harder, *Ecology* **88**, 271 (2007).
25. C. Kremen, K. S. Ullman, R. W. Thorp, *Conserv. Biol.* **25**, 607 (2011).
26. K. S. Delaplane, D. F. Mayer, *Crop Pollination by Bees* (CABI, New York, 2000).
27. C. Kremen *et al.*, *Ecol. Lett.* **10**, 299 (2007).
28. R. Winfree, N. M. Williams, J. Dushoff, C. Kremen, *Ecol. Lett.* **10**, 1105 (2007).
29. A. Aebi *et al.*, *Trends Ecol. Evol.* **27**, 142 (2012).
30. S. D. Wratten, M. Gillespie, A. Decourtye, E. Mader, N. Desneux, *Agric. Ecosyst. Environ.* **159**, 112 (2012).

Acknowledgments: Funding acknowledgments and author contributions are listed in the supplementary materials. The data used in the primary analyses are available in the supplementary materials, including tables S1 and S2.

Supplementary Materials

www.sciencemag.org/cgi/content/full/science.1230200/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S13
Tables S1 to S5
References (*31*–*79*)
Database S1

14 September 2012; accepted 5 February 2013
Published online 28 February 2013;
10.1126/science.1230200

Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function

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Using historic data sets, we quantified the degree to which global change over 120 years disrupted plant-pollinator interactions in a temperate forest understory community in Illinois, USA. We found degradation of interaction network structure and function and extirpation of 50% of bee species. Network changes can be attributed to shifts in forb and bee phenologies resulting in temporal mismatches, nonrandom species extinctions, and loss of spatial co-occurrences between extant species in modified landscapes. Quantity and quality of pollination services have declined through time. The historic network showed flexibility in response to disturbance; however, our data suggest that networks will be less resilient to future changes.

Almost 90% of flowering plant species, including many important crop species (*1*), rely on animal pollinators (*2*). Plant-pollinator interaction networks may be particularly susceptible to anthropogenic changes, owing to their sensitivity to the phenology, behavior, physiology, and relative abundances of multiple species (*3*). Alternatively, the overall structure of plant-pollinator networks might be robust to perturbations because of a high degree of nestedness and redundancy in interactions (*4*).

Several authors have speculated about how changes in biodiversity (*5*) and phenology (*6*–*8*) might translate into changes in the structure (*9*, *10*) and stability (*11*) of complex interaction networks. However, there has been a lack of historical data on plant-pollinator networks and phenologies for both plants and insects in the same community. By using an extensive and unique data set, we were able to examine changes in plant-pollinator network structure and phenologies of forbs and bees across more than a century of anthropogenic change.

In the late 1800s, Charles Robertson meticulously collected and categorized insect visitors to plants, as well as plant and insect phenologies, in natural habitats near Carlinville, Illinois, USA (*12*–*14*). Over the next century, this region experienced severe habitat alteration, including conversion of most forests and prairies to agriculture, and moderate climatic warming of 2°C in winter and spring. In 2009 and 2010, we revisited the area studied by Robertson and re-collected data on the phenologies and structure of a subset of this network—26 spring-blooming forest understory forbs and their 109 pollinating bees (*15*). Hence, we could quantify changes in network structure, local bee diversity, and phenologies of forbs and bees. Further analyses and a null model determined the degree to which changes in network structure and bee diversity were attributed to species' traits, phenological mismatches, and land-use factors that spatially separate interacting species. To examine shifts in the quantity of pollinator services, we used a second historical data set from Carlinville collected in the early 1970s (*16*), examining the diversity and visitation rate of bees to the most important floral resource in this network (*Claytonia virginica*).

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www.sciencemag.org/cgi/content/full/science.1230200/DC1

Supplementary Materials for

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Published 28 February 2013 on *Science* Express
DOI: 10.1126/science.1230200

This PDF file includes:

Materials and Methods
Supplementary Text
Figs. S1 to S13
Tables S1 to S5
References (*31*–*79*)
Caption for Database S1

Other Supplementary Material for this manuscript includes the following:

Database S1 [Database_S1.txt]

Materials and Methods

Crop systems and pollinator species

We sampled 600 fields of 41 crop systems in 19 countries from all continents except Antarctica (Fig. 1 and table S1). Crop systems are defined as a given crop species in a particular region subject to similar management (table S1). We restricted our study to field data to analyze the impact of wild insect loss on a global scale. We collected data matching the following selection criteria: (1) data sampled from at least three spatially separated fields, (2) direct standardized observations of insect species visiting crop flowers in the sampled fields, and (3) a standardized estimate of pollination success, i.e. pollen deposition and (or) seed or fruit set, for sampled fields. The crops considered include a wide array of annual and perennial fruit, seed, nut, and stimulant crops that are pollinator dependant to some degree (fig. S2 and table S1). Crops pollinated primarily by wind were not studied. Crop systems were selected to represent the spectrum of management practices (traditional, intensive agriculture, organic certified agriculture, sun *vs.* shade), landscape settings (cleared, simple, complex landscapes), crop species and varieties (growth form, breeding system, pollinator dependence), abiotic and biotic variables, and we also included crops in their native and non-native (exotic crops) range (fig. S2 and table S1). Fields also encompassed a wide contrast of pollination management practices, from high densities of honey bees managed exclusively for pollination to fields with low densities of honey bees. For example, in California (USA), surveyed fields ranged from extensive monocultures of almonds with honey-bee stocking rates of 6.5 hive ha^{-1} to small fields of organic-certified tomato production without honey-bee management (table S1). We also included examples of traditional agriculture in diversified landscapes, such as pumpkin growing in smallholder vegetable gardens of Indonesia (fig. S2 and table S1).

Apis mellifera was the only managed pollinator, except for coffee_ 1_B and coffee_1_D (lowland coffee in India), for which *Apis cerana indica* was the common managed pollinator species. For coffee_1_B and coffee_1_D we excluded *A. cerana indica* from the analysis to evaluate the relation of fruit set to wild insects only, and we use "honey bee" in reference to only *Apis mellifera*. Managed colonies of honey bees were present in the landscapes of 52% of the systems, and in half of those systems colonies were managed purposefully for pollination of the studied crop (table S2).

Our study included many wild insect species, and fields with contrasting diversity and abundance of wild insects (fig. S3 and table S2). Most of the wild insects observed visiting flowers on the 41 crop systems were bees (Hymenoptera: Apoidea, Apiformes). Bee taxa observed regularly included stingless bees (Apidae: Meliponini), bumble bees (Apidae: *Bombus* spp.), apex-furrowed (or sweat) bees (Halictidae), plasterer bees (Colletidae), carpenter bees (Apidae: Xylocopini), small carpenter bees (Apidae: Ceratinini), *Andrena* bees (Andrenidae) and the giant honey bee (*Apis dorsata*) (bee taxonomy follows (*31*)). In some crop systems, syrphid flies (Diptera: Syrphidae), other flies, ants (Hymenoptera: Formicidae), and various beetle species (Coleoptera) occurred as dominant wild flower visitors (table S2).

In some agricultural landscapes, our samples may include more fields with high abundance of wild insects than is typical, because we sought to explore the roles of wild pollinators. This possibility is most likely for crops grown typically as extensive monocultures, with an attendant low abundance of wild insects. Our samples covered these situations, but also included fields with higher abundances of wild insects. This sampling emphasis does not invalidate the conclusions drawn from our study. On the contrary, it provided the contrast required to quantify the general relation of fruit set to flower visitation and the consequences of the loss of wild insects, rather than to quantify the relative importance of honey bees and wild insects for current agricultural production (e.g. tonnes per country). In addition, analysis of a subset of crop systems produced qualitatively similar results to the analysis of all systems (fig. S7), indicating that our conclusions are not biased by selection of crop systems. Furthermore, the relations of fruit set to visitation by honey bees and wild insects did not vary with sample sizes of individual crop systems (fig. S8), the relative frequency of honey bees in the pollinator assemblage (dominance), the pollinator dependence of crops, or whether the crop species were herbaceous or woody, native or exotic (fig. S9).

Variables

In multiple fields of each of the 41 animal-pollinated crop systems (Fig 1 and tables S2 and S3), we measured insect visitation rate, pollen deposition, and (or) fruit set to quantify different aspects of reproduction. Visitation rate (hereafter visitation) to crop flowers per insect species (or morphospecies) was measured as the number of visits per unit time and flower number. In nine systems, namely, blueberry_A, blueberry_C, buckwheat_A, cherry_A, cranberry, pigeon pea, strawberry, turnip rape, and watermelon_A (table S1), visitation was standardized with respect to a measure other than flower number (such as number of branches or standardized area), because, for example, some crops have hundreds of small flowers per plant, so visits could not be counted accurately per flower. This methodological difference should not introduce any bias in our analyses, as we focused on relative changes within each system through z-scores (see below). We analyzed visitation by honey bees and all other insects (referred to as wild insects) separately. Our analyses treated honey bees as a single group, because workers from managed or feral colonies cannot be distinguished in field observations of crop flowers.

We estimated richness as the number of species of flower visitors per field (mean = 9 species, SE = 1 species). We estimated five indices of evenness, because various indices of evenness have different properties and weight rare and abundant species differently. In particular, we employed the four indices proposed by (*32*), $E_{1/D}$, E’, Eq, Evar, and the widely used Pielou’s *J* (*33*). As the five indices showed similar patterns (fig. S12), we present results for only Evar, as recommended by (*32*). We included honey bees in estimates of both species richness and evenness.

Pollen deposition was measured in 14 crop systems as the number of crop pollen grains deposited per stigma in several open-pollinated flowers per field, except for four systems (blueberry_A, cranberry, tomato_B, and watermelon_B) for which aggregate pollen deposition for each pollinator species was measured as the product of the number of visits and the mean number of pollen grains deposited during a single visit (table S1). The latter systems showed the same patterns as those for which pollen deposition was measured on open-pollinated stigmas (fig. S4). Mature fruit set, the percentage of flowers setting fruits or seeds at ripeness or harvest, was measured in 32 crop systems (table S1 provides detailed information about the systems in which we measured pollen deposition and [or] fruit set). Fruit set was the main measure of pollination success and is an important component of fruit or seed yield per plant (yield = number × weight per fruit; see Fig S1). Given that we measured fruit set in several plants or plots per field (table S1) subjected to open pollination, our results properly represent mean (or coefficient of variation, see below) field conditions and are not biased by resource translocation within the plants to different flowers. For systems for which visitation, pollen deposition or fruit set data were available for more than one year, we selected the year with most fields as the first criterion and most within-field measures as the second criterion to avoid pseudo-replication.

We assessed the influences of predictors (see Statistical analyses below) on both mean fruit set (or pollen deposition) per field, and its variation, as measured by the coefficient of variation (CV) (*5*). We estimated the temporal or spatial CV using data from different days during the flowering season or from different plant individuals or transects in each field, respectively, depending on data availability for the system (table S1). Observations for each variable (y) in each field (j) in each system (i) were standardized using z-scores ($\frac{y_{ji}-\overline{y}_i}{SD_i}$) to allow comparison, despite contrasting means ($\overline{y}_i$) and standard deviations (SD_i) among systems, and differences in methodology (table S1 shows additional methods for each system). Unlike other standardizations (such as logarithms), z-scores do not modify the functional form (e.g. linear or non-linear) of the relation between response and predictor variables.

Additional information concerning unpublished studies

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

Insect visitation to flowers of acerola, annatto and cotton (tables S1 and S2) was assessed following the same general methodology by choosing four (annatto) to five (acerola and cotton) plants at random, monitoring floral visitors during a fixed period, and counting the flowers they visited. Plants were monitored at different times of the day according to anthesis and floral longevity for each plant species. Acerola flowers were monitored five times per day (6, 9, 12, 15, 18 h), cotton flowers six times (7, 9, 11, 13, 15, 17 h) and annatto seven times (5, 6, 7, 8, 9, 10, 11 h) during at least six days per month during the blooming season. Each observation lasted 15 min and floral visitors were recorded, captured using sweep nets, and fixed in ethyl acetate. Later, they were pinned and identified. Pollination success was assessed as the percentage of flowers setting fruits at harvest.

In the Cucumber system in Indonesia (tables S1 and S2), insect visitation to flowers was assessed in 2011 on 25 fields. Visitors to five plants per field were counted during a

5-min observation period per day, between 9 and 14h during three days within the two-week flowering period. All insects were caught for identification. Fruit set was calculated as the ratio of the number of harvested fruits to the number of flowers.

In the Mango_A system in South Africa (tables S1 and S2), insect visitation was assessed by walking slowly (0.1-0.2 $m^2 s^{-1}$) along a 60 x 2 m transect composed of two linear 30 m sections parallel to the crop rows. All flower visitors that contacted the stigma or anthers were counted for a minimum of 5s. Visitation was surveyed during peak flowering season (August and September 2009; two surveys per plot about four weeks apart) in orchards with >75% of inflorescences in the plot in bloom, on warm, still, dry days (temperatures 20 – 39 °C, wind speed < 4 $km.h^{-1}$) between 8 and 16h. When possible, flower visitors were collected, sorted to morphospecies and subsequently sent to professional taxonomists for identification. Farmers counted the commercially suitable fruits.

In the Pigeon pea system in Kibwezi District (Eastern Kenya; tables S1 and S2), bees visiting pigeon-pea flowers at each field were recorded along three, 100-m transects (2 m wide) laid in a North to South orientation, each separated by >10 m. Each transect was sampled for insects for 10 min, twice a day (between 9 and 16h) once weekly from April to June 2009. All visitors were identified in the field to species, or recognizable taxonomic level. Voucher specimens of unknown species were taken to the National Museums of Kenya for specialist identification. No floral visitors were observed other than insects. Fruit set attributable to insects was quantified for the plants at 5, 50 and 95m along each transect. Each selected plant had at least two 50-cm branches with unopened flower buds. The pods set on open-pollinated plants were counted at the end of the experiment.

In the Watermelon_A system (tables S1 and S2), data were collected during May-June 2011 in the Judean Foothills, a Mediterranean region in central Israel. The cultivar ‘Malali’, which has hermaphrodite and male flowers, was grown for seed production and studied in 5 fields located >1 km apart. Weather conditions were almost always suitable for bee activity, with only a single rainy day and temperatures constantly above 20°C during daylight. Most farmers in the region do not rent hives for watermelon pollination, but honey bees from nearby hives are usually abundant (feral colonies are absent). A few hives were placed along the edge of one field. Bee visits to randomly chosen clusters of 1-2 hermaphrodite and 3-5 male flowers were recorded during 3-min observations conducted 2-4 times every hour from 8 to 14 h during three days. The main wild bee visitors at all fields were *Lasioglossum malachurum* and *L. politum*, which are small semi-social species. Fruit set by open-pollinated flowers was evaluated for 10-20 randomly selected hermaphrodite flowers in each field. All other hermaphrodite flowers and previously set fruits on the experimental plants were removed on the day of the experiment. Monitored flowers that developed into mature fruits and were not aborted 30 days post-anthesis were considered as setting fruits.

In the Watermelon_C system (tables S1 and S2), visitation was measured on 3 days per field during bloom in central California, USA during June-August 2010. Observers used visual scans along a 50-m transect in the crop row bordering a field margin. The transect was sampled for 17 min four times on each date. After each scan, bees visiting watermelon flowers were collected for voucher specimens. The pollination function provided per flower visit per bee species was estimated by counting pollen grains deposited by individual bees during single visits to unvisited flowers. Stigmas were stained using fuchsin dye and pollen grains counted under a light microscope (*34*).

In the Blueberry_A system (tables S1 and S2), insect visitation was measured by walking slowly along a 200-m transect comprising four 50-m segments of blueberry bush rows. Walking pace was standardized to 10 m min^{-1}. During an observation period, observers scanned all visible flowers along one side of a row for bees, so that a given cluster of flowers was observed only once per observation bout. Both native bees and honey bees were recorded. Observation was repeated three times during a field-visit day for a total of 60 min. Each field was visited three times during 2010. All data were collected on days with sunny to partly cloudy skies and temperatures above 17ºC by 12h. Pollen deposition per visit was measured by offering unvisited flowers to bees foraging on blueberry bushes within the same planting block as the transect. After a single visit, the stigma was collected and stained with aniline blue. Pollen grains attached to the stigma by pollen tubes and pollen grains elsewhere on the slide with pollen tubes were counted.

In the Blueberry_C system (tables S1 and S2), at each field, all bees visiting blueberry flowers were collected by net for 1 h on three days corresponding to early, middle and late flowering of the crop during 2009. All collections were done between 10 and 15h on sunny and light-overcast days with temperatures >16 °C. On the same days, 45 blueberry stigmas were harvested per field and stained with basic fuchsin. Pollen tetrads deposited on stigmas were counted to determine the percent pollination of each blueberry field.

In Cranberry system (tables S1 and S2), all insects observed visiting flowers along two 1 x 60-m transects were collected using a hand net at each field. One transect was adjacent and parallel to natural habitat, whereas the second one was located in the interior of the field. Transects were walked for 30 min two times per day for a total of 120 min per field per day. Each field was visited twice during 2009. Pollen deposition was measured by presenting unvisited flowers to foraging bees. After a single visit, stigmas were stained with aniline blue dye and the number of pollen grains on the stigma and in the sample but with pollen tubes were counted.

In the Cherry_B system (tables S1 and S2), insect visitation to flowers and fruit set were measured during 2011 on experimentally planted, 7-year-old trees (*35*). Insect visitation was estimated per field using 30 min of video (Sony HDR-CX115E), recorded at three times (10-12, 12-14, 14-16 h) and each recording time on a separate day. After recording, vouchers of flower-visiting insects were captured with sweep nets. Fruit set was assessed on 4 trees per field as the percentage of flowers developing into swollen green fruit (~1 month after flowering period).

In the Pumpkin system (tables S1 and S2), insect visitation to flowers was assessed by walking slowly between two rows of plants along a 45-m transect and surveying the bees visiting flowers in both rows. Visitation was estimated at three transects per field, every two weeks during the blooming period (mid-July through August) for a total of three surveys per field. Surveys were conducted on still, dry days from 6 - 11h, or until flowers closed. In the same fields, *Cucurbita pepo* var. Gladiator transplants were planted into commercial fields two weeks after farmers had planted seeds, so that fruit set was recorded for a single variety.

In the Red clover system (tables S1 and S2), insect visitors to flowers were counted as described in (*36*). Fruit (seed) set was estimated from 20 flower heads per field as the proportion of flowers on a flower head that produced mature seeds. Seed set estimates were compensated for different levels of seed predation between fields and flower heads by excluding flowers that had been attached by seed predating *Apion* weevils (*37*).

In the Tomato_B system (tables S1 and S2), insect visitors to flowers were counted as described in (*38*). Pollen deposition was measured by presenting unvisited flowers to foraging bees. After a single visit, stigmas were stained with aniline blue dye and the pollen grains were counted.

Statistical analyses

We analyzed general linear mixed-effects models of the influences of species richness, species evenness, visitation rate ("visitation") by wild insects, visitation by honey bees, and all interactions (double, triple, and quadruple) on pollen deposition or fruit set and their CVs using R software (version 2.15.1, lme4 package, lmer function, Gaussian error distribution: this approach produces similar results to Bayesian hierarchical models when uninformative priors are employed, especially with large samples, as in our case) (*39–42*). Of particular interest was whether visitation by wild insects and honey bees affected reproduction additively or had interacting effects. A positive statistical interaction would suggest synergistic influences (facilitation) of wild insects and honey bees on pollination, i.e. the effects of wild insects on fruit set are higher when honey bees are more abundant. A negative interaction would suggest antagonistic influences, which would be expected if high abundance of honey bees maximizes pollination and therefore could be used to replace the services provided by wild insects, or vice versa. In contrast, the absence of interaction indicates that managed honey bees supplement, rather than substitute for, pollination provided by wild insects (see predictions in the main text).

We used AIC to select best-fitting models for combinations of the four predictor variables (tables S3, S4) to test the four predictions outlined in the main text (*43, 44*). AIC values (tables S3, S4) were obtained based on maximum-likelihood estimates of regression coefficients, because models differed in the fixed structure but shared the same random structure (random intercepts for different crop systems, see below), whereas parameter estimates for final models presented in figures were obtained using the restricted maximum likelihood method, as recommended by (*45*). Given the large number of fields (table S1), no correction was needed for small samples, AICc (*43*), and this correction showed no clear improvement in simulation studies despite low ratio of independent observations to estimated parameters (*44*). For visitation, we tested models with both linear and curvilinear (i.e., predictor variables log-transformed prior to z-transformation) forms; a curvilinear relation would be expected from a positive, but decelerating relation of fruit set to visitation (*10–12*). We found no clear improvement (i.e. lower AIC) when considering curvilinear relations in mixed-effect models, and therefore we present only models with linear forms (tables S3, S4). For models with CV as the response variable, the inclusion of an additional factor to differentiate trends between temporal and spatial CV increased model AIC and therefore was excluded from analyses.

In general, mixed-effects models are effective for integrated analysis of data from different studies (*42, 46, 47*). By including crop system as a random variable, our models estimated different intercepts (α_i) for each system (i) to account for the hierarchical data structure and differences among systems (random intercept models) (*40-42*). Each overall partial regression coefficient (β_+) was considered a fixed effect reflecting the influence of a predictor (e.g. visitation by wild insects) on fruit set (or pollen deposition) over all crop systems. Inclusion of system-specific partial regression coefficients (β_i) for one of the four predictor variables in this complete model selection analysis (tables S3, S4) would be an arbitrary decision; whereas inclusion of system-specific partial regression coefficients for each predictor (and interactions) would result in over-parameterization (we estimated β_i in reduced models as described below). In all the analyses described above we included only crop systems for which both wild insects and honey bees were active flower visitors, i.e. at least 5% of total visitation by either group. We tested the Gaussian and homoscedasticity assumptions for the standardized residuals of the models (*45*) with graphical analyses and Kolmogorov-Smirnov tests (Type I error rate = 0.05) and these assumptions were valid in all cases.

To quantify variation among crop systems in the influences of individual predictor variables (wild-insect visitation, honey-bee visitation, species richness, or species evenness) on fruit set, pollen deposition and their CVs, we estimated intercepts (α_i) and slopes (β_i) for each system (i) (*40*). These estimates were appropriate, as models with interactive effects did not fit better (i.e. lower AIC) than the same models without interactions (tables S3, S4). In these general linear mixed-effects models, the overall slope (μ_β) reflects a weighted average over crop systems (β_i), where the relative influence of each system increases with the precision of its local model fit and its sample size (*40-42*). These models also allowed inclusion of data from systems for which either honey bees or wild insects were the only active flower visitors (Fig. 2B).

To understand the spatial association of honey bees and wild insects, we modeled visitation by wild insects as a function of visitation by honey bees with the same hierarchical models and estimated different α_i and β_i for each system (i). A negative β_i could indicate spatial segregation caused by competition for resources, or that farmers use more honey bees at fields with fewer wild insects.

Supplementary Text

Full acknowledgements

The authors declare no competing financial interests. This research was funded by Agencia Nacional de Promoción Científica y Tecnológica (PICT 01300), Consejo Nacional de Investigaciones Científicas y Técnicas (PIP 114-201101-00201, PIP 112-200801-01623), CNPq Brasília-Brazil (305062/2007-7), Fundação de Amparo a Pesquisa do Estado da Bahia (FAPESB - ET 33/2004), German Academic Exchange Service, Germany Science Foundation (KL 1849/4-1, KL 1849/10-1, TS 45/32-1), Global

Environment Research Fund (S-9) of the Ministry of the Environment of Japan, EU FP6 project ALARM (GOCE-CT-2003-506675, http://www.alarmproject.net), EU FP7 project STEP (244090, www.STEP-project.net), EU FP 7 project SCALES (226852, http://www.scales-project.net/), Israel Science Foundation (919/09), Israel Ministry of Agriculture (824-0112-08), National Science Foundation of the United States (BIO-DEB 0554790 and 0516205), Natural Sciences and Engineering Research Council of Canada, Projeto Conservação e Utilização Sustentável da Diversidade Biológica Brasileira (PROBIO - Convênio: 0126.00/04), Swedish Research Council Formas, Swiss National Science Foundation (FRAGMENT, 3100A0-127632), Universidad de Buenos Aires (UBACYT 20020100300014), Universidad Nacional del Comahue (B152/04), Universidad Nacional de Río Negro (PI 40-B-259), and United States Department of Agriculture (NIFA-AFRI 2009-65104-05782, Multi-state project 08204). L.A.G. and A.M.K. compiled data, L.A.G. and L.D.H. analyzed data, L.A.G., I.S.D., R.W., M.A.A., R.B., S.A.C., C.K., L G.C, L.D.H. and A.M.K discussed and revised earlier versions of the project and manuscript. The authors named between O.A. and N.W., are listed alphabetically, as they contributed equally, gathering field data, providing several important corrections to subsequent manuscript drafts, and discussing ideas.

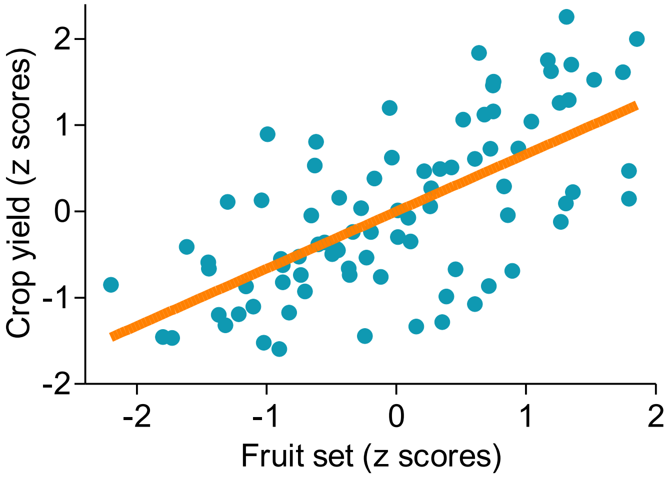

Fig. S1

Crop yield consistently increased with fruit set ($\beta_+ = 0.67$, $CI_{95\%} = 0.50 - 0.82$) across 85 agricultural fields from six crop systems for which yield data were available (namely, Cucumber, Mango_A, Pumpkin, Red clover, Spring rape, and Strawberry; see Table S1). Yield was measured as kg of harvest (fruits or seeds) per hectare for Mango_A, Red clover, and Strawberry, and as kg of harvest per plant for Cucumber, Pumpkin, and Spring rape. Data from individual crop systems were analyzed with a general linear mixed-effect model and standardized by z-scores prior to analysis.
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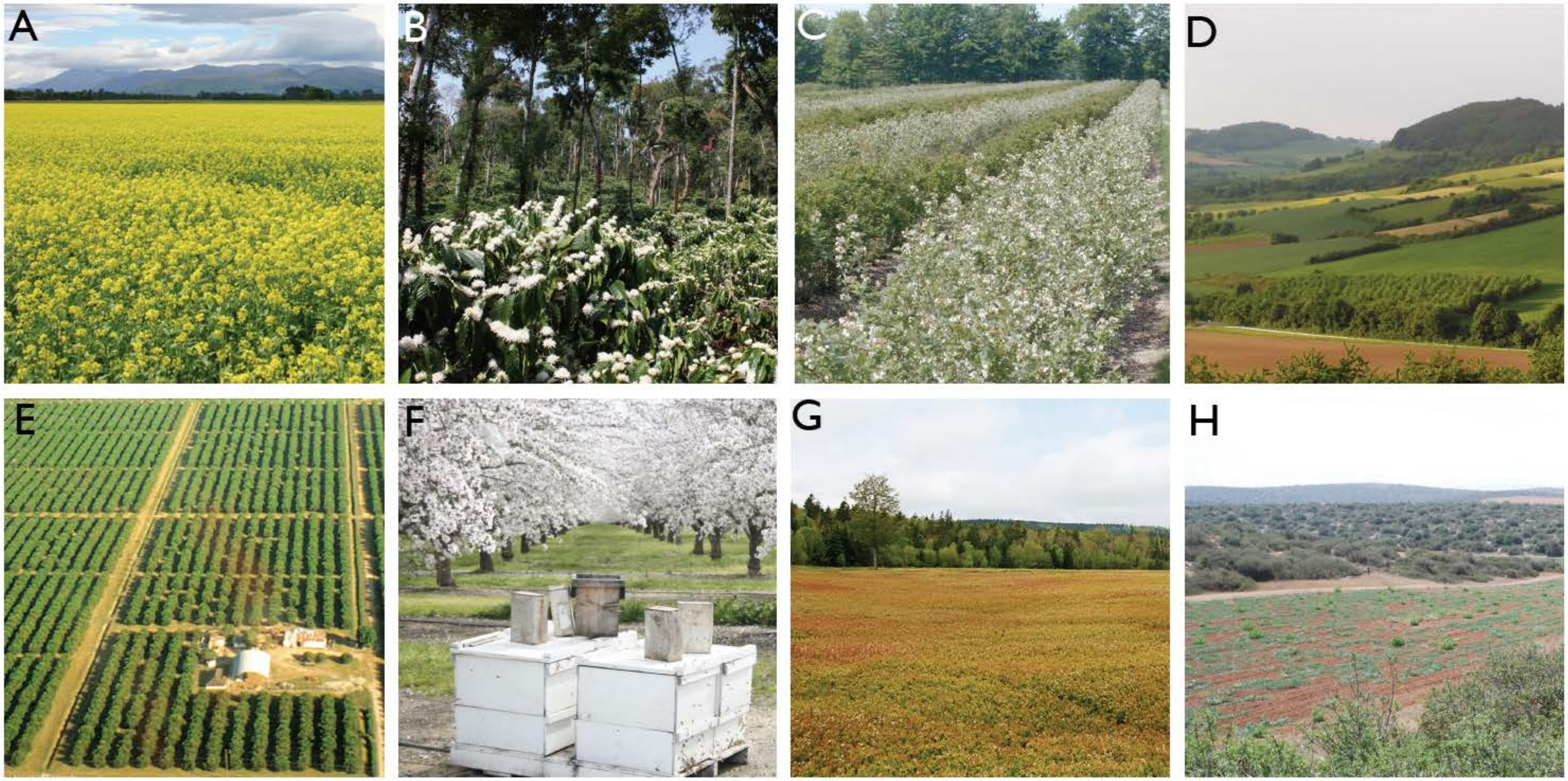

Fig. S2

Examples of crop systems reported in table S1. (**A**) Turnip rape field in New Zealand. (**B**) Coffee grown under native forest shade in India. (**C**) Highbush blueberry field with two cultivars that differ in their bloom phenology in USA. (**D**) Cherry orchard (after bloom; in the lower half of the picture) in a heterogeneous landscape in Germany. (**E**) Grapefruit plantation in Argentina. (**F**) Almond orchard with managed honey bees in USA. (**G**) Commercial lowbush blueberry field in Canada. (**H**) Watermelon field in Israel.

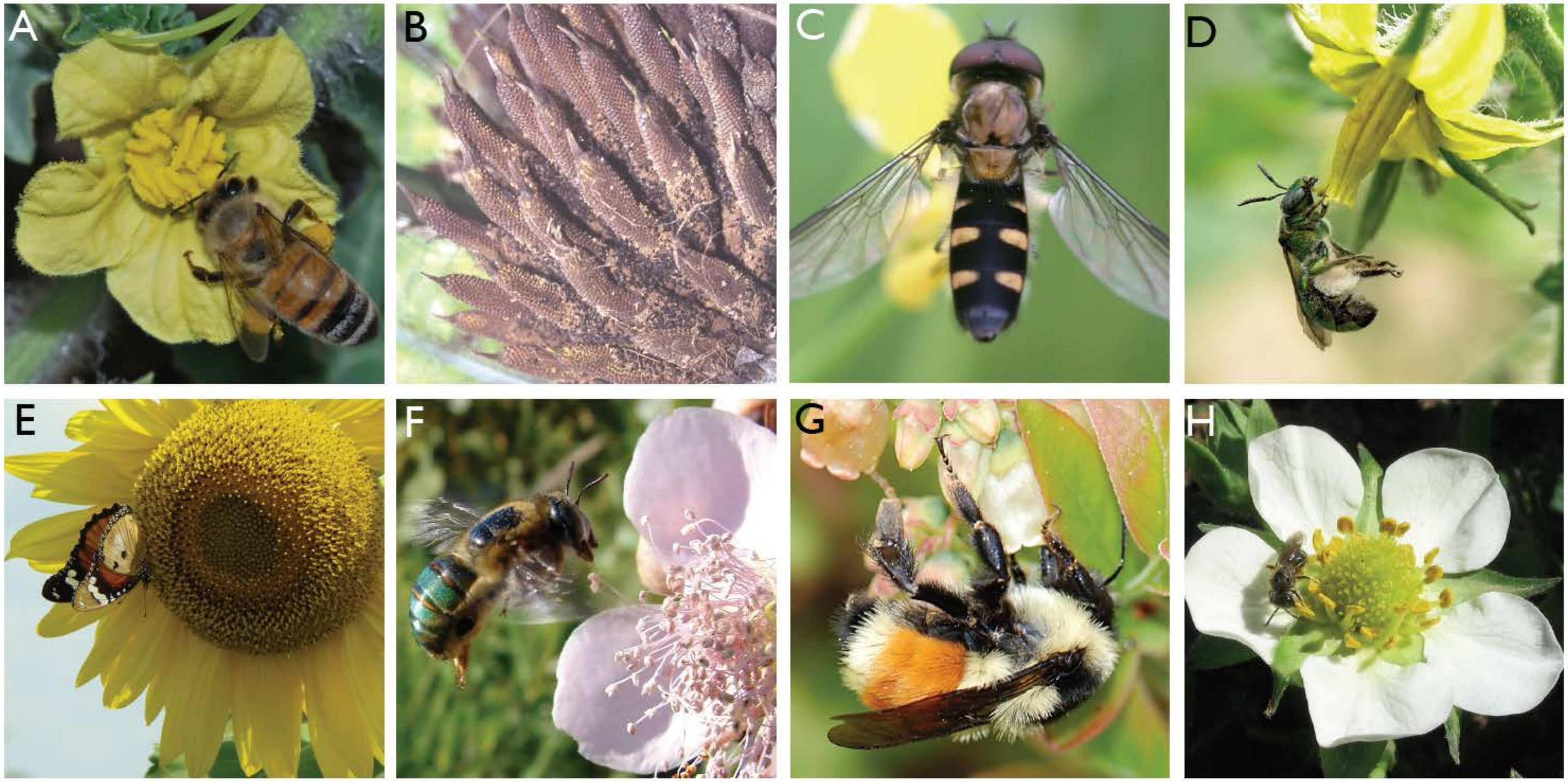

Fig. S3

Examples of pollinators reported in table S2. (**A**) Honey bee (*Apis mellifera*) visiting watermelon, Israel. (**B**) Oil palm weevils (*Elaeidobius kamerunicus*) visiting male oil palm flowers, Costa Rica. (**C**) New Zealand black hoverfly (*Melangyna novaezelandiae*) visiting Turnip rape, New Zealand. (**D**) Augochlorine bee visiting tomato, USA. (**E**) Diadem butterfly (*Hypolimnas misippus*) visiting sunflower, South Africa. (**F**) *Oxaea* sp. hovering in front an annato flower, Brazil. (**G**) Orange-belted bumblebee (*Bombus ternarius*) visiting lowbush blueberry, Canada. (**H**) Mining bee (*Andrena subopaca*) visiting strawberry, Germany.

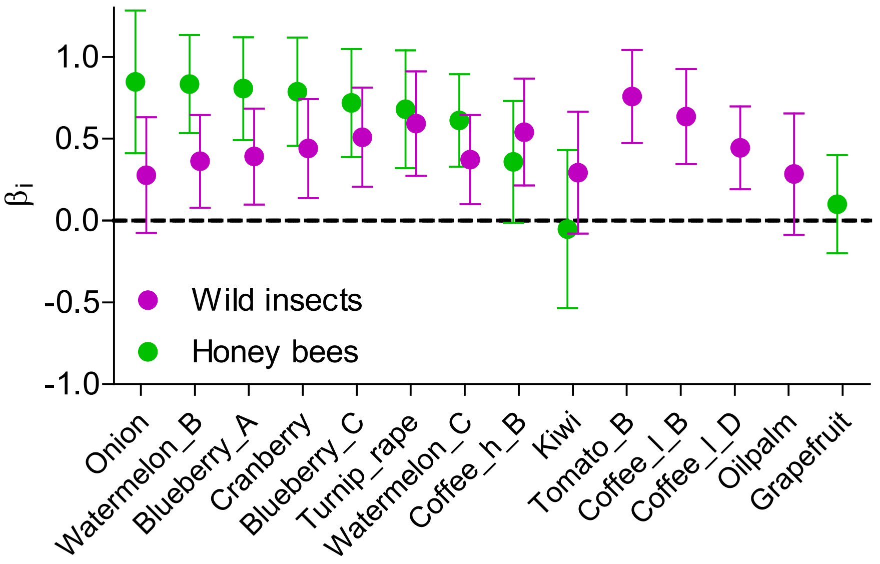

Fig. S4

Pollen deposition generally increases with higher visitation rate by wild insects or honey bees, as indicated by positive slopes (β_i ± 95% confidence interval) for individual crop systems. Cases on the right are systems in which only wild insects or only honey bees were present. Data from individual crop systems were standardized by z-scores prior to analysis, permitting direct comparison of slopes.

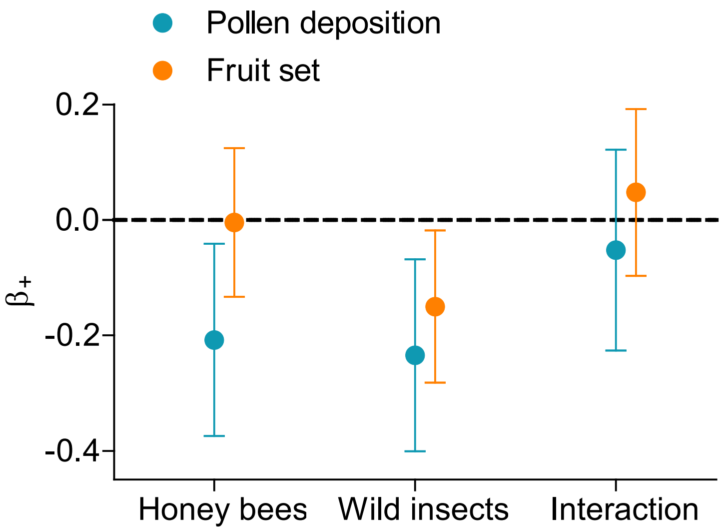

Fig. S5

Variation (CV) in fruit set decreased with visitation rate to crop flowers by wild insects, but not with visitation by honey bees. Overall partial regression coefficients (β_+ ± 95% confidence interval) for CV of pollen deposition or fruit set as a function of visitation by honey bees, by wild insects, or their interaction. Data from individual crop systems were standardized by z-scores prior to analysis, permitting direct comparison of regression coefficients.

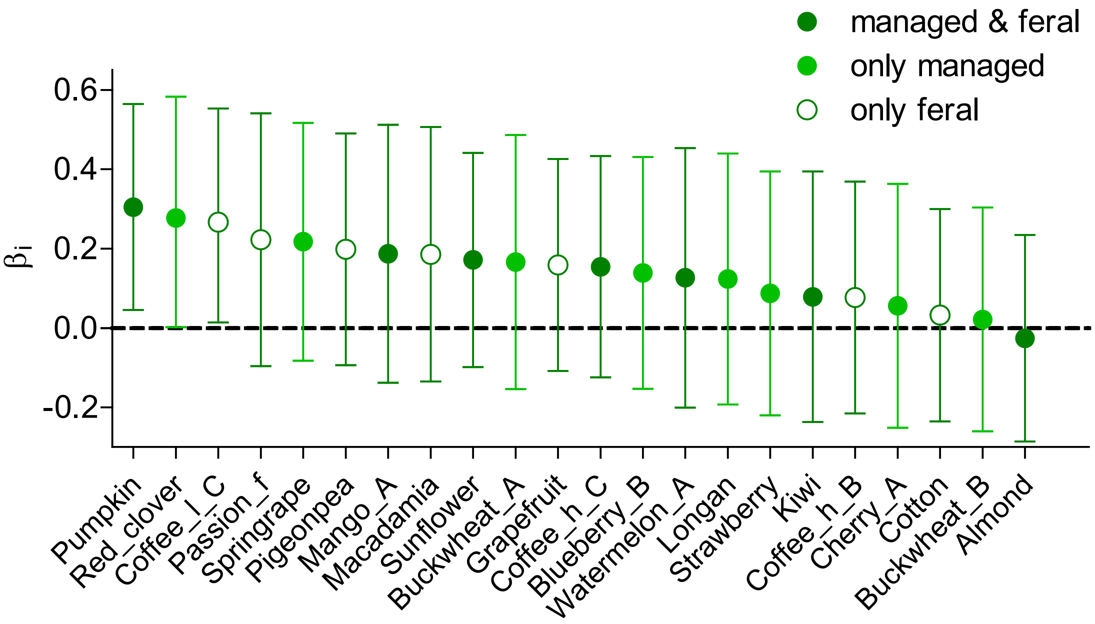

Fig. S6

Slopes (β_i ± 95% confidence interval) for the effect of visitation rate by honey bees on fruit set for individual crop systems do not differ between managed or feral honey bees. Pigeon pea, Mango_A and Sunflower are crop systems for which feral honey bees were native. Data from individual crop systems were standardized by z-scores prior to analysis, permitting comparison of slopes.

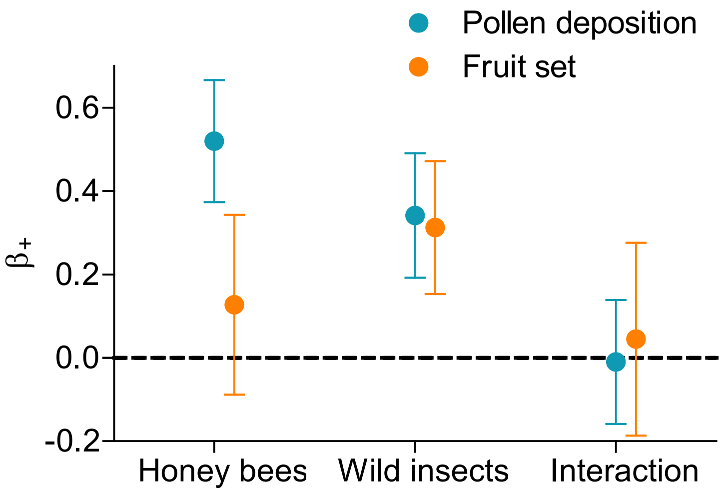

Fig. S7

Overall partial regression coefficients (β_+ ± 95% confidence interval) for pollen deposition or fruit set as a function of visitation rate by wild insects, honey bees, or their interaction. Data include only crops for which both pollen deposition and fruit set data were sampled, namely blueberry, coffee, grapefruit, kiwi, tomato and watermelon. For coffee_h_b, coffee_l_B, coffee_l_D, grapefruit, and kiwi, pollen deposition and fruit set data were measured at the same fields, whereas for other systems the two types of data were collected in different fields. These results are qualitatively similar to those from the complete data set (Fig. 2A), suggesting that the general result is robust to the choice of crop systems. Data from individual crop systems were standardized by z-scores prior to analysis, permitting direct comparison of regression coefficients.

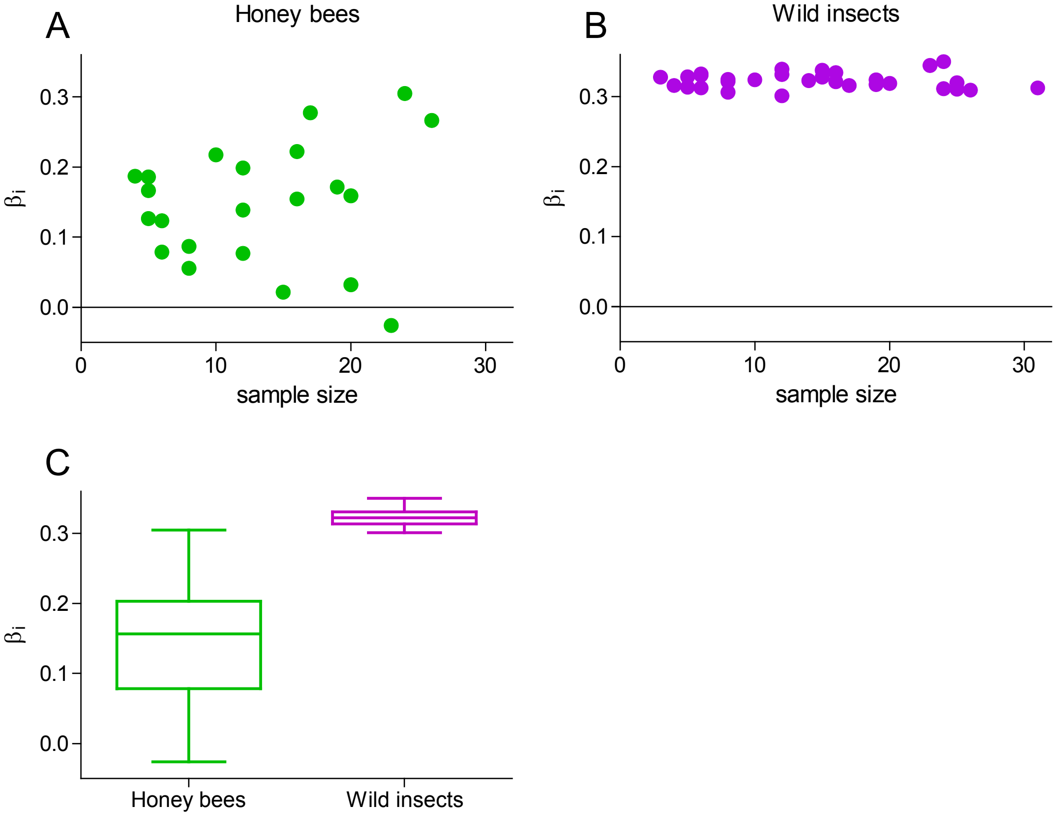

Fig. S8

Slopes (β_i) represent the effects of visitation by wild insects or honey bees on fruit set for individual crop systems. (**A**, **B**) Slopes for each crop system do not vary systematically with sample size (number of fields). (**C**) Box plot for slopes (whiskers are minimum and maximum values). Data from individual crop systems were standardized by z-scores prior to analysis, permitting comparison of slopes in all panels.

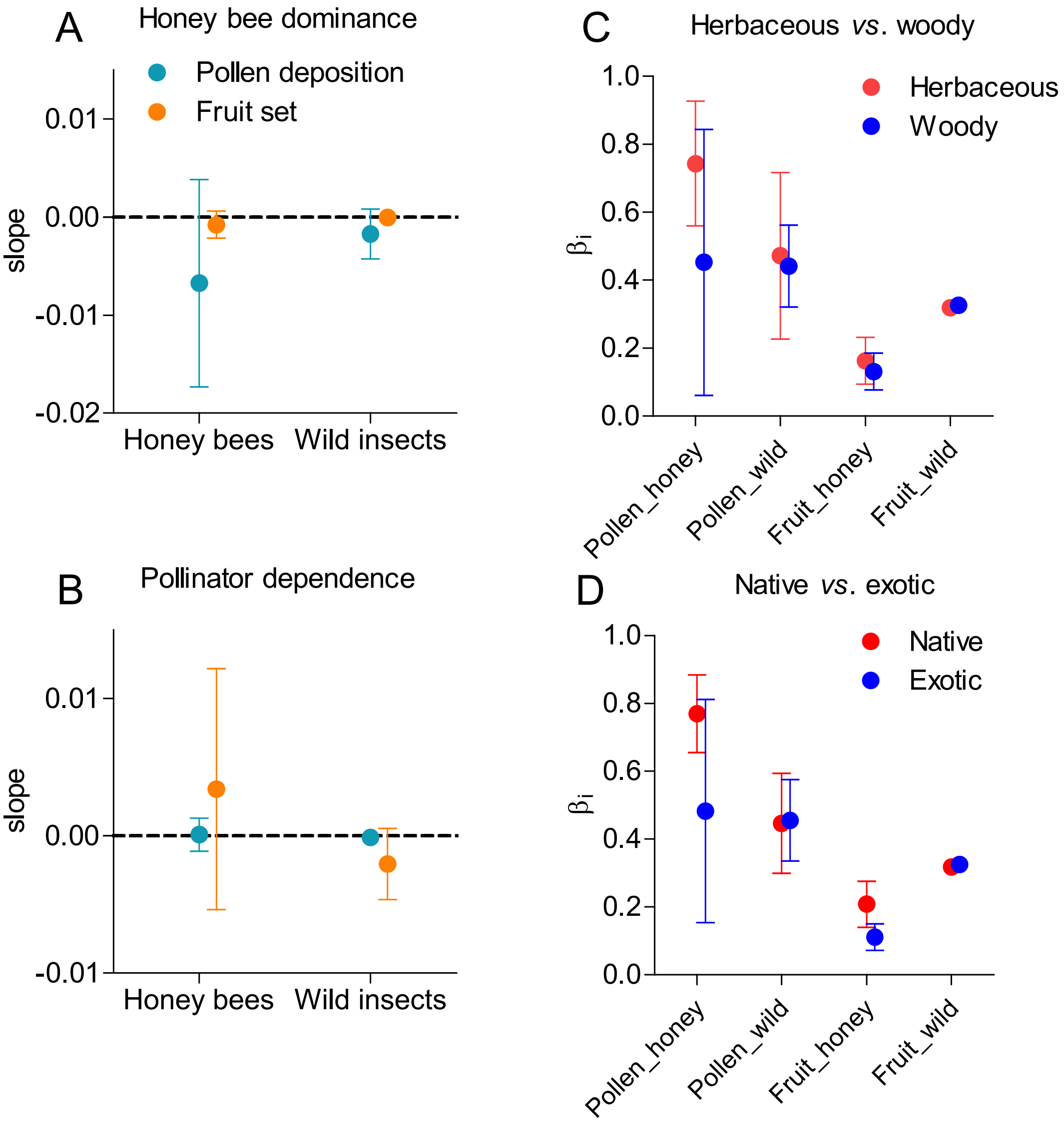

Fig. S9

Differences among crop systems in the relative abundance of honey bees (dominance), pollinator dependence, life form or origin of the crop do not influence individual system slopes (β_i) of pollen deposition or fruit set with visitation rate. (**A**, **B**) Slopes (± 95% confidence interval) estimated from linear regression of β_i (for fruit set or pollen deposition on visitation by honey bees or wild insects as indicated in the x-label) as a function of honey bee dominance or degree of pollinator dependence, respectively. Honey bee dominance is the percentage of total visits to crop flowers contributed by honey bees in the system, whereas the pollinator dependence for each crop is the percentage of fruit set reduction in the absence of pollinators (table S1). (**C**, **D**) Mean (± 95% confidence interval) of β_i for herbaceous or woody crops, native or exotic crops, respectively. “Pollen_honey” or “Fruit_honey”, respectively refer to pollen deposition or fruit set as a function of visitation by honey bees, whereas “Pollen_wild” and “Fruit_wild”, respectively refers to pollen deposition or fruit set as a function of visitation by wild insects.

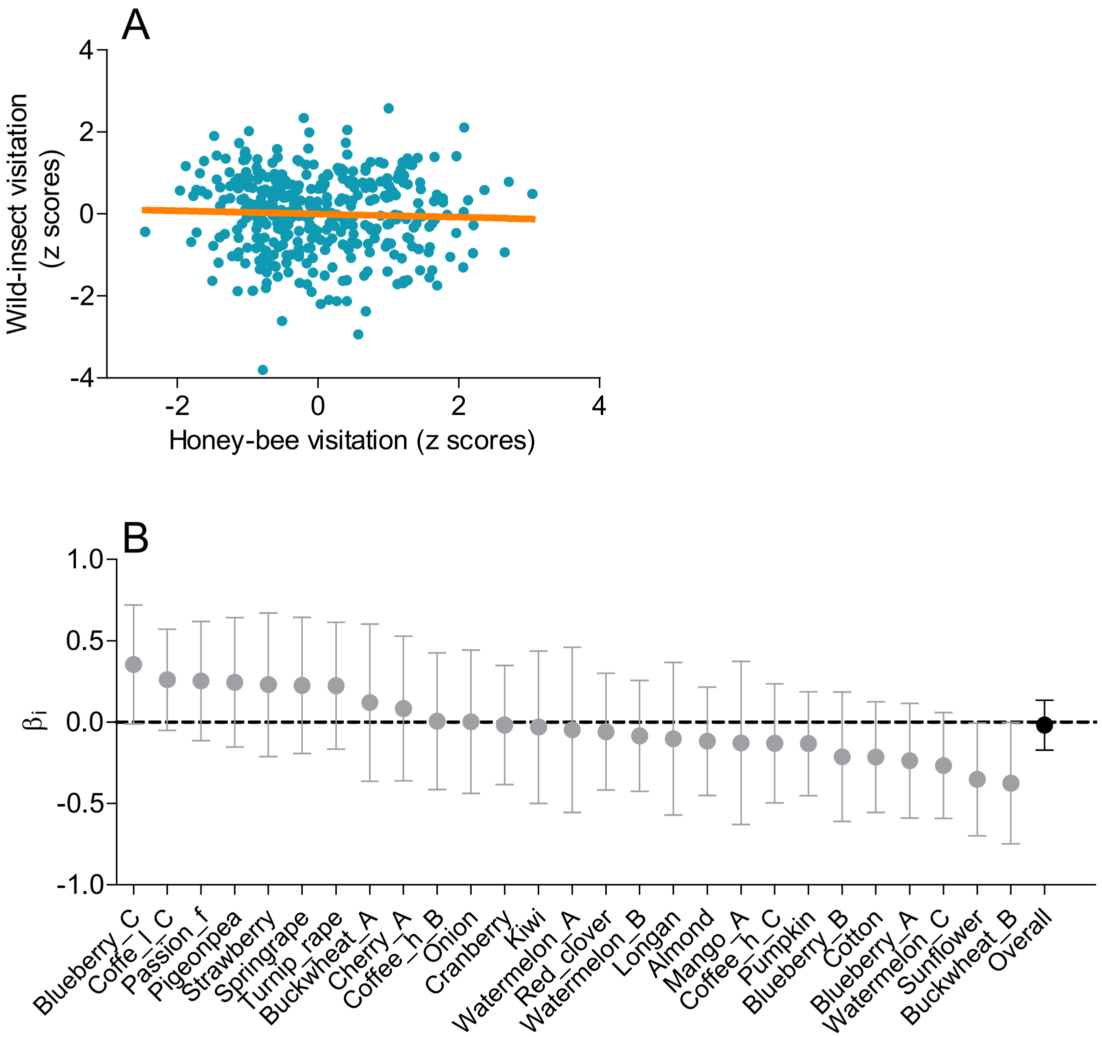

Fig. S10

Visitation rate by wild insects varies independently of visitation by honey bees both (**A**) overall and (**B**) within crop systems. (**A**) The line is the overall regression, and each point is a field in a crop system. (**B**) Slopes (β_i ± 95% confidence interval) of the relations of wild-insect visitation to honey-bee visitation for individual crop systems. Data from individual crop systems were standardized by z-scores prior to analysis (after log-transformation for visitation), permitting direct comparison of slopes.

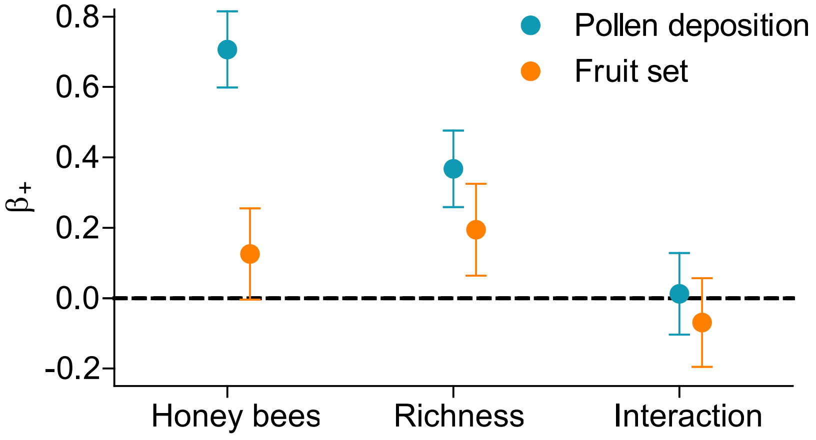

Fig. S11

Overall partial regression coefficients (β_+ ± 95% confidence interval) for mean pollen deposition or fruit set as functions of honey-bees visitation, flower-visitor richness, and their interaction (models *L* in tables S3, S4).

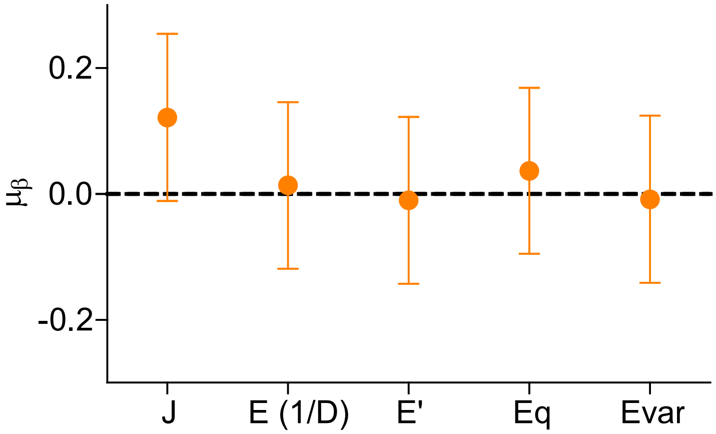

Fig. S12

Overall slopes (μ_β ± 95% confidence interval) for fruit set as a function of species evenness of flower visitor assemblages. Fruit set did not vary significantly with any of the five evenness indices considered (J, $E_{1/D}$, E’, Eq or Evar; see Material and Methods), even though they weight rare species differently, and exhibit generally different properties (*32*). Therefore, we present only Evar in further analyses, as recommended by (*32*). Data from individual crop systems were standardized by z-scores prior to analysis, permitting direct comparison of slopes.

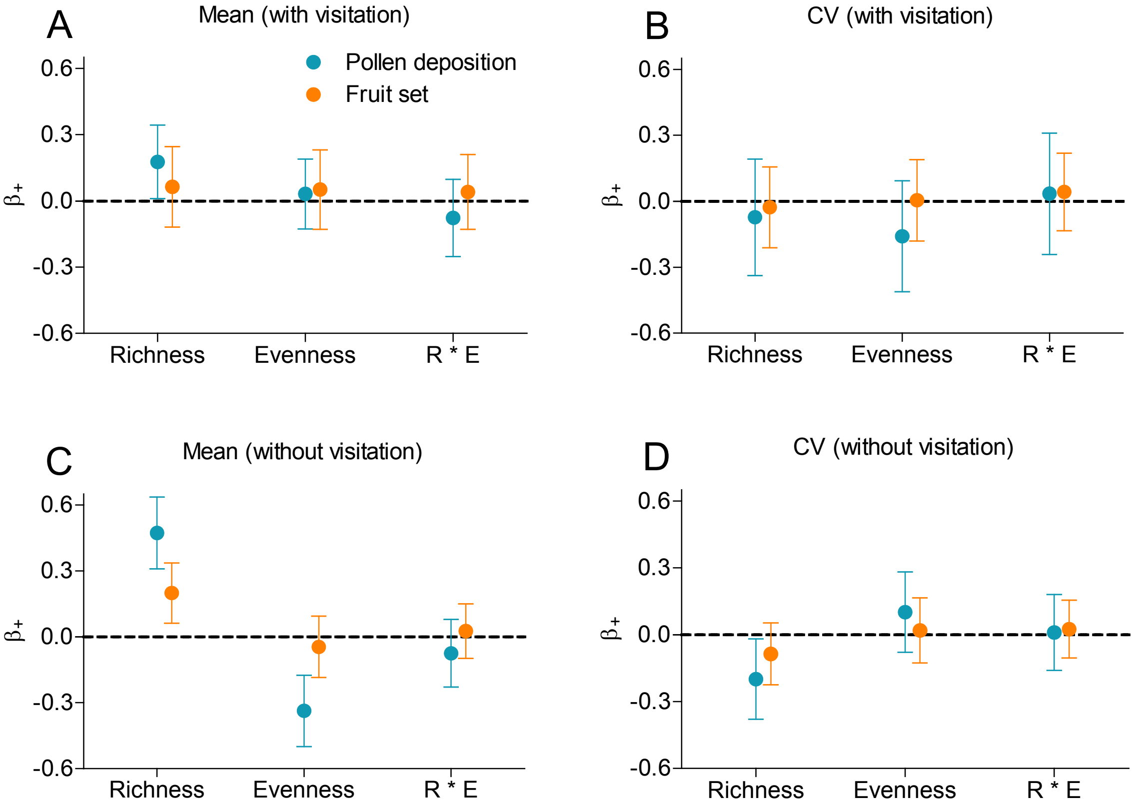

Fig. S13

Overall partial regression coefficients (β_{+} ± 95% confidence interval) for mean or variation (CV) of pollen deposition or fruit set as functions of flower-visitor richness, evenness (Evar), and their interaction (R * E). (**A**, **B**) Influences of richness and evenness on the mean or CV when visitation rate by wild insects is included as predictor in the same model. (**C**, **D**) Influences of richness and evenness without including visitation by wild insects in the model. Data from individual crop systems were standardized by z-scores prior to analysis, permitting direct comparison of regression coefficients.

Table S1.

Description of each of the 41 crop systems analyzed.

Crop and system code	**Reference and (or) data holder contact**	**Crop species**	**Breeding system**[*]	**Pollinator dependence (%)**[*]	**Growth form**	**Native or exotic crop**	**Study location**	**No. fields, within field measures**	**Reproduction measure**[‡]
Tropical and subtropical biomes									
Acerola	Freitas, freitas@ufc.br	*Malpighia emarginata*	Hermaphrodite, low degree of self pollination	50	Perennial evergreen shrub	Exotic	Brazil, Ceará	8 fields, 5 plants	Fruit set
Annato	Freitas, freitas@ufc.br	*Bixa orellana*	Hermaphrodite, varying degrees of self pollination	50	Perennial evergreen shrub	Native	Brazil, Ceará	6 fields, 4 plants	Fruit set
Coffee highland (A)	(*48, 49*) Klein, aklein@uni.leuphana.de	*Coffea arabica*	Hermaphrodite, mainly autonomous self pollination	25	Perennial evergreen shrub	Exotic	Indonesia, Sulawesi	24 fields, 4 plants	Fruit set
Coffee highland (B)	(*50, 51*) Ricketts, taylor.ricketts@uvm.edu	*Coffea arabica*	Hermaphrodite, mainly autonomous self pollination	25	Perennial evergreen shrub	Exotic	Costa Rica	12 fields, 5 plants	Fruit set, pollen
Coffee highland (C)	(*52*) Vergara, carlosh.vergara@udlap.mx	*Coffea arabica*	Hermaphrodite, mainly autonomous self pollination	25	Perennial evergreen shrub	Exotic	Mexico, Veracruz	16 fields, ----	Fruit set
Coffee lowland (A)	(*53*) Klein, aklein@uni.leuphana.de	*Coffea canephora*	Hermaphrodite, mainly wind pollination	25	Perennial evergreen shrub	Exotic	Indonesia, Sulawesi	15 fields, 4 plants	Fruit set
Coffee lowland (B)	(*54*) Krishnan, smitha.krishnan@env.ethz.ch	*Coffea canephora*	Hermaphrodite, mainly wind pollination	25	Perennial evergreen shrub	Exotic	India, Kodagu	19 fields, 4 transects	Fruit set, pollen
Coffee lowland	(*55*) Munyuli,	*Coffea*	Hermaphrodite,	25	Perennial	Native	Uganda,	26 fields, 3	Fruit set

(C)	tmunyuli@yahoo.com	*canephora*	mainly wind pollination		evergreen shrub		Mukono, Wakiso, Mpigi, Nakaseke, Kamuli, Masaka	plants	
Coffee lowland (D)	(*56*) Boreux, boreux@leuphana.de	*Coffea canephora*	Hermaphrodite, mainly wind pollination	25	Perennial shrub	Exotic	India, Kodagu	31, fields, ----	Fruit set, pollen
Cotton	Freitas, freitas@ufc.br	*Gossypium hirsutum*	Hermaphrodite, mainly autonomous self pollination	25	Perennial evergreen shrub, grown annually	Exotic	Brazil, Ceará	20 fields, 5 plants	Fruit set
Cucumber	Motzke, iris.motzke@agr.uni-goettingen.de	*Cucumis sativus*	Monoecious or andro-monoecious, self-compatible	75	Annual, herbaceous vine	Exotic	Indonesia, Sulawesi	25 fields, 3 days	Fruit set
Grapefruit	(*11, 57*) Chacoff, nchacoff@gmail.com	*Citrus paradisi*	Hermaphrodite, varying degrees of self-compatibility depending on variety	5	Perennial evergreen tree	Exotic	Argentina, Salta	20 fields, 10 plants	Fruit set, pollen
Longan	(*58*) Cunningham, Saul.Cunningham@csiro.au	*Dimocarpus longan*	Polygamous, autonomous self pollination, wind pollination	5	Perennial evergreen tree	Exotic	Australia, Queensland	6 fields, 4 plants	Fruit set
Macadamia	(*58*) Cunningham, Saul.Cunningham@csiro.au	*Macadamia integrifolia*	Hermaphrodite, largely self-incompatible	>95	Perennial evergreen tree	Native	Australia, Queensland	5 fields, 4 plants	Fruit set
Mango (A)	(*59*) Carvalheiro, lgcarvalheiro@gmail.com	*Mangifera indica*	Andro-monoecious, variable self-compatibility among varieties, autonomous self- and wild-pollination occurs	75	Perennial evergreen tree	Exotic	South Africa, Limpopo	4 fields, 2 plots	Fruit set

Mango (B)	(*60*) Sousa, jhdsousa@yahoo.com	*Mangifera indica*	Andro-monoecious, variable self-compatibility among varieties, autonomous self- and wild-pollination occurs	75	Perennial evergreen tree	Exotic	Brazil, Bahia	3 fields, ----	Fruit set
Oil palm	(*61*) Mayfield, m.mayfield@uq.edu.au	*Elaeis guineensis*	Monoecious, male and female flower production temporally separated	5	Perennial evergreen palm	Exotic	Costa Rica, Puntarenas	6 fields, 3 days	Pollen
Passion fruit	(*62*) Viana, blande.viana@gmail.com	*Passiflora edulis*	Hermaphrodite, most varieties largely self-incompatible	>95	Perennial evergreen vine	Native	Brazil, Bahia	16 fields, 3 days	Fruit set
Pigeon pea	Otieno, M.Otieno@pgr.reading.ac.uk	*Cajanus cajan*	Hermaphrodite, mainly autonomous self pollination	5	Perennial evergreen herb, grown annually	Exotic	Kenya, Kibwezi District	12 fields, 3 transects	Fruit set
Sunflower	(*16*) Carvalheiro, lgcarvalheiro@gmail.com	*Helianthus annuus*	Dichogamous, variable level of self-compatibility among varieties, autonomous self pollination low	25	Annual herb	Exotic	South Africa, Limpopo	19 fields, 9 plants	Fruit set
Mediterranean biome									
Almond	(*63*) Klein, aklein@uni.leuphana.de	*Prunus dulcis*	Hermaphrodite, self-incompatible, very low autonomous self pollination	>75	Perennial deciduous tree	Exotic	USA, California	23 fields, 2 transects	Fruit set
Tomato (A)	(*64*) Kremen, ckremen@gmail.com	*Solanum lycopersicum*	Hermaphrodite, self-compatible, buzz-pollination	5	Perennial shrub, grown annually	Exotic	USA, California	14 fields, 4 transects	Fruit set
Watermelon (A)	Mandelik, Yael.Mandelik@mail.huji.ac	*Citrullus lanatus*	Mostly monoecious, self-compatible	>95	Annual, herbaceous vine	Exotic	Central Israel	5 fields, 3 days	Fruit set
Watermelon	Williams,	*Citrullus*	Mostly monoecious,	>95	Annual,	Exotic	USA,	20 fields, 3	Pollen

(B)	nmwilliams@ucdavis.edu	*lanatus*	self-compatible		herbaceous vine		California	days	
Other temperate biomes†									
Blueberry (A) highbush	Benjamin, faye.benjamin@gmail.com	*Vaccinium corymbosum*	Hermaphrodite, self-compatible, varying degree of self-incompatibility, buzz-pollination	75	Perennial deciduous or evergreen shrub	Native	USA, New Jersey	18 fields, 3 days	Pollen
Blueberry (B) highbush	(*65*) Isaacs, isaacsr@msu.edu	*Vaccinium corymbosum*	Hermaphrodite, self-compatible, varying degree of self-incompatibility, buzz-pollination	75	Perennial deciduous or evergreen shrub	Native	USA, Michigan	12 fields, 2 transects	Fruit set
Blueberry (C) lowbush	Javorek, steve.javorek@agr.gc.ca	*Vaccinium angustifolium*	Hermaphrodite, self-compatible, varying degree of self-incompatibility, buzz-pollination	75	Perennial deciduous shrub	Native	Canada, Prince Edward Island	16 fields, 3 days	Pollen
Buckwheat (A)	(*66*) Szentgyorgyi, hajnalka.szentgyorgyi@uj.edu.pl	*Fagopyrum esculentum*	Hermaphrodite, self-incompatible (distylous)	75	Annual or perennial herbaceous plant	Exotic	Poland, Lubelszczyzna	5 fields, 10 transects	Fruit set
Buckwheat (B)	(*67*) Taki, htaki@affrc.go.jp	*Fagopyrum esculentum*	Hermaphrodite, self-incompatible (distylous)	75	Annual or perennial herbaceous plant	Exotic	Japan, Ibaraki	15 fields, 10 plants	Fruit set
Cranberry	Cariveau, cariveau@rci.rutgers.edu	*Vaccinium macrocarpon*	Hermaphrodite, self-compatible, buzz-pollination	75	Perennial evergreen shrub	Native	USA, New Jersey	16 fields, 2 transects	Pollen
Cherry (A)	(*68*) Holzschuh, andrea.holzschuh@uni-wuerzburg.de	*Prunus avium*	Hermaphrodite, mostly self-incompatible	75	Perennial deciduous tree	Native	Germany, Hesse	8 fields, 4 trees	Fruit set
Cherry (B)	Schüepp,	*Prunus*	Hermaphrodite,	75	Perennial	Native	Switzerland,	25 fields, 4	Fruit set

	christof.schueepp@iee.unibe.ch	*avium*	mostly self-incompatible		deciduous tree		BE and SO	plants	
Kiwi fruit	(*69*) Mayfield, m.mayfield@uq.edu.au	*Actinidia deliciosa*	Dioecious	>95	Perennial vine	Exotic	New Zealand, North island	6 fields, 7 plants	Fruit set, pollen
Onion	(*70*) Howlett, brad.howlett@plantandfood.co.nz	*Allium cepa*	Hermaphrodite, partly self-compatible[§]	75	Perennial or biannual herb	Exotic	New Zealand, North & South islands	8 fields, 5 plants	Pollen
Pumpkin	Petersen, jdp245@cornell.edu	*Cucurbita pepo*	Monoecious, varying degrees of self incompatibility depending on variety	75	Annual vine	Native	USA, New York	24 fields, 3 transects	Fruit set
Red clover	(*36*) Rundlöf, maj.rundlof@biol.lu.se	*Trifolium pratense*	Hermaphrodite, self-incompatible	>95	Perennial herb	Native	Sweden, Skåne	17 fields, 2 transects	Fruit set
Spring rape	(*71*) Bommarco, Riccardo.Bommarco@slu.se	*Brassica napus*	Hermaphrodite, self compatible	25	Annual herb	Native	Sweden, Uppland	10 fields, 6 transects	Fruit set
Strawberry	(*66*) Krewenka, kkrewen@gwdg.de	*Fragaria x ananassa*	Hermaphrodite (most varieties), self-compatible	25	Perennial herb, grown annually	Exotic	Germany, Lower Saxony	8 fields, 6 transects	Fruit set
Tomato (B)	Bartomeus, nacho.bartomeus@gmail.com	*Solanum lycopersicum*	Hermaphrodite, self-compatible, buzz-pollination	5	Perennial shrub, grown annually	Exotic	USA, NJ and PA	20 fields, ----	Pollen
Turnip rape	(*72, 73*) Rader, rominarader@gmail.com	*Brassica rapa*	Hermaphrodite, largely self-compatible	75	Annual herb	Exotic	New Zealand, South Island	13 fields, 5 transects	Pollen
Watermelon (C)	(*27, 38*) Winfree, rwinfree@rutgers.edu	*Citrullus lanatus*	Mostly monoecious, self-compatible	>95	Annual, herbaceous vine	Exotic	USA, NJ and PA	23 fields, 40 quadrats	Pollen

[*] Information on the breeding system and pollinator dependence (i.e. percentage of fruit set reduction in the absence of pollinators) was obtained from *3*, *26*, and *74-79*.

[†] Includes all crop systems located in temperate latitudes (>23.5º and <66.5º), except those with Mediterranean climate (warm to hot, dry summers, and mild to cold, wet winters).

[‡] We measured fruit set at harvest (mature fruit set) for all crop systems, except for Coffe_h_A, Coffee_l_A, Mango_A, Mango_B and Cherry_B where we measured initial fruit set. Note that Fig.2B shows that results for these studies were similar to those measuring mature fruit set. For Mango_A, yield was also measured and showed a positive correlation with initial fruit set (Fig. S1).

[§] The studied crop system in New Zealand grows onion as a hybrid crop requiring cross pollination. Seed harvested from umbels that are male sterile, ensuring pollination can only occur from the transfer of pollen from male fertile umbels (different cultivar).

Table S2.

Flower visitors observed most commonly in each crop system.

Crop and system code	Honey bees and wild insects >5% visits?	Managed or feral honey bees?	Dominant pollinator (species, % visits)		2nd dominant pollinator (species, % visits)		3rd dominant pollinator (species, % visits)	
Tropical and subtropical biomes								
Acerola	Only wild insects	------	*Trigona spinipes*	33%	*Centris aenea*	24%	*Centris flavifrons*	17%
Annato	Only wild insects	------	*Trigona spinipes*	20%	*Augochloropsis* spp.	14%	*Eulaema nigrita*	11%
Coffee highland (A)	Only wild insects	------	*Apis nigrocinta binghami*	18%	*Apis cerana*	13%	*Apis dorsata*	11%
Coffee highland (B)	Yes	Feral	*Apis mellifera*	44%	*Plebeia jatiformis*	22%	*Plebeia frontalis*	10%
Coffee highland (C)	Yes	Managed for pollination and feral	*Apis mellifera*	91%	*Scaptotrigona mexicana*	2%	Syrphidae	1%
Coffee lowland (A)	Only wild insects	------	*Apis nigrocinta binghami*	18%	*Apis dorsata*	12%	*Lepidotrigona terminata*	10%
Coffee lowland (B)	Only wild insects and *Apis cerana indica*	------	*Apis dorsata*	59%	*Apis cerana*	27%	*Tetragonula iridipennis*	11%
Coffee lowland (C)	Yes	Feral	*Hypotrigona gribodoi*	62%	*Meliponula ferruginea*	14%	*Apis mellifera scutellata*	6%
Coffee lowland (D)	Only wild insects and *Apis cerana indica*	-----	*Apis dorsata*	57%	*Tetragonula iridipennis*	22%	*Apis cerana*	20%
Cotton	Yes	Feral	*Lithurgus huberi*	38%	*Ceratina* spp.	20%	*Melitomella murihirta*	5%
Cucumber	Only wild insects	------	*Curvinomia* spp.	38%	*Ceratinidia cognata*	22%	*Xylocopa aesturns*	9%
Grapefruit	Only honey bees	Feral	*Apis mellifera*	96%	*Melipona* spp.	3%	*Bombus* spp.	<1%

Longan	Yes	Feral	*Apis mellifera*	49%	*Trigona* spp.	45%	other	<1%
Macadamia	Only honey bees	Feral	*Apis mellifera*	>99%	Other	<1%		
Mango (A)	Yes	Managed for pollination and feral	*Anoplolepis* spp.	37%	*Macrocoma apicicornis*	9%	Apionidae Gen. spp.	8%
Mango (B)	Only wild insects	------	Empididae Gen. spp.	39%	*Muscidae* spp.	23%	Vespidae Gen. spp.	9%
Oil palm	Only wild insects	------	*Elaeidobius kamerunicus*	67%	Formidicae spp.	18%	Diptera	10%
Passion fruit	Yes	Feral	*Xylocopa* spp.	47%	*Trigona spinipes*	28%	*Apis mellifera*	25%
Pigeon pea	Yes	Feral	*Apis mellifera*	20%	*Ceratina* spp.	18%	*Megachile flavipennis*	5%
Sunflower	Yes	Managed for honey and feral	*Apis mellifera*	83%	*Astylus atromaculatus*	6%	*Hypolimnas misippus*	1%
Mediterranean biome								
Almond	Yes	Managed for pollination and feral	*Apis mellifera*	64%	Syrphidae Gen. spp.	11%	*Andrena cerasifolii*	2%
Tomato (A)	Only wild insects	------	*Bombus* spp.	50%	*Anthophora urbana*	46%	*Dialictus* spp.	3%
Watermelon (A)	Yes	Managed for honey and feral	*Apis mellifera*	88%	*Lasioglossum politum*	7%	*Lasioglossum malachurum*	3%
Watermelon (B)	Yes	Managed for pollination and feral	*Apis mellifera*	79%	*Dialictus* spp.	10%	*Halictus tripartitus*	4%
Other temperate biomes[*]								
Blueberry (A) highbush	Yes	Managed for pollination	*Apis mellifera*	87%	*Xylocopa virginica*	3%	*Habropoda laboriosa*	2%
Blueberry (B) highbush	Yes	Managed for pollination	*Apis mellifera*	85%	*Bombus* spp.	6%	*Andrena* spp.	3%
Blueberry (C) lowbush	Yes	Managed for pollination	*Apis mellifera*	38%	*Megachile rotundata*	21%	*Andrena* spp.	12%

Buckwheat (A)	Yes	Managed for honey	*Apis mellifera*	71%	Syrphidae Gen. spp.	17%	*Episyrphus balteatus*	3%
Buckwheat (B)	Yes	Managed for honey	*Apis cerana*	24%	*Apis mellifera*	23%	*Formica japonica*	14%
Cranberry	Yes	Managed for pollination	*Apis mellifera*	75%	*Bombus griseocollis*	6%	*Bombus bimaculatus*	5%
Cherry (A)	Yes	Managed for honey	*Apis mellifera*	67%	*Andrena jacobi*	5%	*Andrena haemorrhoa*	5%
Cherry (B)	Only wild insects	------	Empididae Gen. spp.	11%	*Andrena haemorrhoa*	9%	Chalcidoidea Gen. spp.	7%
Kiwi fruit	Yes	Managed for honey and feral	*Apis mellifera*	88%	Syrphidae Gen. spp.	4%	*Bombus* spp.	2%
Onion	Yes	Managed for pollination and feral	*Apis mellifera*	65%	*Delia platura*	7%	*Lasioglossum sordidum*	6%
Pumpkin	Yes	Managed for pollination and feral	*Peponapis pruinosa*	60%	*Apis mellifera*	27%	*Bombus impatiens*	9%
Red clover	Yes	Managed for honey	*Apis mellifera*	49%	*Bombus terrestris*	30%	*Bombus lapidarius*	8%
Spring rape	Yes	Managed for honey	*Apis mellifera*	78%	Syrphidae Gen. spp.	4%	*Bombus terrestris*	2%
Strawberry	Yes	Managed for honey	*Apis mellifera*	62%	*Bombus terrestris*	9%	*Bombus lapidarius*	7%
Tomato (B)	Only wild insects	------	*Lasioglossum* spp.	40%	*Augochlora pura*	21%	*Augochlorella aurata*	10%
Turnip rape	Yes	Managed and feral	*Apis mellifera*	40%	*Melangyna novaezelandiae*	19%	*Eristalis tenax*	10%
Watermelon (C)	Yes	Managed for pollination	*Apis mellifera*	30%	*Augochlora pura*	16%	*Melissodes bimaculata*	14%

[*] Includes all crop systems located in temperate latitudes (>23.5º and <66.5º), except those with Mediterranean climate (warm to hot, dry summers, and mild to cold, wet winters).

Table S3.

Akaike's Information Criterion (AIC) for mixed effects models of the potential influences on crop pollen deposition, including visitation rate by wild insects (*w*), visitation rate by honey bees (*h*), species richness (R) and species evenness (E). The Δ column depicts the difference between a model's AIC and that of the best-fitting model. Different intercepts (α_i) 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	**AIC**	**Δ**	***w***	***h***	**R**	**E**	**R * E**	**R * *w***	**R * *h***	**E * *w***	**E * *h***	***w* * *h***	**R * E *_w_**	**R * E *_h_**	**R * _w_ *_h_**	**E * _w_ *_h_**	**R* E *_w_ *_h_**
A	364	138	Null model including only a random intercept term to account for differences among systems														
Models lacking insect abundance																	
B	333	107			X	X											
C	334	108			X	X	X										
D	347	121			X												
E	361	135				X											
Models with wild insect abundance, but not honey-bee abundance																	
F	334	108	X			X											
G	336	110	X			X				X							
H	344	118	X														
I	344	118	X		X												
J	346	120	X		X			X									
Models with honey-bee abundance, but not wild insect abundance																	
K	240	14		X	X												
L	242	16		X	X				X								
M	272	46		X		X											
N	274	48		X		X					X						
O	278	52		X													
Models with both wild insect and honey-bee abundance																	
P	226	0	X	X	X	X											
Q	229	3	X	X													
R	230	4	X	X								X					
S	235	9	X	X	X	X	X	X	X	X	X	X					
T	240	14	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
U	242	16	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Table S4.

Akaike's Information Criterion (AIC) for mixed effects models of the potential influences on crop fruit set, including visitation rate by wild insects (*w*), visitation rate by honey bees (*h*), species richness (R) and species evenness (E). The Δ column depicts the difference between a model's AIC and that of the best-fitting model. Different intercepts (α_i) 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	**AIC**	**Δ**	***w***	***h***	**R**	**E**	**R * E**	**R * *w***	**R * *h***	**E * *w***	**E * *h***	***w* * *h***	**R * E **w***	**R * E **h***	**R * *w* **h***	**E * *w* **h***	**R* E **w* **h***
A	605	23	Null model including only a random intercept term to account for differences among systems														
Models lacking insect abundance																	
B	595	13			X												
C	596	14			X	X											
D	598	16			X	X	X										
E	603	21				X											
Models with wild insect abundance, but not honey-bee abundance																	
F	584	2	X														
G	585	3	X		X												
H	586	4	X			X											
I	587	5	X			X				X							
J	587	5	X		X			X									
Models with honey-bee abundance, but not wild insect abundance																	
K	593	11		X	X												
L	594	12		X	X				X								
M	600	18		X													
N	601	19		X		X											
O	602	20		X		X					X						
Models with both wild insect and honey-bee abundance																	
P	582	0	X	X													
Q	584	2	X	X								X					
R	585	3	X	X	X	X											
S	594	12	X	X	X	X	X	X	X	X	X	X					
T	600	18	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
U	601	19	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Table S5.

Overall Pearson's correlation coefficients among studied variables in crop systems for which both wild insects and honey bees were active flower visitors, i.e. at least 5% of total visitation by either group. Significant (*P* < 0.05) correlations are shown in bold.

		Mean				CV			
	Evenness	Wild insect visits	Honey bee visits	Fruit set	Pollen deposition	Wild insect visits	Honey bee visits	Fruit set	Pollen deposition
Richness	**0.20**	**0.56**	-0.04	**0.18**	**0.36**	**-0.33**	-0.07	-0.06	-0.17
Evenness		0.03	**-0.46**	-0.01	**-0.20**	**-0.18**	0.06	0.06	0.01
Mean wild insect visits			-0.03	**0.28**	**0.39**	**-0.38**	0.04	**-0.15**	**-0.23**
Mean honey bee visits				**0.14**	**0.69**	<0.01	**-0.25**	<0.01	**-0.20**
Mean fruit set					**0.46**	**-0.14**	0.02	**-0.48**	**-0.55**
Mean pollen deposition						**-0.22**	-0.17	**-0.57**	**-0.39**
CV wild insect visits							**0.11**	0.11	**0.23**
CV honey bee visits								<0.01	**0.51**
CV fruit set									0.36

Additional Data table S1 (separate file)

Database_S1.txt: Data used in the primary analyses of this article. Note that for some analyses a subset of these data was used (e.g. only crop systems including both wild insects and honey bees). See Material and Methods for further information.

References

1. L. Roberts, 9 billion? *Science* 333, 540 (2011). doi:10.1126/science.333.6042.540 Medline

2. D. Tilman *et al.*, Forecasting agriculturally driven global environmental change. *Science* 292, 281 (2001). doi:10.1126/science.1057544 Medline

3. A.-M. Klein *et al.*, Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. London Ser. B* 274, 303 (2007). doi:10.1098/rspb.2006.3721 Medline

4. S. G. Potts *et al.*, Global pollinator declines: Trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345 (2010). doi:10.1016/j.tree.2010.01.007 Medline

5. L. A. Garibaldi *et al.*, Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 1062 (2011). doi:10.1111/j.1461-0248.2011.01669.x Medline

6. R. A. Morse, Honeybees forever. *Trends Ecol. Evol.* 6, 337 (1991). doi:10.1016/0169-5347(91)90043-W Medline

7. R. M. Goodwin, H. M. Cox, M. A. Taylor, L. J. Evans, H. M. McBrydie, Number of honey bee visits required to fully pollinate white clover (*Trifolium repens*) seed crops in Canterbury, New Zealand. *New Zeal. J. Crop Hort.* 39, 7 (2011). doi:10.1080/01140671.2010.520164

8. R. R. Rucker, W. N. Thurman, M. Burgett, Honey bee pollination markets and the internalization of reciprocal benefits. *Am. J. Agric. Econ.* 94, 956 (2012). doi:10.1093/ajae/aas031

9. M. A. Aizen, L. D. Harder, The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. *Curr. Biol.* 19, 915 (2009). doi:10.1016/j.cub.2009.03.071 Medline

10. L. A. Garibaldi, M. A. Aizen, A.-M. Klein, S. A. Cunningham, L. D. Harder, Global growth and stability of agricultural yield decrease with pollinator dependence. *Proc. Natl. Acad. Sci. U.S.A.* 108, 5909 (2011). doi:10.1073/pnas.1012431108 Medline

11. N. P. Chacoff, M. A. Aizen, V. Aschero, Proximity to forest edge does not affect crop production despite pollen limitation. *Proc. R. Soc. London Ser. B* 275, 907 (2008). doi:10.1098/rspb.2007.1547 Medline

12. W. F. Morris, D. P. Vázquez, N. P. Chacoff, Benefit and cost curves for typical pollination mutualisms. *Ecology* 91, 1276 (2010). doi:10.1890/08-2278.1 Medline

13. R. Winfree, C. Kremen, Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proc. R. Soc. London Ser. B* 276, 229 (2009). doi:10.1098/rspb.2008.0709 Medline

14. P. Hoehn, T. Tscharntke, J. M. Tylianakis, I. Steffan-Dewenter, Functional group diversity of bee pollinators increases crop yield. *Proc. R. Soc. London Ser. B* 275, 2283 (2008). doi:10.1098/rspb.2008.0405 Medline

15. N. Blüthgen, A.-M. Klein, Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. *Basic Appl. Ecol.* 12, 282 (2011). doi:10.1016/j.baae.2010.11.001

16. L. G. Carvalheiro *et al.*, Natural and within-farmland biodiversity enhances crop productivity. *Ecol. Lett.* 14, 251 (2011). doi:10.1111/j.1461-0248.2010.01579.x Medline

17. S. S. Greenleaf, C. Kremen, Wild bees enhance honey bees' pollination of hybrid sunflower. *Proc. Natl. Acad. Sci. U.S.A.* 103, 13890 (2006). doi:10.1073/pnas.0600929103 Medline

18. B. J. Cardinale *et al.*, Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443, 989 (2006). doi:10.1038/nature05202 Medline

19. A.-M. Klein, C. Müller, P. Hoehn, C. Kremen, in *Biodiversity, Ecosystem Functioning, and Human Wellbeing: An Ecological and Economic Perspective*, D. E. Bunker, A. Hector, M. Loreau, C. Perrings, S. Naeem, Eds. (Oxford Univ. Press, Oxford, 2009), pp. 195–208.

20. T. Tscharntke, A.-M. Klein, A. Kruess, I. Steffan-Dewenter, C. Thies, Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol. Lett.* 8, 857 (2005). doi:10.1111/j.1461-0248.2005.00782.x

21. H. Hillebrand, D. M. Bennett, M. W. Cadotte, Consequences of dominance: A review of evenness effects on local and regional ecosystem processes. *Ecology* 89, 1510 (2008). doi:10.1890/07-1053.1 Medline

22. B. J. Cardinale *et al.*, Biodiversity loss and its impact on humanity. *Nature* 486, 59 (2012). doi:10.1038/nature11148 Medline

23. See supplementary materials on *Science* Online.

24. M. A. Aizen, L. D. Harder, Expanding the limits of the pollen-limitation concept: Effects of pollen quantity and quality. *Ecology* 88, 271 (2007). doi:10.1890/06-1017 Medline

25. C. Kremen, K. S. Ullman, R. W. Thorp, Evaluating the quality of citizen-scientist data on pollinator communities. *Conserv. Biol.* 25, 607 (2011). doi:10.1111/j.1523-1739.2011.01657.x Medline

26. K. S. Delaplane, D. F. Mayer, *Crop Pollination by Bees* (CABI, New York, 2000).

27. C. Kremen *et al.*, Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecol. Lett.* 10, 299 (2007). doi:10.1111/j.1461-0248.2007.01018.x Medline

28. R. Winfree, N. M. Williams, J. Dushoff, C. Kremen, Native bees provide insurance against ongoing honey bee losses. *Ecol. Lett.* 10, 1105 (2007). doi:10.1111/j.1461-0248.2007.01110.x Medline

29. A. Aebi *et al.*, Back to the future: *Apis* versus non-*Apis* pollination. *Trends Ecol. Evol.* 27, 142 (2012). doi:10.1016/j.tree.2011.11.017

30. S. D. Wratten, M. Gillespie, A. Decourtye, E. Mader, N. Desneux, Pollinator habitat enhancement: Benefits to other ecosystem services. *Agric. Ecosyst. Environ.* 159, 112 (2012). doi:10.1016/j.agee.2012.06.020

31. C. D. Michener, *The Bees of the World* (Johns Hopkins Univ. Press, Baltimore, 2000).

32. B. Smith, J. B. Wilson, A consumer's guide to evenness indices. *Oikos* 76, 70 (1996). doi:10.2307/3545749

33. E. C. Pielou, *Ecological Diversity* (Wiley, New York, 1975).

34. C. Kremen, N. M. Williams, R. W. Thorp, Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. U.S.A.* 99, 16812 (2002). doi:10.1073/pnas.262413599 Medline

35. C. Schüepp, J. D. Herrmann, F. Herzog, M. H. Schmidt-Entling, Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. *Oecologia* 165, 713 (2011). doi:10.1007/s00442-010-1746-6 Medline

36. R. Bommarco, O. Lundin, H. G. Smith, M. Rundlöf, Drastic historic shifts in bumble-bee community composition in Sweden. *Proc. R. Soc. London Ser. B* 279, 309 (2012). doi:10.1098/rspb.2011.0647 Medline

37. O. Lundin, M. Rundlöf, H. G. Smith, R. Bommarco, Towards integrated pest management in red clover seed production. *J. Econ. Entomol.* 105, 1620 (2012). doi:10.1603/EC12179 Medline

38. R. Winfree, N. M. Williams, H. Gaines, J. S. Ascher, C. Kremen, Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J. Appl. Ecol.* 45, 793 (2008). doi:10.1111/j.1365-2664.2007.01418.x

39. R Development Core Team, R: A Language and Environment for Statistical Computing (2011) (www.r-project.org).

40. A. Gelman, J. Hill, *Data Analysis Using Regression and Multilevel/Hierarchical Models* (Cambridge Univ. Press, Cambridge, 2007).

41. D. Bates, M. Maechler, B. Bolker, lme4: Linear Mixed-Effects Models Using s4 Classes (2011).

42. S. S. Qian, T. F. Cuffney, I. Alameddine, G. McMahon, K. H. Reckhow, On the application of multilevel modeling in environmental and ecological studies. *Ecology* 91, 355 (2010). doi:10.1890/09-1043.1 Medline

43. J. B. Johnson, K. S. Omland, Model selection in ecology and evolution. *Trends Ecol. Evol.* 19, 101 (2004). doi:10.1016/j.tree.2003.10.013 Medline

44. S. A. Richards, Testing ecological theory using the information-theoretic approach: Examples and cautionary results. *Ecology* 86, 2805 (2005). doi:10.1890/05-0074

45. A. F. Zuur, E. N. Ieno, N. J. Walker, A. A. Saveliev, G. M. Smith, *Mixed Effects Models and Extensions in Ecology with R* (Springer, New York, 2009).

46. D. O. Stram, Meta-analysis of published data using a linear mixed-effects model. *Biometrics* 52, 536 (1996). doi:10.2307/2532893 Medline

47. S. A. Smith-Warner *et al.*, Methods for pooling results of epidemiologic studies: The pooling project of prospective studies of diet and cancer. *Am. J. Epidemiol.* 163, 1053 (2006). doi:10.1093/aje/kwj127 Medline

48. A.-M. Klein, I. Steffan-Dewenter, T. Tscharntke, Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc. R. Soc. London Ser. B* 270, 955 (2003). doi:10.1098/rspb.2002.2306 Medline

49. A.-M. Klein, Nearby rainforest promotes coffee pollination by increasing spatio-temporal stability in bee species richness. *For. Ecol. Manage.* 258, 1838 (2009). doi:10.1016/j.foreco.2009.05.005

50. T. H. Ricketts, Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv. Biol.* 18, 1262 (2004). doi:10.1111/j.1523-1739.2004.00227.x

51. T. H. Ricketts, G. C. Daily, P. R. Ehrlich, C. D. Michener, Economic value of tropical forest to coffee production. *Proc. Natl. Acad. Sci. U.S.A.* 101, 12579 (2004). doi:10.1073/pnas.0405147101 Medline

52. E. I. Badano, C. H. Vergara, Potential negative effects of exotic honey bees on the diversity of native pollinators and yield of highland coffee plantations. *Agric. For. Entomol.* 13, 365 (2011). doi:10.1111/j.1461-9563.2011.00527.x

53. A.-M. Klein, I. Steffan-Dewenter, T. Tscharntke, Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *J. Appl. Ecol.* 40, 837 (2003). doi:10.1046/j.1365-2664.2003.00847.x

54. S. Krishnan, C. G. Kushalappa, R. U. Shaanker, J. Ghazoul, Status of pollinators and their efficiency in coffee fruit set in a fragmented landscape mosaic in South India. *Basic Appl. Ecol.* 13, 277 (2012). doi:10.1016/j.baae.2012.03.007

55. M. B. T. Munyuli, Micro, local, landscape and regional drivers of bee biodiversity and pollination services delivery to coffee (*Coffea canephora*) in Uganda. *Int. J. Biodivers. Sci. Ecosyst. Serv. Manage.* 8, 190 (2012). doi:10.1080/21513732.2012.682361

56. V. Boreux, S. Krishnan, K. G. Cheppudira, J. Ghazoul, Impact of forest fragments on bee visits and fruit set in rain-fed and irrigated coffee agro-forests. *Agric. Ecosyst. Environ.* 10.1016/j.agee.2012.05.003 (2012). doi:10.1016/j.agee.2012.05.003 Medline

57. N. P. Chacoff, M. A. Aizen, Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *J. Appl. Ecol.* 43, 18 (2006). doi:10.1111/j.1365-2664.2005.01116.x

58. K. R. Blanche, J. A. Ludwig, S. A. Cunningham, Proximity to rainforest enhances pollination and fruit set in orchards. *J. Appl. Ecol.* 43, 1182 (2006). doi:10.1111/j.1365-2664.2006.01230.x

59. L. G. Carvalheiro, C. L. Seymour, S. W. Nicolson, R. Veldtman, Creating patches of native flowers facilitates crop pollination in large agricultural fields: Mango as a case study. *J. Appl. Ecol.* 49, 1373 (2012). doi:10.1111/j.1365-2664.2012.02217.x

60. J. Hipólito de Sousa, C. M. Pigozzo, B. F. Viana, Polinizaçao de manga (*Mangifera indica* L. - Anacardiaceae) variedade Tommy Atkins, no vale do Sao Francisco, Bahia. *Oecol. Austral.* 14, 165 (2010). doi:10.4257/oeco.2010.1401.09

61. M. M. Mayfield, The importance of nearby forest to known and potential pollinators of oil palm (*Elaeis guineënsis* Jacq.; Areceaceae) in southern Costa Rica. *Econ. Bot.* 59, 190 (2005). doi:10.1663/0013-0001(2005)059[0190:TIONFT]2.0.CO;2

62. T. H. Ricketts *et al.*, Landscape effects on crop pollination services: Are there general patterns? *Ecol. Lett.* 11, 499 (2008). doi:10.1111/j.1461-0248.2008.01157.x Medline

63. A.-M. Klein *et al.*, Wild pollination services to California almond rely on semi-natural habitat. *J. Appl. Ecol.* 49, 723 (2012).

64. S. S. Greenleaf, C. Kremen, Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biol. Conserv.* 133, 81 (2006). doi:10.1016/j.biocon.2006.05.025

65. R. Isaacs, A. K. Kirk, Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *J. Appl. Ecol.* 47, 841 (2010). doi:10.1111/j.1365-2664.2010.01823.x

66. G. Carré *et al.*, Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agric. Ecosyst. Environ.* 133, 40 (2009). doi:10.1016/j.agee.2009.05.001

67. H. Taki *et al.*, Effects of landscape metrics on *Apis* and non-*Apis* pollinators and seed set in common buckwheat. *Basic Appl. Ecol.* 11, 594 (2010). doi:10.1016/j.baae.2010.08.004

68. A. Holzschuh, J. H. Dudenhöffer, T. Tscharntke, Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biol. Conserv.* 153, 101 (2012). doi:10.1016/j.biocon.2012.04.032

69. T. H. Ricketts, N. M. Williams, M. M. Mayfield, in *Connectivity for Conservation*, M. Sanjayan, K. Crooks, Eds. (Cambridge Univ. Press, Cambridge, 2006), pp. 255–289.

70. B. G. Howlett, M. K. Walker, L. E. Newstrom-Lloyd, B. J. Donovan, D. A. J. Teulon, Window traps and direct observations record similar arthropod flower visitor assemblages in two mass flowering crops. *J. Appl. Entomol.* 133, 553 (2009). doi:10.1111/j.1439-0418.2009.01395.x

71. R. Bommarco, L. Marini, B. E. Vaissière, Insect pollination enhances seed yield, quality, and market value in oilseed rape. *Oecologia* 169, 1025 (2012). doi:10.1007/s00442-012-2271-6 Medline

72. R. Rader, B. G. Howlett, S. A. Cunningham, D. A. Westcott, W. Edwards, Spatial and temporal variation in pollinator effectiveness: Do unmanaged insects provide consistent pollination services to mass flowering crops? *J. Appl. Ecol.* 49, 126 (2012). doi:10.1111/j.1365-2664.2011.02066.x

73. R. Rader *et al.*, Alternative pollinator taxa are equally efficient but not as effective as the honeybee in a mass flowering crop. *J. Appl. Ecol.* 46, 1080 (2009). doi:10.1111/j.1365-2664.2009.01700.x

74. R. da Silva Guedes *et al.*, Déficit de polinização da aceroleira no período seco no semíarido paraibano. *Rev. Bras. Frutic.* 33, 465 (2011). doi:10.1590/S0100-29452011005000060

75. J. B. Free, *Insect Pollination of Crops* (Academic Press, London, 1993).

76. N. Joseph, E. A. Siril, G. M. Nair, Reproductive characterization and preliminary studies on controlled breeding of Annatto (*Bixa orellana* L.). *Plant Syst. Evol.* 298, 239 (2012). doi:10.1007/s00606-011-0541-0

77. K. M. Medeiros de Siquiera *et al.*, Estudo comparativo da polinização em variedades de aceroleiras (*Malpighia emarginata* DC, Malpighiaceae). *Rev. Caatinga* 24, 18 (2011).

78. R. Rivera-Madrid *et al.*, Preliminary studies toward genetic improvement of annatto (*Bixa orellana* L.). *Sci. Hortic.* 109, 165 (2006). doi:10.1016/j.scienta.2006.03.011

79. D. W. Roubik, *Pollination of Cultivated Plants in the Tropics* (Food and Agriculture Organization of the United Nations, Rome, 1995).