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Crop production in the USA is frequently limited by a lack of pollinators

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Most of the world's crops depend on pollinators, so declines in both managed and wild bees raise concerns about food security. However, the degree to which insect pollination is actually limiting current crop production is poorly understood, as is the role of wild species (as opposed to managed honeybees) in pollinating crops, particularly in intensive production areas. We established a nationwide study to assess the extent of pollinator limitation in seven crops at 131 locations situated across major crop-producing areas of the USA. We found that five out of seven crops showed evidence of pollinator limitation. Wild bees and honeybees provided comparable amounts of pollination for most crops, even in agriculturally intensive regions. We estimated the nationwide annual production value of wild pollinators to the seven crops we studied at over $1.5 billion; the value of wild bee pollination of all pollinator-dependent crops would be much greater. Our findings show that pollinator declines could translate directly into decreased yields or production for most of the crops studied, and that wild species contribute substantially to pollination of most study crops in major crop-producing regions.

1. Introduction

Pollination by insects is a critical ecosystem service that is necessary for production of most crops, including those providing essential micronutrients,

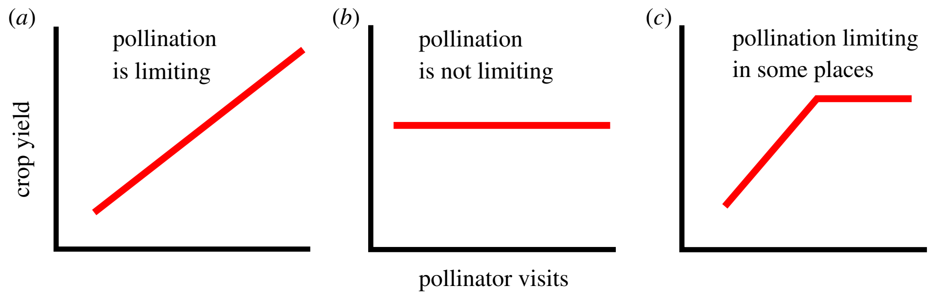

Figure 1. Conceptual figure showing the general relationship between pollinator visitation (or pollen deposition) and crop yield. As the number of visits from pollinators increases, crop yield is expected to increase until the crop is fully pollinated, at which point the relationship reaches an asymptote. Data from a particular farm or set of farms may indicate the full asymptotic relationship, as shown in (*c*), or they may fit a strictly positive relationship (*a*), or no relationship at all (*b*), corresponding to lower or higher sections of the full visits versus yield relationship in (*c*). (Online version in colour.)

and is thus essential for food security [1]. In the USA, the production of pollinator-dependent crops is valued at over $50 billion per year [2,3]. Recent evidence that both European honeybees (*Apis mellifera*) and some native wild bee species are declining [4–6] raises concern about negative impacts on crop yield (amount produced per area). However, a decline in pollinators will only affect crop yield if yield is limited by a lack of pollination. Research on pollinator limitation, or the degree to which a lack of pollinators is restricting full seed or fruit production, has focused mainly on wild plant species [7–8], with little information available about the frequency or circumstances in which pollination limits crop production [9–13].

Theoretically, for any pollinator-dependent crop, we expect a relationship between pollination and crop yield, such that yield increases with pollination until the crop is fully pollinated, at which point additional pollinators contribute no further service (figure 1) [7]. When a crop is pollination limited, we expect a positive relationship between pollination and yield, such that crop fields receiving more pollination also produce higher yields. Conversely, if pollination is not limiting, we expect no relationship between pollination and yield. Across farms that differ in pollination, we would expect farms with lower visitation to show lower yield, but there might not be a relationship between visitation and yield among farms with high visitation rates. Pollination may not be limiting for two fundamentally different reasons. First, yield is not pollination limited if the crop plant's pollination threshold is met (i.e. the number of pollen grains deposited is sufficient for maximum fruit production under ideal growth conditions). Second, even if the plant's pollination threshold is not met, pollination will not be a limiting factor if some other factor is more limiting to yield (e.g. [14–16]). Common limiting factors for crop production include a lack of water or nutrients (fertilizer) and injury from plant pests and diseases [7,17]. When other factors are limiting, crop yield will not increase with increasing pollination, even if pollination is insufficient. Thus, we expect that commercial farms, which typically have high inputs for irrigation, fertilizer and pest management, would be particularly sensitive to deficits in pollination. However, whether intensively managed crops in major production areas are in fact limited by pollination has rarely been tested (but see [12]).

In many agricultural situations, pollination is provided by a combination of managed honeybees (or sometimes other managed bees) and wild insects (primarily wild bees). While honeybees have long been considered the most economically valuable pollinators, recent global syntheses have revealed that wild pollinators are often as abundant as honeybees on crop flowers [18–20], and that the diversity of wild bee visitors is higher when crops are grown in their biogeographic region of origin [21]. Furthermore, flower visits by wild bees are more strongly correlated with crop yields than are visits by honeybees [18,22,23]. The reason for this association is not known, but could include some wild bee species depositing more pollen per visit than honeybees [22,24], wild bees moving more often between compatible plants, or wild bees increasing the pollination provided by honeybees through interspecific interactions [25,26]. Wild pollinators might be contributing significantly to crop pollination at the national scale in the USA, but this has not been evaluated in a comprehensive way.

An ideal nationwide assessment of crop pollination should study multiple economically important bee-pollinated crops, each in its main region(s) of production. An assessment should also capture the effects of typical management practices, including honeybee stocking rates. We expect high stocking density in major production regions because in intensively managed landscapes many wild bee species have reduced abundance or fail to persist [24,27–30]. Thus, in the settings where most crop production occurs, the contribution of wild bees might be considerably less than that of honeybees.

The economic value of honeybees and wild bees can be estimated based on their relative contributions to crop pollination. The production value method, which has most often been used to economically value pollination [2,31], begins with the market value (price × quantity) of the crop and attributes to pollinators the fraction of this value that would be lost in the absence of pollination. This fraction can be less than the entire market value for crops that still produce some yield when pollinators are absent [32]. This total economic value can then be partitioned into components attributable to honeybees and to wild bees. Estimates from the production value method are best interpreted as short term, on a time scale in which alternative strategies such as switching to less pollinator-dependent varieties are not available [33].

In this paper, we report the results of a national-scale empirical study of seven pollinator-dependent crops and 131 commercially managed fields across the USA and part of Canada. We answer the following questions. (i) How prevalent is pollinator limitation? (ii) What are the relative contributions of wild bees and the honeybees to crop production or yields? (iii) How do these contributions translate into economic value?

2. Methods

(a) Study design

We collected data on insect pollination and crop production for highbush blueberry (*Vaccinium corymbosum*), apple (*Malus pumila*), sweet cherry (*Prunus avium*), tart cherry (*Prunus cerasus*), almond (*Prunus dulcis*), watermelon (*Citrullus lanatus*) and pumpkin (*Cucurbita pepo*) at farms across the USA and part of Canada (electronic supplementary material, figure S1). All of these crops depend very strongly or absolutely on insect pollination [32]. For each crop, we selected study farms within economically important areas for the national production of that crop, so these farms were representative of the majority of production in terms of growing conditions, pollinator communities and farm management practices. In addition, the individual farm fields selected were reasonably large and well-maintained as per standard agricultural practice, and were growing a regionally common cultivar. All fields were stocked with honeybee hives at rates typical for the region. For pumpkin and apple in Pennsylvania, not all farmers routinely stock honeybees because native bees are thought to provide sufficient pollination (e.g. [34]). However, even when honeybees were not stocked at our study sites, they were still found on crop flowers.

(b) Data collection: pollinator visitation rates and crop production metrics

Within each crop field, insect pollinators were observed during bloom along four 100 m transects, positioned approximately 0, 25, 50 and 100 m into the field from one edge. Along each transect, observers stopped every few metres and observed a small patch of flowers to which all visiting bees could reliably be counted. Each visiting bee was identified to an on-the-wing species group, such as '*Bombus*', '*Xylocopa*' or 'green bee' (electronic supplementary material, table S2). Bee species were grouped based on body size and hairiness, which are the two main predictors of pollen deposition per visit [35,36]. Honeybees were always identified uniquely to species. In each year (two or three years depending on crop), bees were counted on up to three different days during peak crop bloom, and up to three times per day, during weather conditions when bees were active. Methods for observing bee visits were standardized to the extent possible, but also tailored to each crop based on, for example, the density and distribution of flowers. Crop-specific visitation assessment protocols are listed in electronic supplementary material, table S3.

Crop production data were collected for each crop field within the same four transects where bee observations were performed. In each transect, production was assessed for a standard number of trees (orchard crops), bushes (berry crops) or quadrats (field crops). For each crop, we measured a crop production variable that was potentially related to pollination and also relevant to economic value. We used fruit weight when available or otherwise fruit set or number of fruit. Thus for some crops (watermelon and pumpkin), our crop production measurements are explicitly per area and thus correspond directly to yield. For the other crops, our measurements are not explicitly per area and are thus better referred to more generally as 'production'. Regardless, our measures of production match commonly used proxies for yield in the insect pollination literature [18,37]. Flower counts were performed during peak bloom, then paired later with post-bloom fruit counts from the same sample locations to determine fruit set. Fruit weights and fruit counts were measured just prior to harvest. Crop-specific protocol details are listed in electronic supplementary material, table S4.

(c) Analysis 1: frequency of pollinator limitation

To measure the frequency of pollinator limitation across all locations for a given crop, we created three potential statistical models relating the number of bee visits observed to crop production and used AIC to choose between them (figure 1; electronic supplementary material, Methods). The three models were: (i) a linear positive relationship, implying that all locations were pollinator limited; (ii) no relationship (an intercept only model), implying that no locations were limited; or (iii) an asymptotic (piecewise) regression model in which production increases with visitation to a certain visit rate breakpoint, then remains flat, implying that the crop is pollinator limited in some locations and not others. If the third model was selected, we estimated the frequency of pollinator limitation as the proportion of locations falling below the breakpoint.

(d) Analysis 2: contribution of honeybees versus wild bees

For each crop, the fraction of total pollen grains deposited by honeybees and each species group of wild bee was estimated by multiplying flower visits by that bee group (data collection described above) with an estimate of pollen grains deposited per visit (pollinator efficiency) for that group, and then calculating the proportion of the total pollination provided by each bee group (details in electronic supplementary material, Methods). Values of pollinator efficiency were taken from the literature and are listed in electronic supplementary material, table S2, along with associated sample sizes.

(e) Analysis 3: economic valuation

The economic value delivered to each crop in each state by honeybees and wild bees was calculated using the equation

$$V_{\text{pollinator}} = V_{\text{crop}} \cdot D \cdot P_{\text{pollinator}}, \tag{2.1}$$

where $V_{\text{pollinator}}$ is the annual economic value attributable to a particular pollinator group (either wild bees or honeybee), V_{crop} is the annual production value of the crop, D is the pollinator dependency value for the crop (the proportion by which yield is reduced in the absence of pollination [32]) and $P_{\text{pollinator}}$ is the proportion of total pollination of the crop provided by the pollinator group, as estimated above.

Our approach updates previous national-scale estimates of the value of wild and honeybee pollination in several ways. First, previous national valuations (e.g. [2,38]) did not have access to empirical data for the percentage of pollinator visits provided by each pollinator group ($P_{\text{pollinator}}$), but rather assumed a P_{honeybee} value of 0.9 for crops in which honeybees were routinely supplied, unless expert opinion suggested the use of a different value [39]. In our study, we actually measured honeybee and wild bee visitation to each crop. Second, most previous studies come from one area in the USA, which often is not within the main production area for the crop. Our field sites were in states that are among the top national producers of each crop (electronic supplementary material, table S5), which is essential when such estimates are used to extrapolate to national value. Third, we based our economic valuations on estimated pollen deposition by each type of pollinator (by weighting flower visitation rates by the number of pollen grains deposited per flower visit), not merely on flower visitation rates, as has been done by most previous national-scale valuations. Details of our valuation methods, including

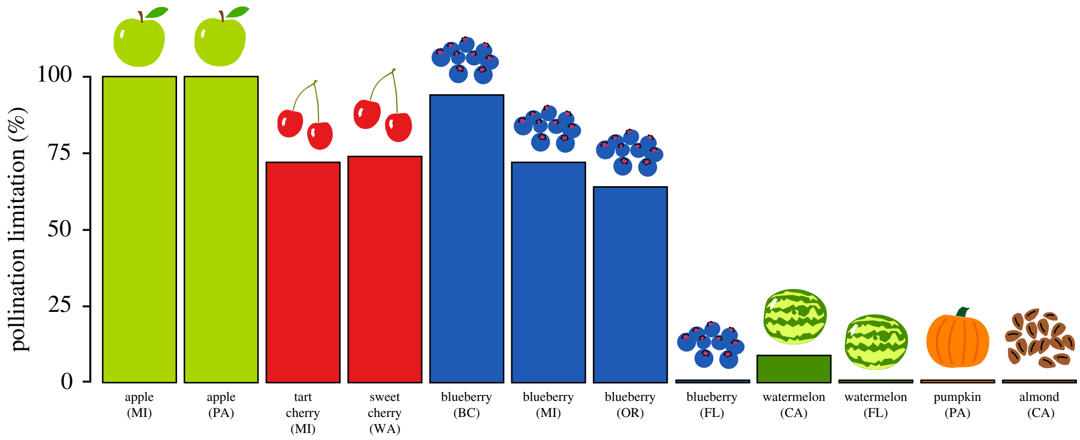

Figure 2. Frequency of study transects predicted to be pollination limited using the AIC selection method. The best of three models were selected by AIC: (i) limitation across all sampling locations; (ii) limitation at no sampling locations; and (iii) limitation at lower levels of visitation, but not at higher levels of visitation. If model 3 was selected, limitation frequency is the percentage of transects occurring below the model-estimated breakpoint between the positive relationship between visits and crop production or yield, and no relationship. (Online version in colour.)

extrapolations to the national level, are discussed in the electronic supplementary material, Methods.

3. Results

(a) Frequency of pollinator limitation

For each crop–state combination in our study, we used AIC model selection to estimate the frequency of pollinator limitation (figure 2; electronic supplementary material, tables S6 and S7). For tart cherry in Michigan, sweet cherry in Washington, and for blueberry in Michigan, Oregon and British Columbia, we found evidence of pollinator limitation for most sampled areas (64–94% of transects). For watermelon, pumpkin and almond, we found little to no evidence of pollinator limitation. For apple in both Michigan and Pennsylvania, the best model was a linear relationship between visitation and crop production across all transects with no evidence of an asymptote, suggesting pollinator limitation across all sampled areas. Apples are typically thinned to achieve fruit that meet fresh-market standards; thus, our apple fruit counts were taken post-thinning to be more directly related to harvestable yield. This is a conservative approach, because post-thinning measurements are less likely than those taken pre-thinning to detect the effect of pollinator limitation. Plots of best-fit lines for each of the three models and estimated breakpoints between limiting and asymptotic pollination are shown in electronic supplementary material, figure S2. For blueberry, we performed a second analysis of pollen limitation using additional field data from hand-pollination experiments (electronic supplementary material, supplementary analysis 3). Results from this analysis were qualitatively similar to the results from the main analysis, in that they showed pollen limitation in farms with lower visitation, but not in farms with higher visitation (i.e. the segmented relationship was selected) for northern blueberry and showed no evidence of pollen limitation in Florida blueberry.

(b) Contribution of honeybees versus wild bees

On average across the 13 crop–state combinations measured in our study, 74% of observed visits were performed by honeybees and the other 26% by wild bees. However, this proportion differed greatly by crop (electronic supplementary material, figure S3). Wild bee visits accounted for the largest proportion in pumpkin (74.6%) and the lowest in almond (0%). The proportion of wild bee visits was higher for cherry and apple (average of 43.5% in sweet cherry, 34.7% in tart cherry, and 32.9% in apple) than for blueberry (average of 8.9%). The proportion of visits from each type of bee was remarkably consistent across states within each crop, with the exception of watermelon, for which wild bees were four times as abundant in Florida as compared with California.

Incorporating the data on pollen deposition per visit into the calculations increased the relative contribution of wild bees for most crops (figure 3). Although visitation rates of honeybees were higher than those of wild bees in apple and tart cherry, the amount of pollen deposited by wild bees was equal or even somewhat greater because wild bee groups deposited an estimated 1.5 to 2 times more pollen per visit in these crops (electronic supplementary material, table S2). Wild bees contributed slightly more in Florida watermelon, and continued to be dominant in pumpkin. Incorporating pollen deposition per visit into calculations for blueberry, almond and California watermelon made little difference due to the low abundance of wild bees. The exception was sweet cherry, in which wild bees provided 43% of visits, but only 28% of pollen deposition. This was because the most abundant wild pollinators in this system were bumblebees, which have been shown to be ineffective pollinators of cherry flowers [40].

(c) Economic valuation

For the crops in our study, a high value of wild bees was estimated when the relative importance of wild bees was greater than that of honeybees (e.g. in pumpkin in Pennsylvania), or when the value of the crop was high overall (e.g. in Washington cherry and Michigan apple). However, for almond, which had the largest total national value, the subset of value attributable to wild bees was negligible because they were very rare or absent in the observations of pollinators in those farms. At the national level, we estimated the value of wild pollinators to be highest in apple, with a value of \$1.06 billion, with significant value also in sweet cherry

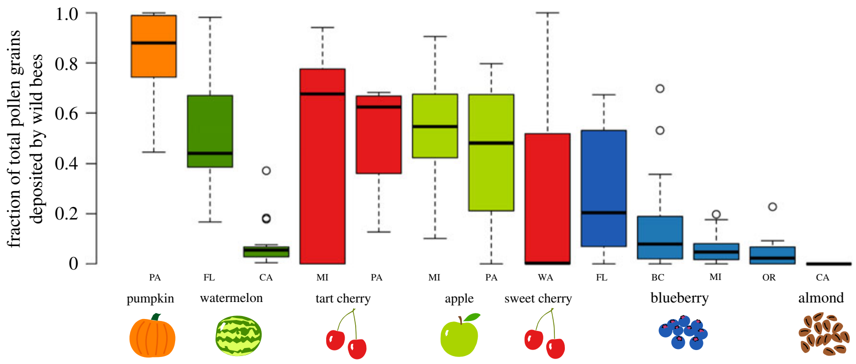

Figure 3. Boxplots of relative pollen deposition rate of wild bees (as a proportion of total pollen deposition) across the crop–region combinations in our study. Estimates of pollen deposition were based on visits × pollen deposition per visit for each type of pollinator observed (electronic supplementary material, table S2), with the remainder of pollen deposition provided by honeybees. Black line is the median, boxes show the first and third quartiles, and whiskers extend to 1.5 times the interquartile range or to the most extreme data point. The number of farms and years differed by crop (electronic supplementary material, table S7). (Online version in colour.)

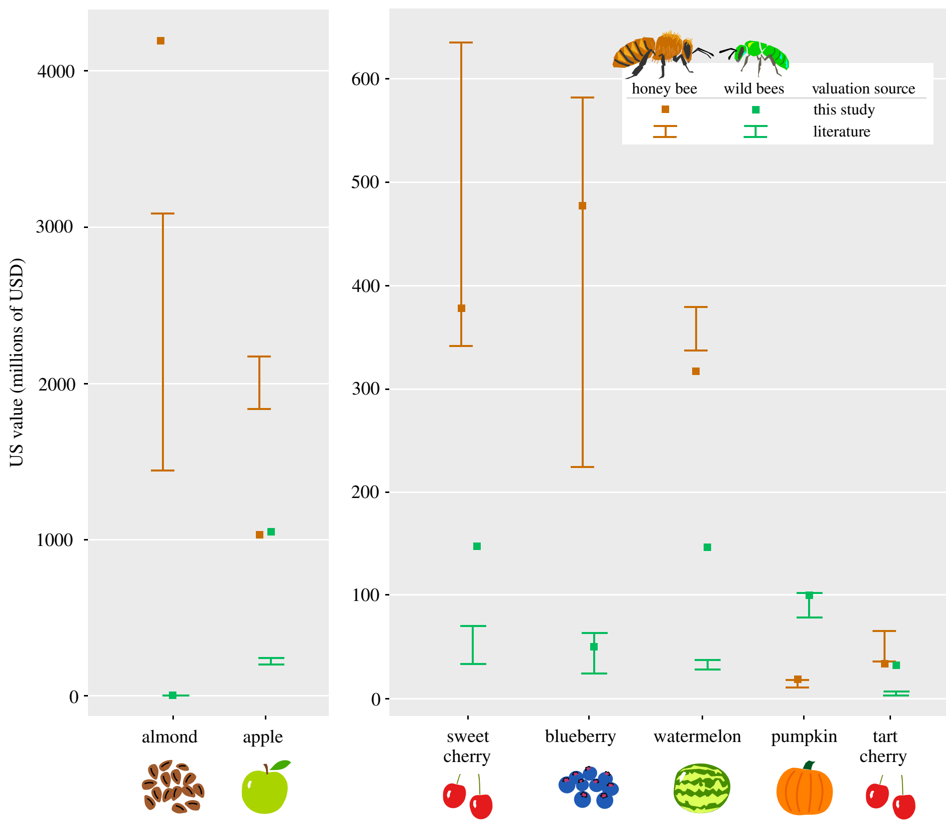

Figure 4. Value estimates for honeybee (orange) and wild bees (green), extrapolated to the level of the United States. Bars encompass the range of estimates in the published literature [2,39]. Square points show our final value estimates. Our estimates differ from literature estimates for several reasons: (i) we used new data on flower visitation rates collected in important production areas for each crop, (ii) we used updated pollinator dependency values from [32], (iii) we transformed our visitation rates into pollen deposition rates by incorporating pollen deposition per visit estimates from the literature and (iv) we sampled in large-scale commercial farms. All values have been adjusted to 2015 dollars. (Online version in colour.)

($145 million), watermelon ($146 million), pumpkin ($101 million), blueberry ($50 million) and tart cherry ($32 million) (figure 4), totalling approximately $1.5 billion across these crops alone. By contrast, wild bees provided very limited value to almond (actually $0 based on our study farms). The economic value of honeybees to crop yield across these crops, when estimated in the same manner, totalled about $6.4 billion, with this value dominated by their $4.2 billion value to almond. An alternative analysis that accounts for the potential for farmers to reduce financial losses by limiting other input costs when pollination fails and the crop will not be harvested is presented as electronic supplementary material, analysis 1. Using this method, estimated values are considerably lower for both wild bees and honeybees because variable production costs are subtracted from the yield value attributable to bees.

4. Discussion

Global reliance on pollinator-dependent crops has increased over the past several decades [1,41], while wild and managed pollinators have declined in many places (e.g. [5,42,43]), prompting concern that pollinator limitation could pose a risk to yield stability and food security [44,45]. In a multi-region study focusing on major production regions for fruits, vegetables and nuts in North America, we found evidence of pollinator limitation in five of the seven pollinator-dependent crops we examined. This is consistent with a growing body of literature that suggests pollination may be limiting across a wide range of crops worldwide [11–13,18,44,46]. An earlier meta-analysis found little or no evidence of limitation in most global crop systems [47], but these conclusions were based on an indirect analysis of temporal trends in yield, rather than measuring the relationship between bee abundance and yield directly. Our new evidence of pollinator limitation is particularly valuable in comparison to previous analyses, because we specifically targeted larger commercial farms that represent the context for the majority of production.

We found the overall contribution of wild bees to be similar to (or higher than) that of honeybees in most of the crops we studied (figure 3). This result is in contrast to our expectation that sampling in agriculturally intensive areas would reveal greatly reduced wild bee contributions to crop pollination. Our data suggest that instead, wild bees are able to persist in many of these managed landscapes and make a significant, although variable, contribution to crop pollination. Furthermore, in all six crops we studied, the wild bee species, on average, deposited more pollen per visit than did the honeybee, by a factor of 1.4 to 3.2. (electronic supplementary material, table S2 and figure S4). We found a predominance of pollination by honeybees in certain crops (blueberry, California watermelon and almond), and this may be due to landscape factors, farm management intensity and/or pesticide use patterns that limit the ability of wild bees to persist and contribute to crop yield in these crops, in addition to differences in honeybee stocking rates. For instance, in California almond, visitation rates by wild bees are much lower (or more often non-existent) in the large-scale orchards we surveyed than in smaller farms surrounded by natural habitat [48] where much of the previous research on wild bees and almond pollination has been conducted. This pattern has also been seen in watermelon [24] and blueberry [10].

Our study reconciles previous conflicting evidence for the relative importance of honeybees, a managed agricultural input that growers must pay for each year, and wild bees, which provide a free ecosystem service, in pollination of crops grown across the United States. Previous national-level studies of the USA have estimated honeybees to be much more important than wild bees [2,38,39], but did not actually measure wild bee abundance in crop fields. By contrast, more recent syntheses of global literature have concluded wild bees may be at least as important as honeybees, if not more so [18,19,28]. We found that wild bee abundance on crop flowers in major US and Canadian production regions is higher than previously thought, and that this, combined with the greater pollination efficiency of many native bees, makes their importance in agricultural pollination more in line with previous estimates from other parts of the world than with previous estimates from the USA.

It is important to note that even when the proportion of visits by wild bees was fairly similar between two crops, including crops that are in the same genus and flower at the same time of year, the actual *species* of wild bee pollinating each crop differed (e.g. [49]). For instance, the vast majority of wild bee visits in sweet cherry in Washington were performed by bumblebees, while most wild insect visits in tart cherry in the eastern USA were performed by distantly related bee species (in this case various species in the genus *Andrena*). Similar differences are also known for squash/pumpkin in the Northeast and mid-Atlantic, where bumblebees and squash bees comprise most of the wild bee visits [50,51], versus California, where bumblebee visits are relatively rare [52]. This variability in bee fauna highlights the need to sample broadly across production regions [49,53] to better understand the role of specific types of wild bees for crop yields.

The natural history of specific crops and pollinators may explain some of the variation in pollinator limitation that we found among crops. The most obvious difference appeared to be between the early spring-blooming tree and perennial bush crops (apple, cherry and blueberry) that generally had much higher levels of pollinator limitation than the later summer-blooming annual crops (watermelon and pumpkin). Early bloom phenology is expected to negatively affect the abundance of both honeybees and wild bees. In the early spring, cool or rainy weather often suppresses bee visitation [54–56], and if too few bees are active when flowers are blooming, pollinator limitation can result. Honeybees, even if maintained at high densities, do not typically fly in inclement weather, making spring-blooming crops more dependent on wild pollinators than those flowering in summer. These include species that are adapted to spring weather, but often do not achieve high abundance both due to lack of suitable habitat or, in the case of *Bombus* spp., because bees present at that time are foraging queens who have yet to produce a worker-filled colony. Later in the season, temperatures are more suitable for bee flight in general, resulting in a greater chance of good foraging weather during bloom of summer crops such as watermelon and pumpkin.

Another possible explanation for the pattern we observed is that apples, cherries and blueberries have intrinsically much higher flower densities than watermelon and pumpkin. This is at least somewhat mitigated by higher recommended honeybee stocking densities [57,58], but nevertheless the bee to flower ratio is likely lower in these crops. An exception to this pattern is almond, which is the earliest blooming crop in its region (February) and yet showed little evidence of limitation at the sites we sampled. One might expect pollination limitation in almond, because wild bees of most local species have not yet emerged from winter diapause. However, an entire beekeeping industry has focused on providing large numbers of honeybees for this crop, and extensive research and management effort is allocated to insure reliable pollination. In fact, during almond bloom, two thirds of all honeybee colonies in the United States are employed for California almond pollination [59].

Given the evidence of widespread pollinator limitation, especially in tree fruits and blueberry, our results suggest that the adoption of practices that conserve or augment wild bees, such as wildflower enhancements [60,61] and the use of alternative managed pollinators [62,63], is likely to be successful for increasing yields. Furthermore, the high value (over $1.5 billion for the crops in this study alone) we estimate for the contribution of wild bees to crops underscores the importance of their conservation, as well as the economic benefits that investment in conservation and augmentation strategies could bring. Increasing investment in honeybee colonies is an alternative approach to reducing pollinator limitation. Traditionally recommended stocking rates could be too low for several reasons, including the use of modern cultivars and horticultural practices that result in greater flower density per unit area, and more intensive agricultural practices, whereby fertilizer, pests and water are often less limiting than in the past. Most recommendations for honeybee stocking densities in fruit and vegetable crops were developed decades ago [57,64] when production levels were lower, honeybee colonies were stronger, and feral honeybees and wild bees were more numerous. Research on optimal honeybee colony stocking density has generally not been updated to keep pace with horticultural advances (but see [65]), even though these changes can have significant implications for yield [66]. In cases where pollination is limiting, there may be little benefit to spending large amounts of money on pest control (US farms currently spend about $9 billion annually on pesticides [67]), fertilizer (about $23 billion [68]), water, or other farming practices without also finding ways to reduce pollinator limitation. Additionally, addressing pollinator limitation should increase yields and food security.

Data accessibility. Datasets used in this study are available online from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hdr7sqvfj [69].

Authors' contributions. R.I., R.W. and J.G. conceived and designed the study. D.R.A., D.B., K.B., N.K.B., C.B., J.B., J.W.C., J.D., E.E., J.D.E., S.J.F., J.G., R.L.G., K.B.G., L.G., G.H., N.J., O.L., K.M., C.M.M., S.S.P., T.L.P.-S., S.R., N.R., L.R., K.L.W., N.M.W. and J.K.W. carried out the observations and experiments. J.R.R. designed and performed the analyses. J.R.R., R.W. and R.I. wrote the manuscript. All authors assisted with interpretation of the data and revision of the manuscript.

Competing interests. We declare we have no competing interests.

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