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

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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. Here we show universally positive associations of fruit set with wild-insect visits to flowers in 41 crop systems worldwide, and thus clearly demonstrate their agricultural value. In contrast, fruit set increased significantly with visitation by honey bees in only 14% of the systems surveyed. Overall, wild insects pollinated crops more effectively, because increase in their visitation enhanced fruit set by twice as much as an equivalent increase in honey bee visitation. Further, visitation by wild insects and honey bees promoted fruit set independently, so high abundance of 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. 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 provided by wild insects is one such vulnerable ecosystem service (*3*), as their abundance and diversity 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 declines in wild pollinators on crop yields is largely unknown, as is whether increasing application of honey bees (*9*) compensates for losses of wild pollinators, or even promotes these losses.

Wild insects may increase the proportion of flowers that develop into mature fruits or seeds (fruit set), and therefore crop yield (e.g., Kg ha^{-1}, fig. S1), by contributing to pollinator abundance, species number (richness), and (or) equity in relative species abundance (evenness). Increased pollinator abundance, and therefore visitation rate to crop flowers, should augment fruit set at a decelerating rate until additional individuals do not further increase (e.g., pollen saturation), or even decrease (e.g., pollen excess) fruit set (*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 assumption 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: (1) for most crops, wild-insect and honey bee visitation enhances pollen deposition on stigmas of flowers; (2) consequently, for most crops, wild-insect and honey bee visitation improves fruit set; (3) visitation by wild insects promotes fruit set only when honey bees visit infrequently (i.e., negatively interacting effects between wild-insect visitation and honey bee visitation); and (4) pollinator assemblages with more species benefit fruit set only when honey bees visit infrequently (i.e., negatively interacting effects 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 wide array of animal-pollinated, annual and perennial fruit, seed, nut, and stimulant crops; predominately wind-pollinated crops were not considered (fig. S2 and table S1). Sampled fields were subject to a diversity of agricultural practices, ranging from extensive monocultures to small and diversified systems (fig. S2 and table S1), fields stocked with low to high densities 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 (a key component of crop yield, 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 based on Akaike's 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, do not include zero) in seven of ten crop systems, and wild insects in ten 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 systems (Fig. 2B). In addition, fruit set increased twice as strongly with visitation by wild insects than by honey bees (Fig. 2A). These partial regression coefficients did not differ simply because of unequal abundance, or 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%; $CI_{95\%}$ = 40-62%), and among-field CVs for visitation by honey bees (mean = 73%; $CI_{95\%}$ = 57-88%) and by wild insects (mean = 79%; $CI_{95\%}$ = 62-96%) 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). Moreover, wild-insect visitation alone predicted fruit set better than honey bee visitation alone (Δ_{AIC} = 16, model F vs. M in table S4). 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 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 exceeds that for wild insects (Fig. 2A), indicating 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 insect foraging behavior, based 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 on fruit set of wild-insect visitation, suggest that management to promote diverse wild insects has great potential to improve global yield of animal-pollinated crops.

The third prediction was also not supported, as fruit set increased consistently 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 both visitation by wild insects and honey bees (model P in table S4), suggesting that managed honey bees supplement the pollination service of wild insects, but cannot replace it. Overall, visitation by wild insects and honey bees were not correlated among fields (fig. S10), providing no evidence for either competition for the resources obtained from crop flowers (pollen, nectar), or 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, although insect polli-

nators appear not to be limited by crop floral resources, 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 (model B vs. G in table S4). However, richness did not enhance model fit when added to a model with wild-insect visitation (model F vs. G in table S4), suggesting that the effects of richness on fruit set reflect increased wild-insect visitation (i.e., co-linear 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 species experience less visitation by wild insects and reduced fruit set, independent of species evenness or honey bee visitation. Globally, wild-insect visitation signals both species richness and pollination services, and is a relatively inexpensive indicator that can be standardized easily 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 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 demonstrate 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 or 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 both wild insects as ecosystem service providers, and 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 semi-natural 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 transcend the supply of pollination services alone and extend to, for example, mitigation against soil erosion, and improved pest control, nutrient cycling and water use efficiency (30). Without such changes, the on-going loss of wild insects (4, 5) is destined to compromise agricultural yields worldwide.

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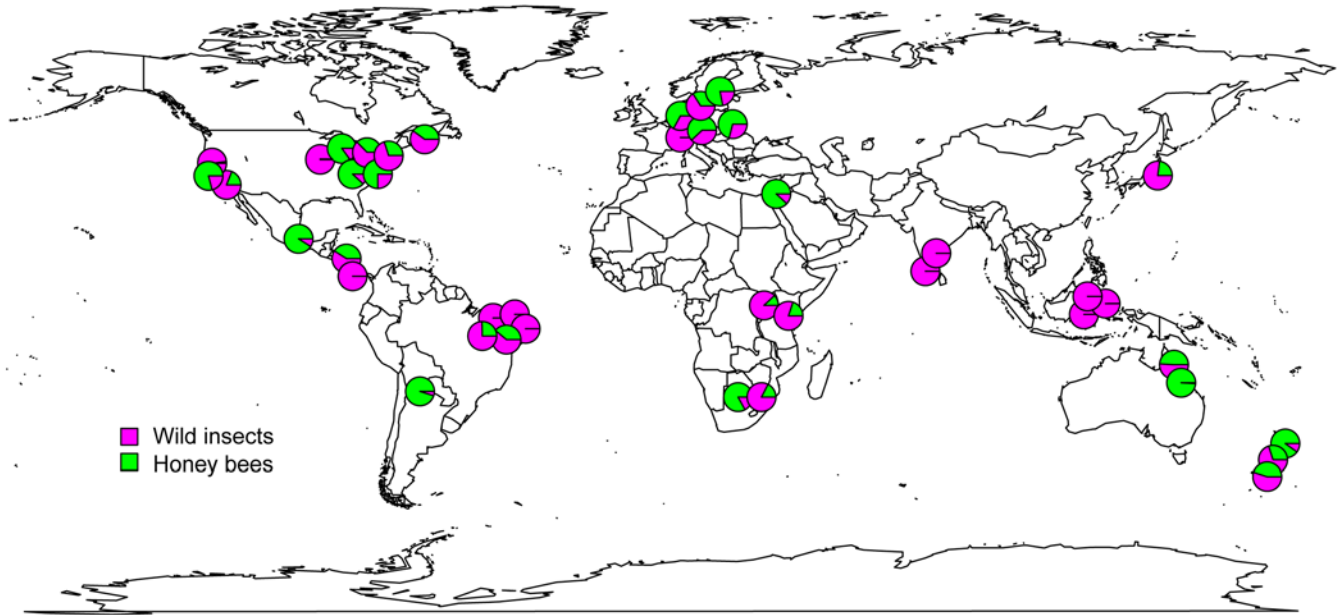
Fig. 1. Locations of the 41 crop systems studied. Symbols indicate the percentage of total visitation rate to crop flowers contributed by honey bees (*Apis mellifera* L.) and wild insects. Honey bees occur as domesticated colonies in transportable hives worldwide, as a native species in Europe (rarely) and Africa, or as feral populations in all other continents, except Antarctica.
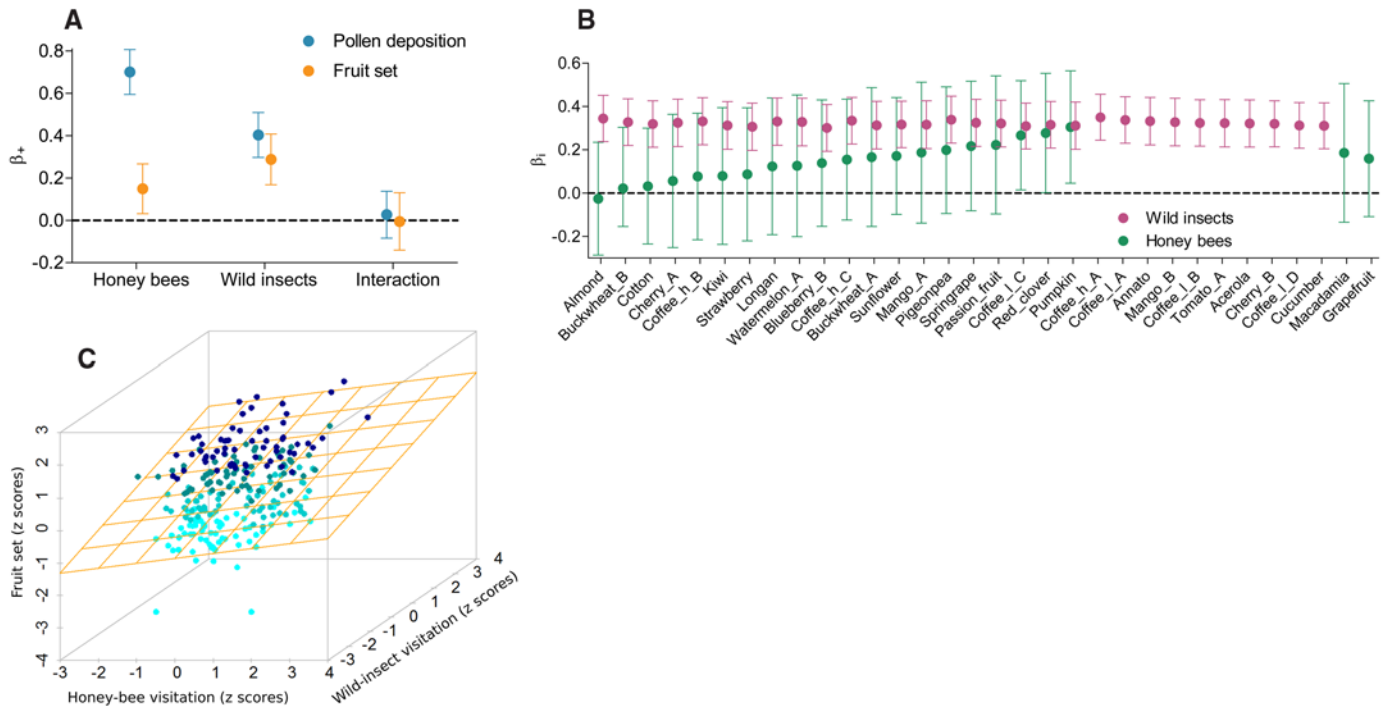
Fig. 2. Visitation rate to crop flowers by wild insects enhances reproduction in all crops examined (regression coefficient, $\beta_i >$ 0), whereas honey bee visitation has weaker effects overall. (**A**) Overall partial regression coefficients ($\beta_+ \pm 95\%$ confidence interval) for the direct 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 ($\beta_i \pm 95\%$ confidence interval) represent the effects of visitation by wild insects or honey bees on fruit set 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 comparison of regression coefficients in all panels. Letters after the crop name 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 side of the figure). 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).
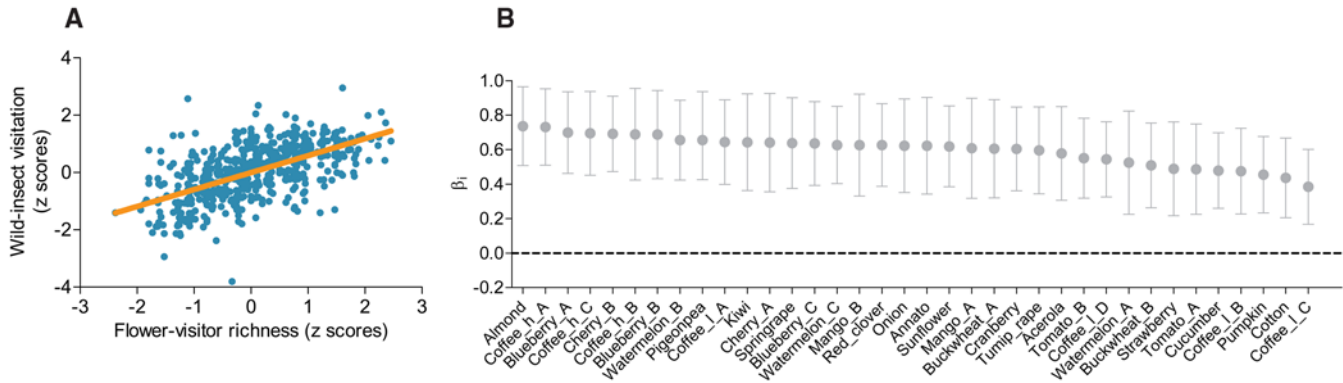
Fig. 3. Globally, visitation rate to crop flowers by wild insects increases with flower-visitor richness. (**A**) The line is the overall regression, and each point is a field in a crop system. (**B**) Slopes (β_i ± 95% confidence interval) represent the effect of richness on wild-insect visitation for 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.