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

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Research

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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.

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1. Introduction

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

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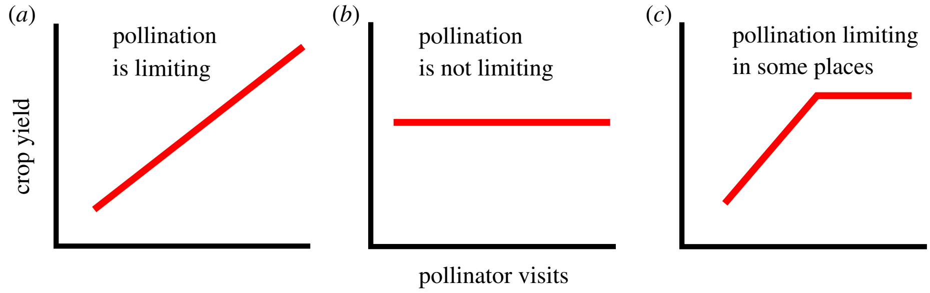

Figure 1. Conceptual figure showing the general relationship between pollinator visitation (or pollen deposition) and crop yield. As the number of visits from pollinators increases, crop yield is expected to increase until the crop is fully pollinated, at which point the relationship reaches an asymptote. 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

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

where $V_{\mathrm{pollinator}}$ 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 $P_{\mathrm{pollinator}}$ 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 ($P_{\mathrm{pollinator}}$), 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

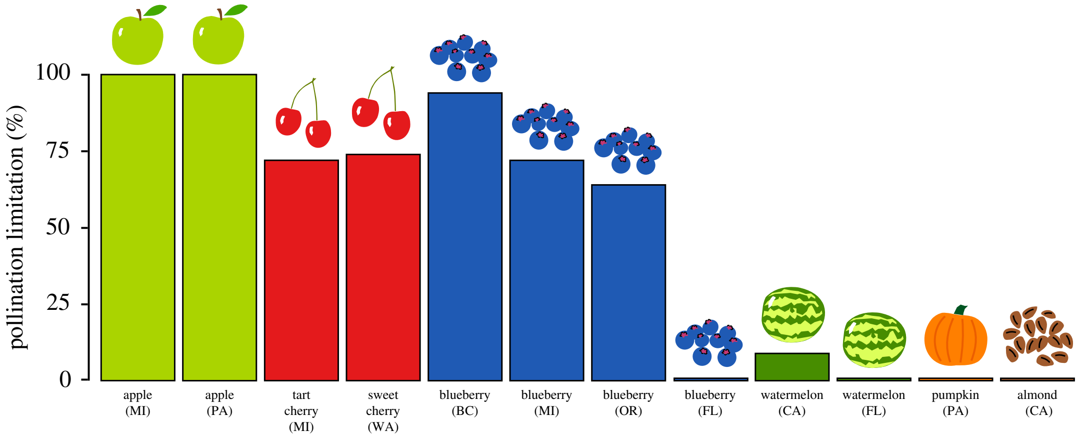

Figure 2. Frequency of study transects predicted to be pollination limited using the AIC selection method. The best of three models were selected by AIC: (i) limitation across all sampling locations; (ii) limitation at no sampling locations; and (iii) limitation at lower levels of visitation, but not 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

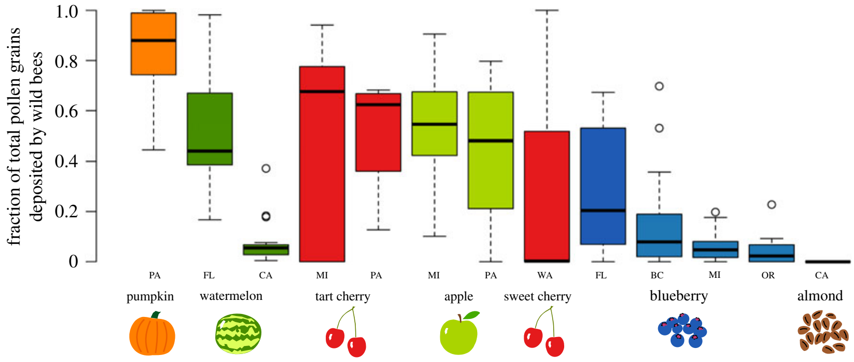

Figure 3. Boxplots of relative pollen deposition rate of wild bees (as a proportion of total pollen deposition) across the crop–region combinations in our study. Estimates of pollen deposition were based on visits × pollen deposition per visit for each type of pollinator observed (electronic supplementary 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.)

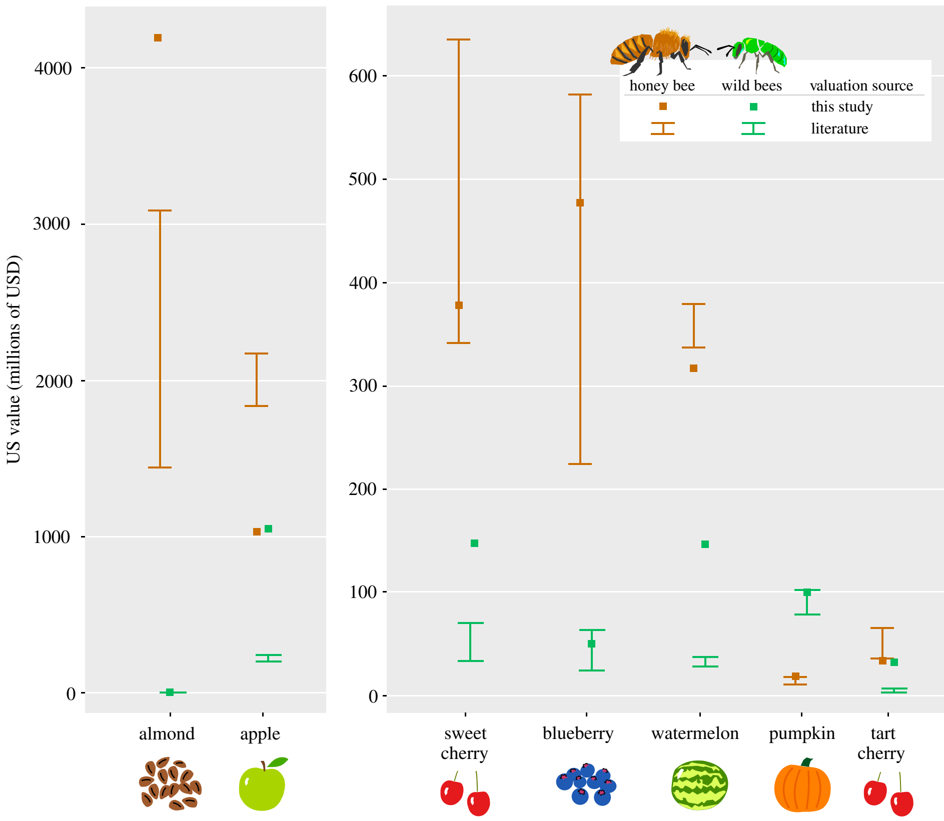

Figure 4. Value estimates for honeybee (orange) and wild bees (green), extrapolated to the level of the United States. Bars encompass the range of estimates in the published literature [2,39]. Square points show our final value estimates. Our estimates differ from literature estimates for several reasons: (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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References

1. IPBES. 2016 *The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production* (eds S Potts, V Imperatriz-Fonseca, H Ngo). Bonn, Germany: IPBES.
2. Calderone N. 2012 Insect pollinated crops, insect pollinators and US agriculture: trend analysis of aggregate data for the period 1992–2009. *PLoS ONE* **7**, 1–27. (doi:10.1371/journal.pone.0037235)
3. Bauer D, Wing I. 2016 The macroeconomic cost of catastrophic pollinator declines. *Ecol. Econ.* **126**, 1–13. (doi:10.1016/j.ecolecon.2016.01.011)
4. van Engelsdorp D, Hayes Jr J, Underwood R. 2008 A survey of honey bee colony losses in the US, Fall 2007 to Spring 2008. *PLoS ONE* **3**, e4071. (doi:10.1371/journal.pone.0004071)
5. Potts S, Biesmeijer J, Kremen C, Neumann P, Schweiger O, Kunin W. 2010 Global pollinator declines: trends, impacts and drivers. *TREE* **25**, 345–353.
6. Cameron S, Lozier J, Strange J, Koch J, Cordes N, Solter L, Griswold T. 2011 Patterns of widespread decline in North American bumble bees. *PNAS* **108**, 662–667. (doi:10.1073/pnas.1014743108)
7. Ashman T *et al.* 2004 Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* **85**, 2408–2421. (doi:10.1890/03-8024)
8. Knight T *et al.* 2005 Pollen limitation of plant reproduction: pattern and process. *Annu. Rev. Ecol. Evol. Syst.* **36**, 467–497. (doi:10.1146/annurev.ecolsys.36.102403.115320)
9. Benjamin F, Winfree R. 2014 Lack of pollinators limits fruit production in commercial blueberry (*Vaccinium corymbosum*). *Environ. Entomol.* **43**, 1574–1583.
10. Isaacs R, Kirk A. 2010 Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *J. Appl. Ecol.* **47**, 841–849. (doi:10.1111/j.1365-2664.2010.01823.x)
11. Garibaldi L *et al.* 2016 Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. *Science* **351**, 388–391. (doi:10.1126/science.aac7287)
12. Garratt M, Bishop J, Degani E, Potts S, Shaw R, Shi A, Roy S. 2018 Insect pollination as an agronomic input: strategies for oilseed rape production. *J. app. ecol.* **55**, 2834–2842. (doi:10.1111/1365-2664.13153)
13. Fijen T, Scheper J, Boom T, Janssen N, Raemakers I, Kleijn D. 2018 Insect pollination is at least as important for marketable crop yield as plant quality in a seed crop. *Ecol. Lett.* **21**, 1704–1713. (doi:10.1111/ele.13150)
14. Haig D, Westoby M. 1988 On limits to seed production. *Am. Nat.* **131**, 757–759. (doi:10.1086/284817)
15. Burd M. 2008 The Haig-Westoby model revisited. *Am. Nat.* **171**, 400–404. (doi:10.1086/527499)
16. Rosenheim J, Williams N, Schreiber S, Rapp J. 2016 Modest pollen limitation of lifetime seed production is in good agreement with modest uncertainty in whole-plant pollen receipt. *Am. Nat.* **187**, 397–404. (doi:10.1086/684849)
17. Klein A, Hendrix S, Clough Y, Scofield A, Kremen C. 2015 Interacting effects of pollination, water and nutrients on fruit tree performance. *Plant Biol.* **17**, 201–208. (doi:10.1111/plb.12180)
18. Garibaldi L *et al.* 2013 Wild pollinators enhance fruit set of crops regardless of honey-bee abundance. *Science* **339**, 1608–1611. (doi:10.1126/science.1230200)
19. Kleijn D *et al.* 2015 Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* **6**, 1–24. (doi:10.1038/ncomms8414)
20. Rader R *et al.* 2016 Non-bee insects are important contributors to global crop pollination. *PNAS* **113**, 146–151. (doi:10.1073/pnas.1517092112)
21. Brown J, Cunningham SA. 2019 Global scale drivers of crop visitor diversity and the historical development of agriculture. *Proc. R. Soc. B* **286**, 20192096. (doi:10.1098/rspb.2019.2096)
22. Winfree R, Williams N, Dushoff J, Kremen C. 2007 Native bees provide insurance against ongoing honey bee losses. *Ecol. Lett.* **10**, 1105–1113. (doi:10.1111/j.1461-0248.2007.01110.x)
23. Blitzer E, Gibbs J, Park M, Danforth B. 2016 Pollination services for apple are dependent on diverse wild bee communities. *Agric. Ecosyst. Environ.* **221**, 1–7. (doi:10.1016/j.agee.2016.01.004)
24. Kremen C, Williams N, Thorp R. 2002 Crop pollination from native bees at risk from agricultural intensification. *PNAS* **99**, 16 812–16 816. (doi:10.1073/pnas.262413599)
25. Greenleaf S, Kremen C. 2006 Wild bees enhance honey bees pollination of hybrid sunflower. *PNAS USA* **103**, 13 890–13 895. (doi:10.1073/pnas.0600929103)

26. Brittain C, Williams N, Kremen C, Klein A. 2013 Synergistic effects of non-*Apis* bees and honey bees for pollination services. *Proc. R. Soc. B* **280**, 1754. (doi:10.1098/rspb.2012.2767)
27. Ricketts T *et al.* 2008 Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* **11**, 499–515. (doi:10.1111/j.1461-0248.2008.01157.x)
28. Garibaldi L *et al.* 2011 Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* **14**, 1062–1072. (doi:10.1111/j.1461-0248.2011.01669.x)
29. Kennedy C *et al.* 2013 A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* **16**, 584–599. (doi:10.1111/ele.12082)
30. Koh I, Lonsdorf E, Williams N, Brittain C, Isaacs R, Gibbs J, Ricketts T. 2016 Modeling the status, trends, and impacts of wild bee abundance in the United States. *PNAS* **113**, 140–145. (doi:10.1073/pnas.1517685113)
31. Gallai N, Salles J, Settele J, Vaissière B. 2009 Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol. Econ.* **68**, 810–821. (doi:10.1016/j.ecolecon.2008.06.014)
32. Klein A, Vaissiere B, Cane J, Steffan-Dewenter I, Cunningham S, Kremen C, Tscharntke T. 2007 Importance of pollinators in changing landscapes for world crops. *Proc. Biol. Sci.* **274**, 303–313. (doi:10.1098/rspb.2006.3721)
33. Winfree R, Gross B, Kremen C. 2011 Valuing pollination services to agriculture. *Ecol. Econ.* **71**, 80–88. (doi:10.1016/j.ecolecon.2011.08.001)
34. Kammerer M, Biddinger D, Rajotte E, Mortensen D. 2015 Local plant diversity across multiple habitats supports a diverse wild bee community in Pennsylvania apple orchards. *Environ. Entomol.* **45**, 32–38. (doi:10.1093/ee/nvv147)
35. Willmer P, Finlayson K. 2014 Big bees do a better job: intraspecific size variation influences pollination effectiveness. *J. Pollination Ecol.* **14**, 244–254. (doi:10.26786/1920-7603(2014)22)
36. Stavert J, Liñán-Cembrano G, Beggs J, Howlett B, Pattemore D, Bartomeus I. 2016 Hairiness: the missing link between pollinators and pollination. *PeerJ* **4**, e2779. (doi:10.7717/peerj.2779)
37. Bartomeus I *et al.* 2014 Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. *PeerJ* **2**, e328. (doi:10.7717/peerj.328)
38. Losey J, Vaughan M. 2006 The economic value of ecological services provided by insects. *Bioscience* **56**, 311–323. (doi:10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2)
39. Morse R, Calderone N. 2000 The value of honey bees as pollinators of US crops in 2000. *Bee Culture* **128**, 15.
40. Eeraerts M, Vanderhaegen R, Smagghe G, Meeus I. 2019 Pollination efficiency and foraging behaviour of honey bees and non-*Apis* bees to sweet cherry. *Agric. For. Entomol.* **22**, 75–82. (doi:10.1111/afe.12363)
41. Aizen M, Garibaldi L, Cunningham S, Klein A. 2009 How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Ann. Botany* **103**, 1579–1588. (doi:10.1093/aob/mcp076)
42. Biesmeijer J *et al.* 2006 Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**, 351–354. (doi:10.1126/science.1127863)
43. Oldroyd B. 2007 What's killing American honey bees? *PLoS Biol.* **5**, 1195–1199. (doi:10.1371/journal.pbio.0050168)
44. Garibaldi L, Aizen M, Klein A, Cunningham S, Harder L. 2011 Global growth and stability of agricultural yield decrease with pollinator dependence. *PNAS* **108**, 5909–5914. (doi:10.1073/pnas.1012431108)
45. Aizen M *et al.* 2019 Global agricultural productivity is threatened by increasing pollinator dependence without an increase in crop diversification. *Glob. Change Biol.* **25**, 3516–3527. (doi:10.1111/gcb.14736)
46. Garibaldi L, Aizen M, Cunningham S, Klein A. 2009 Pollinator shortage and global crop yield: looking at the whole spectrum of pollinator dependency. *Commun. Integr. Biol.* **2**, 37–39. (doi:10.4161/cib.2.1.7425)
47. Aizen M, Garibaldi L, Cunningham S, Klein A. 2008 Long-term global trends in crop yield and production reveal no current pollination shortage but increasing pollinator dependency. *Curr. Biol.* **18**, 1572–1575. (doi:10.1016/j.cub.2008.08.066)
48. Klein A, Brittain C, Hendrix S, Thorp R, Williams N, Kremen C. 2012 Wild pollination services to California almond rely on semi-natural habitat. *J. Appl. Ecol.* **49**, 723–732.
49. Gibbs J, Elle E, Bobiwash K, Haapalainen T, Isaacs R. 2016 Contrasting pollinators and pollination in native and non-native regions of highbush blueberry production. *PLoS ONE* **11**, e0158937. (doi:10.1371/journal.pone.0158937)
50. McGrady C, Troyer R, Fleischer S. 2019 Wild bee visitation rates exceed pollination thresholds in commercial *Cucurbita* agroecosystems. *J. Econ. Entomol.* **113**, 562–574. (doi: 10.1093/jee/toz295)
51. Schuler R, Roulston T, Farris G. 2005 Farming practices influence wild pollinator populations on squash and pumpkin. *J. Econ. Entomol.* **98**, 790–795. (doi:10.1603/0022-0493-98.3.790)
52. Tepedino V. 1981 The pollination efficiency of the squash bee (*Peponapis pruinosa*) and the honey bee (*Apis mellifera*) on summer squash (*Cucurbita pepo*). *J. Kansas Entomol. Soc.* **54**, 359–377.
53. Winfree R, Reilly J, Bartomeus I, Cariveau D, Williams N, Gibbs J. 2018 Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science* **359**, 791–793. (doi:10.1126/science.aao2117)
54. Blüthgen N, Klein A. 2011 Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic Appl. Ecol.* **12**, 282–291. (doi:10.1016/j.baae.2010.11.001)
55. Rader R, Reilly J, Bartomeus I, Winfree R. 2013 Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Glob. Change Biol.* **19**, 3103–3110. (doi:10.1111/gcb.12264)
56. Fründ J, Dormann C, Holzschuh A, Tscharntke T. 2013 Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology* **94**, 2042–2054. (doi:10.1890/12-1620.1)
57. Delaplane K, Mayer D. 2000 *Crop pollination by bees*. New York, NY: CABI Publishing.
58. Woodcock T. 2012 Pollination in the Agricultural Landscape: Best Management Practices for Crop Pollination. Canadian Pollination Initiative (NSERC-CANPOLIN): University of Guelph.
59. American Beekeeping Federation. 2018 Pollination facts. See http://www.abfnet.org/page/PollinatorFacts.
60. Blaauw B, Isaacs R. 2014 Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.* **51**, 890–898. (doi:10.1111/1365-2664.12257)
61. Grab H, Poveda K, Danforth D, Loeb G. 2018 Landscape context shifts the balance of costs and benefits from wildflower borders on multiple ecosystem services. *Proc. Roy. Soc. B* **285**, 20181102. (doi:10.1098/rspb.2018.1102)
62. Isaacs R, Williams N, Ellis J, Pitts-Singer T, Bommarco R, Vaughan M. 2017 Integrated crop pollination: combining strategies to ensure stable and sustainable yields of pollination-dependent crops. *Basic Appl. Ecol.* **22**, 44–60. (doi:10.1016/j.baae.2017.07.003)
63. Pitts-Singer T, Artz D, Peterson S, Boyle N, Wardell G. 2018 Examination of a managed pollinator strategy for almond production using *Apis mellifera* (Hymenoptera: Apidae) and *Osmia lignaria* (Hymenoptera: Megachilidae). *Environ. Entomol.* **47**, 364–377. (doi:10.1093/ee/nvy009)
64. McGregor S. 1976 Insect pollination of cultivated crop-plants. *USDA Agriculture Handbook* **496**, 93–98.
65. Eaton L, Nams V. 2012 Honey bee stocking numbers and wild blueberry production in Nova Scotia. *Can. J. Plant. Sci.* **92**, 1305–1310. (doi:10.4141/cjps2012-045)
66. Geslin B, Aizen M, Garcia N, Pereira A, Vaissiere B, Garibaldi L. 2017 The impact of honey bee colony quality on crop yield and farmers' profit in apples and pears. *Agric. Ecosyst. Environ.* **248**, 153–161. (doi:10.1016/j.agee.2017.07.035)
67. EPA. 2017 *Pesticides industry sales and usage: 2008–2012 market estimates*. Washington, DC: EPA.
68. USDA-NASS. 2017 QuickStats online database. See https://quickstats.nass.usda.gov.
69. Reilly JR *et al.* 2020 Data from: Crop production in the USA is frequently limited by a lack of pollinators. Dryad Digital Repository. (doi:10.5061/dryad.hdr7sqvfj)

Electronic Supplementary Information (ESM)

Supplementary Methods

Analysis 1: frequency of pollinator limitation

To measure the frequency of pollinator limitation across all locations for a given crop, we used AIC to choose between three models that relate the number of pollinators observed to our crop-specific yield or production variable (see Fig. 1): 1) a linear positive relationship, implying that all locations were pollination-limited, 2) no relationship (an intercept only model), implying that no locations were limited, or 3) 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 pollination-limited in some locations and not others. If the third model was selected, we estimated the frequency of pollinator limitation as the fraction of locations falling below the breakpoint.

For all models, we used the transect as the unit of analysis for the flower visitation-yield relationship, because this was the most highly resolved scale at which observations of visitation and subsequent production measurements could be paired. In principle, within a given crop in our study, pollination could be limiting at all transects, at a subset of transects, or at no transects. Linear regressions and intercept-only models were performed using the glm() function in R version 3.3.2 (R Core Team 2016). Piecewise regressions were performed using the segmented() function in the segmented package (Muggeo 2003, 2008) in R. The breakpoint between the linear and intercept-only portions of the curve was not specified beforehand, but was estimated automatically by the segmented() function to maximize the model fit. For this analysis, we selected the model with the lowest AIC, even in cases where another model was close, because the different structure of the three models meant model averaging would not be appropriate. Tart cherry in Pennsylvania was not included in this analysis due to insufficient data. Investigation of temporal effects in pollinator limitation is beyond the scope of this manuscript. It should also be noted that site and cultivar are necessarily confounded in this analysis because a large number of cultivars are grown for many of our crops, and because cultivar must be matched to the environmental conditions at a given farm. From our perspective this is not necessarily undesirable because we simply intended our data to be a representative sample of what exists in each growing region, and did not intend to make inferences about particular cultivars. Our goal was to make our sample as representative as possible by spreading sampling over many locations in each region.

All crop regions were analyzed separately except for northern highbush blueberry (i.e. transects from British Columbia, Michigan, and Oregon), where the data from all three regions was pooled together in order to extend the range of bee visitation values on the x-axis as widely as possible, given that transects with low bee visitation were only present in British Columbia (Fig. S6). We felt this was appropriate given that our sampling methods were exactly the same across all three regions and that all bushes were of the same cultivar (Bluecrop), and because estimation across the full range of visitation values should result in a more reliable breakpoint value than if each dataset were analyzed separately. Results for each blueberry region analyzed separately are reported in Supplementary analysis 2. The Florida blueberry dataset was not combined with the other regions because it is a different species (southern highbush blueberry).

For blueberry in all four regions, as a check on the patterns of pollinator limitation suggested by our analysis, we performed an additional parallel analysis using the data from hand-pollination experiments. These experiments were performed in the same transects where open-pollinated bushes were measured, such that each transect had individual measurements for open, bagged, and hand-pollinated bushes. The results of this analysis are reported in Supplementary analysis 3.

Analysis 2: contribution of honey bees versus wild bees

For each crop, the fraction of total pollen grains deposited by honey bees and each species group of wild bee was estimated by multiplying flower visits by that group with an estimate of relative pollen grains deposited per visit (pollinator efficiency), then dividing by the total to give a proportion:

$$P_{pollinator} = \frac{R_{pollinator} \cdot E_{pollinator}}{\sum(R_{pollinator} \cdot E_{pollinator})} \quad \text{(S1)}$$

where $P_{pollinator}$ is the proportion of pollen grains deposited by each pollinator group, $R_{pollinator}$ is the visitation rate (expressed as a proportion of total observed visits contributed by a given pollinator group), and $E_{pollinator}$ is the number of pollen grains deposited per visit (by that pollinator group; expressed as a fraction of pollen grains deposited by the honey bee). Table S1 illustrates these calculations for one of our study systems.

Table S1. An example of pollinator contribution calculations based on Florida watermelon.

pollinator	R	E	R x E	P
Honey_bee	0.561	1.0	0.561	0.480
Tiny_bee	0.287	1.2	0.344	0.295
Green_bee	0.102	1.1	0.112	0.096
Bumble_bee	0.029	3.6	0.104	0.089
Large_bee	0.010	0.9	0.009	0.008
Small_bee	0.009	2.0	0.018	0.015
Xylocopa	0.002	12.1	0.019	0.017
Megachilid	0.0004	1.4	0.001	0.000
sum	1		1.169	1

Values of E (pollinator efficiency, i.e., pollen deposition per visit) were taken from the following literature sources (see Table S2): watermelon (Winfree et al. 2007, Winfree et al. 2015), pumpkin (Artz and Nault 2011), almond (Thomson and Goodell 2001), apple (Park et al. 2016), and blueberry (Javorek et al. 2002, Benjamin et al. 2014). Values of E for the wild bee groups were expressed as relative to the E of the honey bee for comparative purposes. For bee species with no available PPV estimates in the literature, we assumed that E was the same as for the honey bee in order to create a conservative estimate of the differences between honey bee and wild bees. No PPV estimates for tart cherry were available in the literature, so the values for sweet cherry (Eeraerts et al. 2019) were substituted.

Analysis 3: Economic valuation

There are multiple methods for valuing pollination services and these vary in their assumptions and data requirements (Winfree et al. 2011, Melathopoulos et al. 2015, Hanley et al. 2015, Breeze et al. 2016). Most studies to date have used the production value method, which starts with the total value of the crop yield and multiplies it by the fraction of total yield that would be lost if pollinators were completely absent (Gallai et al. 2009, Calderone 2012). We used the production value method in order to make our results comparable to previous studies that have calculated the value of honey bee and/or wild bee pollination (Losey and Vaughn 2006, Morse and Calderone 2000). Another potential valuation method is the replacement value method, which values the cost of substituting native pollinators with additional honey bees (e.g. Winfree et al. 2011) or hand pollination (Allsopp et al. 2008). Replacement with honey bees is not relevant for our study, as the value contribution of honey bees is one of our measurements of interest. Furthermore, our analysis is best interpreted over a relatively short time scale over which large-scale economic factors remain constant, and the future development of mechanical pollination technologies is not relevant.

Using the production value method, the economic value delivered to each crop in each state was calculated for wild pollinators and honey bees using the following equation, as described in the main text (as equation 1):

$$V_{pollinator} = V_{crop} \cdot D \cdot P_{pollinator} \tag{S2}$$

Where $V_{pollinator}$ is the annual economic value attributable to a particular pollinator group (either wild bees or honey bee), 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; from Klein et al. 2007), and $P_{pollinator}$ is the fraction of total pollination of the crop provided by the pollinator group. Production values for each crop-state combination (from 2013-2015) were obtained from the USDA-NASS database (USDA-NASS 2017). It is important to note that there remains considerable uncertainty in this equation. For instance, the data used by Klein et al. (2007) to specify pollinator dependency values do not account for some factors that affect pollinator dependence and may differ by farm, such as the crop cultivar used.

As discussed in the main text, our approach updates previous national-scale estimates of the value of wild and honey bee pollination (Losey and Vaughn 2006, Calderone 2012) by incorporating both relative visitation rates and per-visit efficiency by each pollinator group, and by using sites that were within the main production regions for the crop.

To extrapolate our state values up to the national level, we followed two steps. First, we needed to estimate the fraction of total pollination for each crop attributable to each pollinator group at the national level ($P_{pollinator,US}$). These fractions were calculated using the proportion of pollination done by each pollinator group ($P_{pollinator}$) and the value of each crop (V_{crop}), both at the state level.

$$P_{pollinator,US} = \sum \left[P_{pollinator,i} \cdot \frac{V_{crop,i}}{\sum V_{crop,i}} \right] \tag{S3}$$

Equation S3 estimates the national value of each type of pollinator by averaging the values $P_{pollinator}$ for each available state i, weighted by the proportion of the national production of that crop that comes from that state $\left(\frac{V_{crop,i}}{\sum V_{crop,i}}\right)$. If only one state was studied for a given crop (e.g. almond), then no averaging was done.

Lastly, we calculated the total production value attributable to each pollinator group at the national level by substituting our fractions from equation S3, along with national-scale crop values, into equation S2, such that

$$V_{pollinator,US} = V_{crop,US} \cdot D \cdot P_{pollinator,US} \tag{S4}$$

where $V_{crop,US}$ is the total national production value for that crop and $P_{pollinator,US}$ is the fraction of pollen deposited by the pollinator group. Total production values for each crop at national scale (from 2013-2015) were obtained from the USDA-NASS database (USDA-NASS 2017).

The value V_{crop} represents the gross production value of the crop. There is a potential for this value to result in an overestimate of the value of pollinators, because if pollination failed farmers might be able to mitigate financial losses by reducing input costs (i.e. variable costs of production), or potentially adopting alternative pollination strategies. Most of the crops we studied, however, were woody perennials (trees and shrubs) for which the variable costs of production, such as irrigation, fertilizer, and pest management, would still be needed in order to maintain plant health for future production. A sensitivity analysis on the effect of subtracting the variable input costs from the production value estimates (Winfree et al. 2011) is described below. Estimates referenced by each of the equations above are provided in Table S11.

Supplementary analysis 1: The effect of subtracting variable costs from crop production values

In the event that crops fail due to a lack of pollination, farmers can potentially save money by abandoning expenditures that will no longer create a benefit. Such expenses are often referred to as variable costs of production, because they can vary depending on how much yield is expected or produced. For instance, harvest costs (an important variable cost) can decline to zero if there is no crop to harvest. However, as discussed above, farm management is a complex business, so some variable costs will not be entirely eliminated and hence subtracting the sum of variable costs as we do below will likely result in an underestimate of pollinator value.

The total variable cost associated with the production of a particular crop across the entire USA TVC_{US} is calculated as

$$TVC_{US} = \sum \left[VCA_i \cdot \frac{A_i}{\sum A_i} \right] \cdot A_{US} \tag{S5}$$

where VCA_i is the variable cost per acre for a state i (one of the states in our study), and where A_i is the number of acres under production for that state, and A_{US} is the total area under production of that crop in the USA. The variable input cost estimates used for each crop and state were calculated using sample budgets published by the university cooperative extension program that was the geographically closest to our study farms (see Table S8). Our objective was to create a mean cost per acre for the USA from a weighted average of the states for which data were available. If only one state was studied for a given crop (e.g. almond), then no averaging was done. For states where we had no bee visitation data or variable cost estimates, we assumed that the situation was similar enough to be approximated by the states where we did have data.

The net production value of a particular crop at the national scale, NPV_{US} , is calculated as

$$NPV_{US} = TPV_{US} - TVC_{US} \tag{S6}$$

where TPV_{US} is the total (gross) production value at the national scale, and TVC is the extrapolated total variable cost from above. Total production values and total acres bearing at the state and national level for 2013-2015 were obtained from the USDA-NASS database (USDA-NASS 2017). The quantity TPV_{US} is equivalent to the quantity $V_{crop,US}$ from equation S4 above.

The fraction of total pollination of each crop nationwide that is attributable to each pollinator group $P_{pollinator,US}$ was calculated as

$$P_{pollinator,US} = \sum \left[P_{pollinator,i} \cdot \frac{NPV_{crop,i}}{\sum NPV_{crop,i}} \right] \tag{S7}$$

an average of the values P_i for each available state, weighted by the relative net production values NPV_i calculated for that state. This matches equation S3 above, but now with net production value substituted for total production value.

Lastly, we calculated the net production value attributable to each pollinator group at the national level by substituting our fractions from equation S7 into equation S2 where V_{crop} is now the net national production value NPV_{US} for that crop from equation S6.

$$V_{pollinator,US} = NPV_{US} \cdot D \cdot P_{pollinator,US} \tag{S8}$$

Result: As a percentage of gross production value, variable input costs averaged 62% (range 29-87%) across the crop-state combinations in our study (Table S8), often leaving less than half of gross production value to be attributed to pollinators. Nevertheless, the remaining net value represented a very large amount at the scale of the state or nation, especially for the higher value crops such as almond and apple. Results of this analysis compared with the version from the main text where variable costs were not subtracted are summarized in Fig. S5.

Our estimates of wild bee pollination value for the USA were higher than previous studies in four of the seven crops studied, and within the range of previous studies in the other 3 crops (Fig. 4). If all of the variable costs were subtracted (see Fig. S5), these higher estimates would persist in only one crop (apple), and three crops would show lower values than previous estimates because on average, subtracting variable production costs would reduce our estimated values by about 70%. Our higher valuations for wild bees were driven by both higher rates of flower visitation and higher pollen deposition per visit compared with the numbers used in previous studies (Losey and Vaughn 2006). Correspondingly, our valuation for honey bees was often lower (four of the crops) than estimated by previous studies and would have been even further reduced if we had subtracted variable production costs.

Supplementary analysis 2: Analysis of the frequency of pollinator limitation for separate regions of northern blueberry.

When the three regions of northern highbush blueberry were analyzed separately, the segmented model was only clearly preferred by AIC in the British Columbia data (deltaAIC=8.7). A linear increasing model was slightly preferred over a segmented model for Oregon (deltaAIC = 1.4) and Michigan (deltaAIC=0.6), but the slopes of these increasing relationships were very shallow. Breakpoints for the separately analyzed regions were 14.4 bees/10 min (BC), 26.7 bees/10 min (MI), and 43.4 bees/min (OR), compared with an estimated breakpoint of 26.3 bees/10 min when analyzed together. Taken together, these results appear reasonably consistent with the results of the main analysis, and reinforce our decision to combine the three regions.

Supplementary analysis 3: Assessing the frequency of pollen limitation using hand pollination experiments in blueberry

For blueberry in British Columbia, Michigan, Oregon, and Florida, we collected crop production data from plants in each transect that had been pollinated by hand, in addition to the plants used in the main analysis that were either open-pollinated or bagged. For these plants, we added pollen to open clusters of flowers multiple times during bloom to ensure maximum pollination. Thus, the pollen we added was in addition to any pollen provided by bees. If pollination were limiting, we would expect hand-pollinated plants to have higher average berry weight than open-pollinated plants. To analyze the frequency of limitation across farms, we followed the same methods described for the main analysis of pollinator limitation, but with a new crop production variable: the difference in average berry weight between hand- and open-pollinated bushes. For this variable, a larger value would represent a larger effect of hand pollination, and thus potentially lower bee visitation. As before, three models were compared by AIC: 1) a linear relationship between bee visitation and the effect of hand pollination, 2) no relationship, and 3) a segmented relationship in which the effect of hand pollination declines with increased bee visitation to a breakpoint, then remains flat.

Result: As in the main analysis, the segmented relationship was strongly preferred by AIC over the linear relationship (deltaAIC = 19.1) and no relationship models (deltaAIC = 52.3) for northern blueberry (OR, MI, BC) (see Fig. S7). Also consistent with the main analysis, the no relationship model was slightly preferred for southern highbush blueberry in Florida (deltaAIC = 1.7). For northern highbush blueberry, the estimated breakpoint occurred at a somewhat lower value of bee visitation than we found in the main analysis (16.7 bees/10 min compared to 26.3 bees/10 min). This discrepancy may be related to a greater difficulty in detecting differences in production between open and hand pollinated bushes when more bees are present, because simultaneous limitation by other factors becomes more likely. The lower breakpoint would lead to lower estimates of pollen/pollinator limitation across farms than reported in the main analysis (see Table S9).

Supplementary References

Artz D, Nault B (2011) Performance of *Apis mellifera*, *Bombus impatiens*, and *Peponapis pruinosa* (Hymenoptera: Apidae) as pollinators of pumpkin. J. Econ. Entomol. 104: 1153-1161.

Breeze T, Gallai N, Garibaldi L, Li X (2016) Economic measures of pollination services: shortcomings and future directions. TREE 31: 927-939.

Benjamin F, Reilly J, Winfree R (2014) Pollinator body size mediates the scale at which land use drives crop pollination services. J. Appl. Ecol. 51: 440-449.

Hanley N, Breeze T, Ellis C, Goulson D (2015) Measuring the economic value of pollination services: principles, evidence and knowledge gaps. Ecosystem Services 14: 124-132.

Homer CG, Dewitz J, Jin S, Xian G, Costello C, Danielson P, Gass L, Funk M, Wickham J, Stehman S, et al. (2020) Conterminous United States land cover change patterns 2001-2016 from the 2016 National Land Cover Database. ISPRS Journal of Photogrammetry and Remote Sensing 162: 184-199.

Javorek S, Mackenzie K, Vander Kloet S (2002) Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). Ann. Entomol. Soc. Am. 95: 345–51.

Melathopoulos A, Cutler G, Tyedmers P (2015) Where is the value in valuing pollination ecosystem services to agriculture? Ecological Economics 109: 59-70.

Muggeo, VM (2003) Estimating regression models with unknown break-points. Statistics in Medicine, 22, 3055-3071.

Muggeo, VM (2008) segmented: an R Package to Fit Regression Models with Broken-Line Relationships.

R News, 8/1, 20-25. URL https://cran.r-project.org/doc/Rnews/.

Park M, Raguso R, Losey J, Danforth B (2016) Per-visit pollinator performance and regional importance of wild *Bombus* and *Andrena* (*Melandrena*) compared to the managed honey bee in New York apple orchards. Apidologie 47: 145-160.

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Thomson J, Goodell K (2001) Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. J. Appl. Ecol. 38: 1032–1044.

USDA-NASS (2017) National Agricultural Statistics Service. United States Department of Agriculture. QuickStats online database: URL https://quickstats.nass.usda.gov/.

Winfree R, Fox J, Williams N, Reilly J, Cariveau D (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecology Letters 18: 626-635.

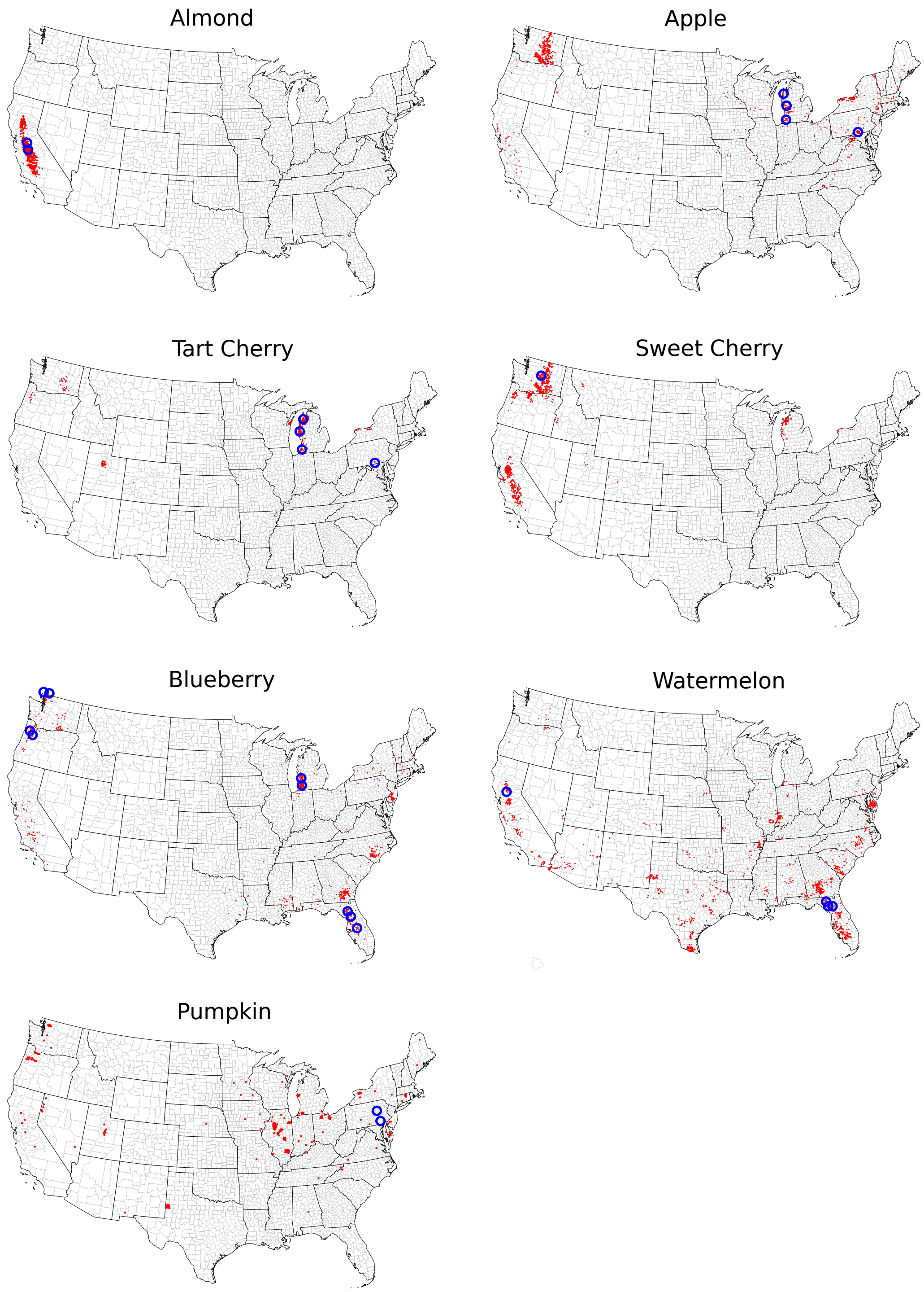

Figure S1. Maps showing the location of our study farms with respect to the major production areas for each crop in the United States. Study farms are marked with a blue circle (often, multiple study farms were located within the same county, so in these cases only a single circlewas drawn for clarity). Crop-specific maps were based on data provided by the United States Department of Agriculture National Agricultural Statistics Service 2012 Census of Agriculture. Each red dot represents 100 acres of a given crop, except in the case of apple where each dot represents 500 acres and almond where each dot represents 1000 acres.

Figure S2 (page 1/4)

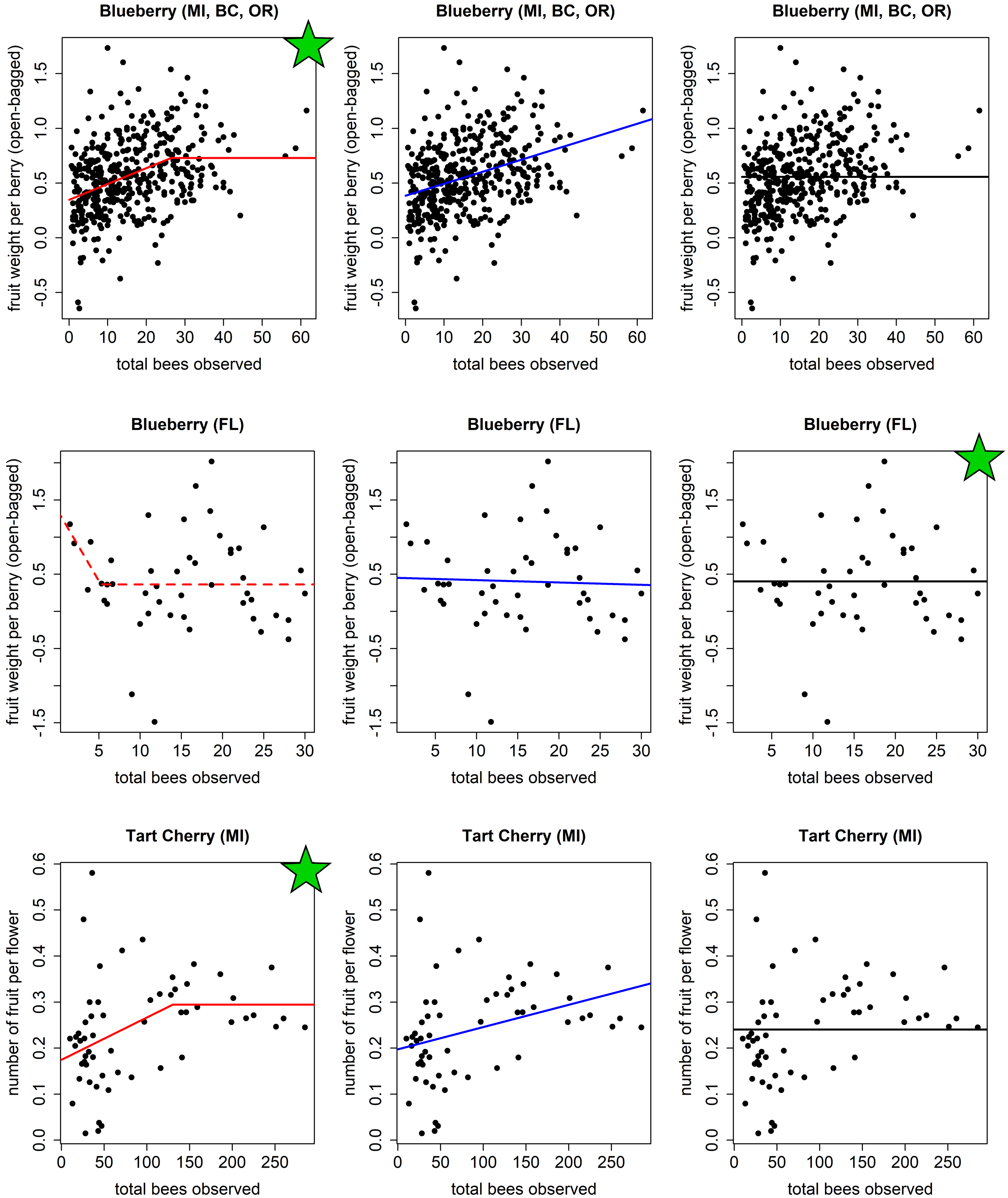

Figure S2 (page 2/4)

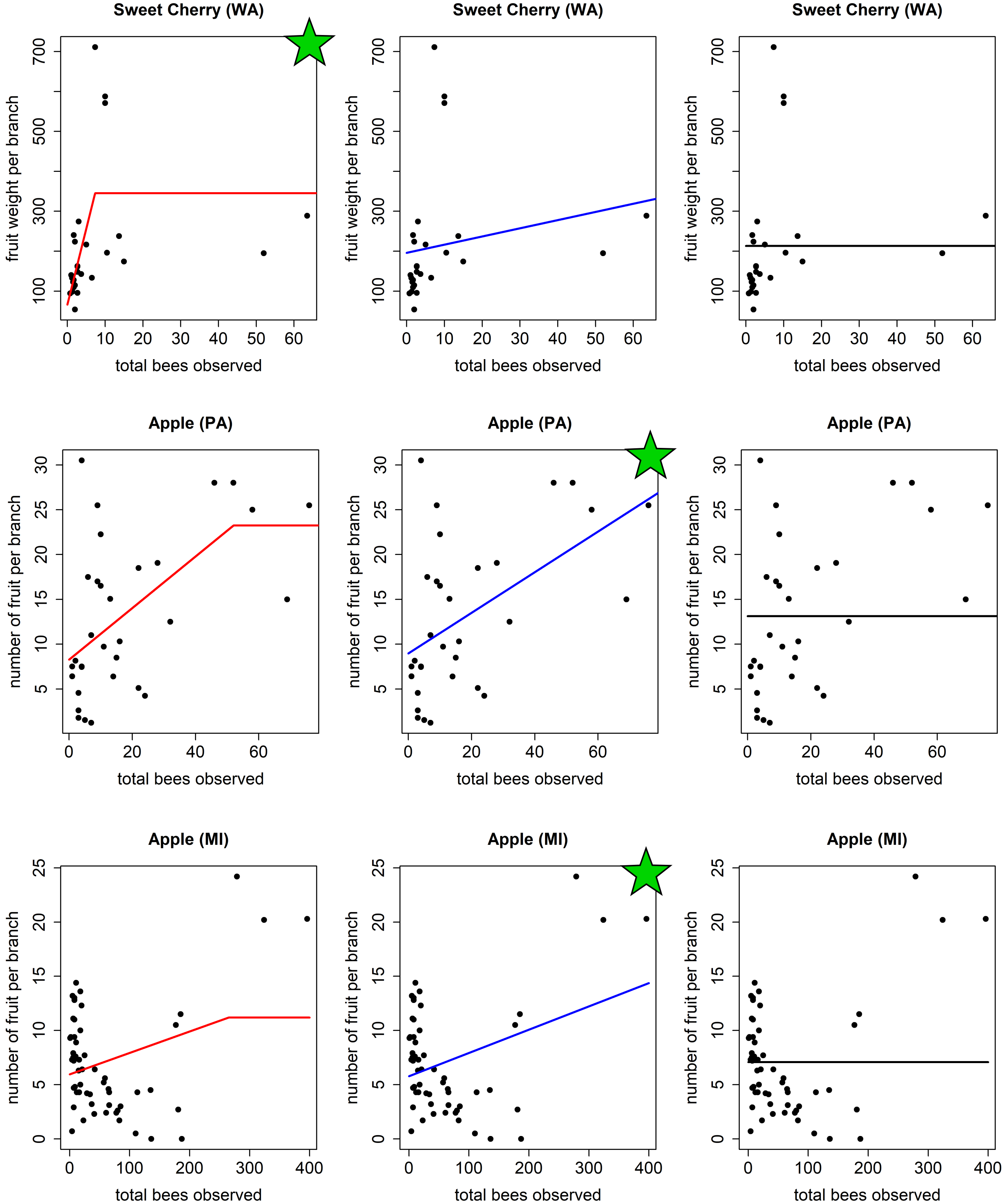

Figure S2 (page 3/4)

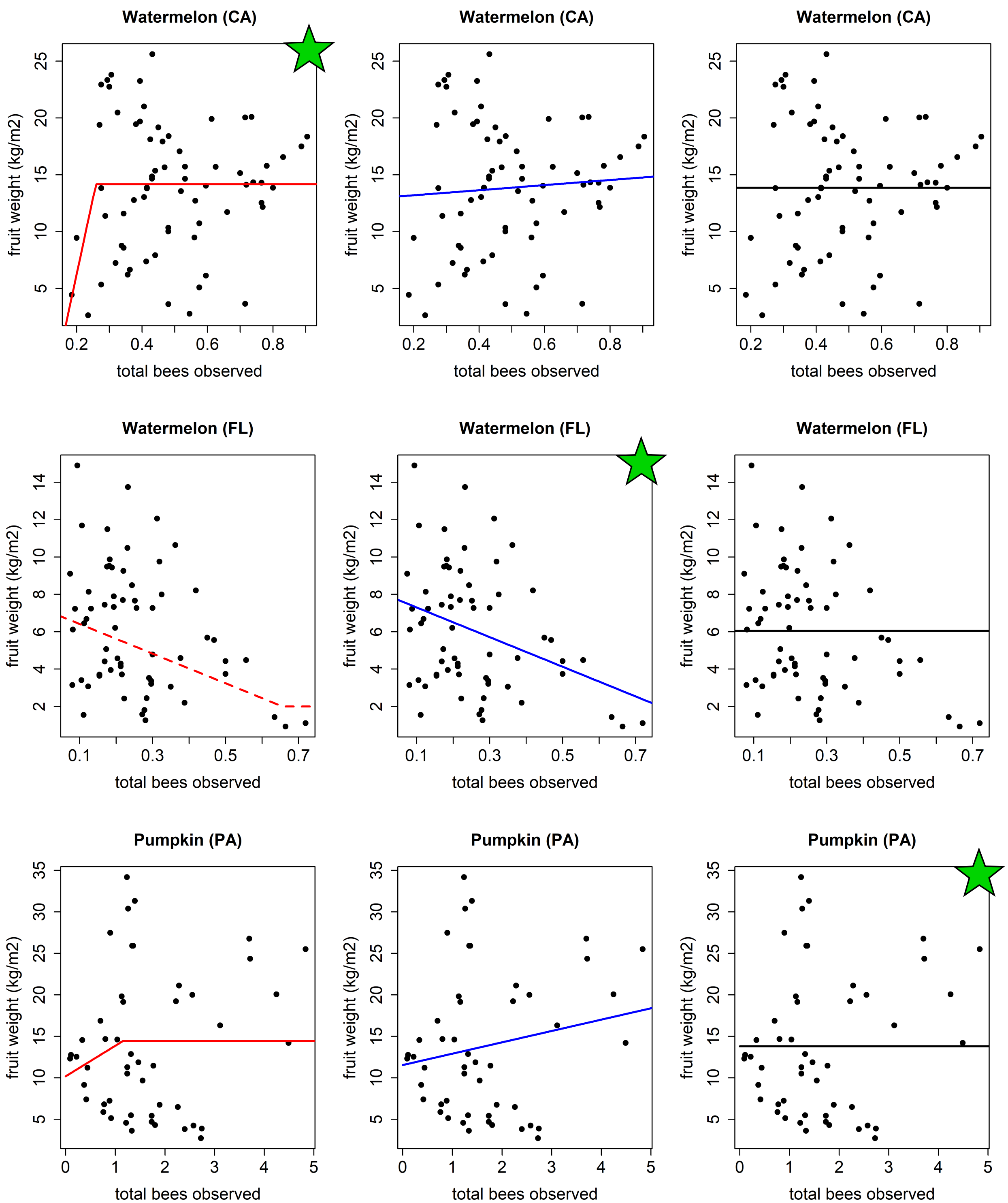

Figure S2 (page 4/4)

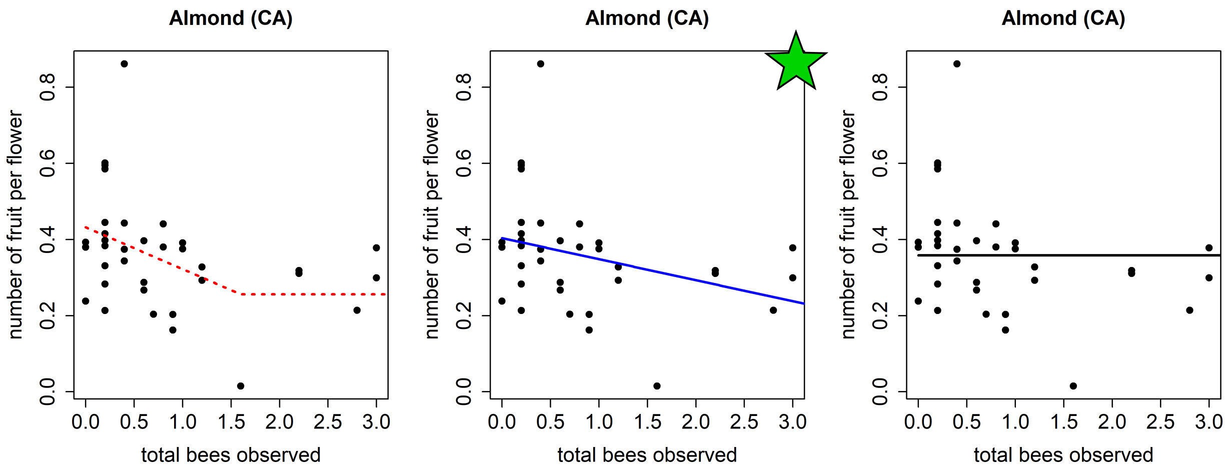

Figure S2. Plots of different potential relationships between visits and yield or production for each crop. In each row, the plots correspond to models of a) a segmented relationship between visits and crop productionwhere there is initially a positive relationship, but after an estimated breakpoint there is no relationship, B) a linear relationship between visits and crop productionacross all sampled locations c) no relationship. AIC model selection was used to select the best model of the three. The green star in the corner denotes which model was selected for a given crop.

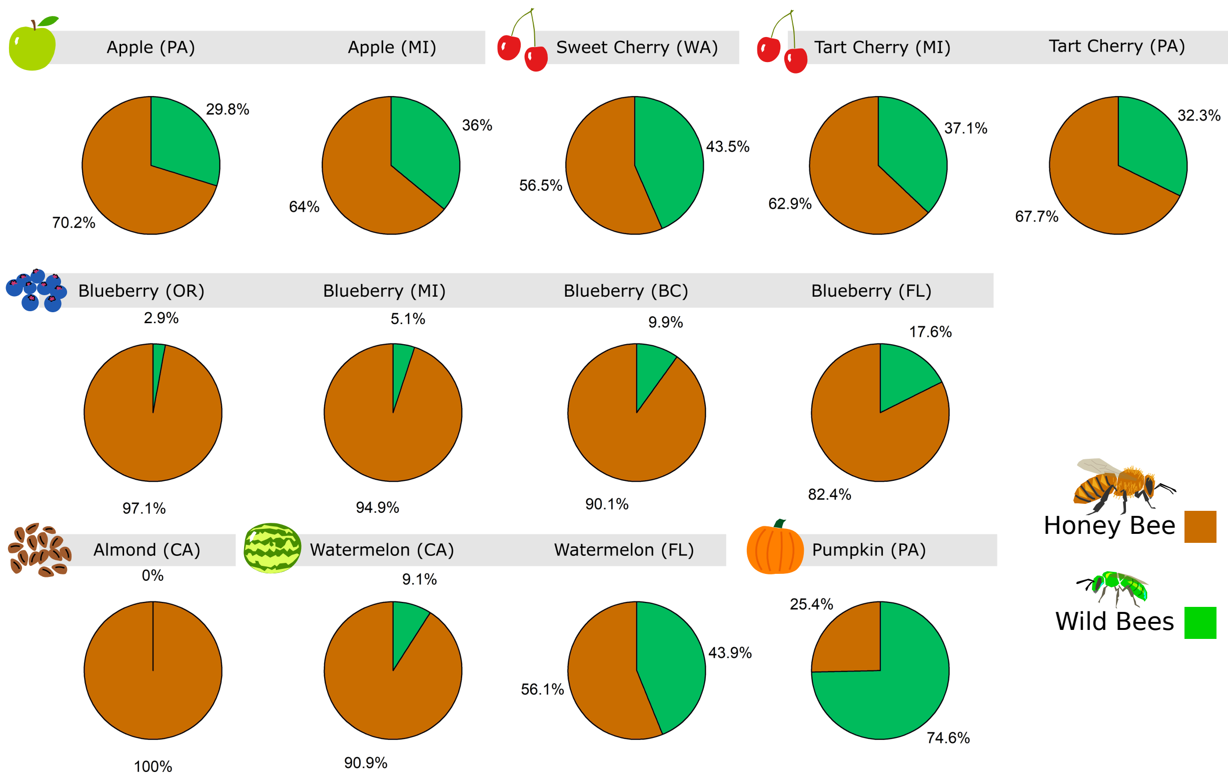

Figure S3. Relative visitation rates of honey beeand wild bees across the crop-region combinations in our study. Percentages were calculated by averaging the number of visits by each pollinator across all the farm-years within that crop. The number of farms and years differed by crop (see Table S3).

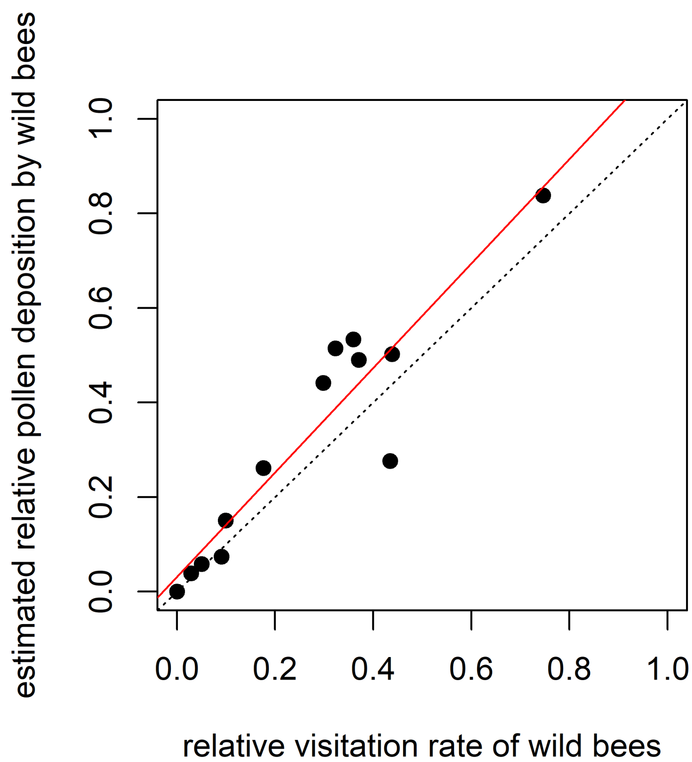

Figure S4. Regression between percent of pollen deposition and percent of visitation by wild bees (where the remainder is provided by the honey bee). Each data point is a crop-state combination from our study. (R^2=0.87, p<0.01) If all bee visits carried the same PPV, the regression would fall along the 1:1 line (dotted). Overall pollen deposition for most crops was somewhat greater than predicted by visit rate alone, hence the regression line (red, slope: 1.10) is somewhat above the 1:1 line. In other words, visitation predicts pollen deposition very well, but there is a positive multiplier of associated with wild bee visitation such that each wild bee visit (on average) results in more pollen deposition than each honey bee visit. The outlier below the line is sweet cherry, where many of the wild bee pollinators were bumble bees (see Table S2) that are not currently thought to be effective pollinators of cherry (Eeraerts et al 2019).

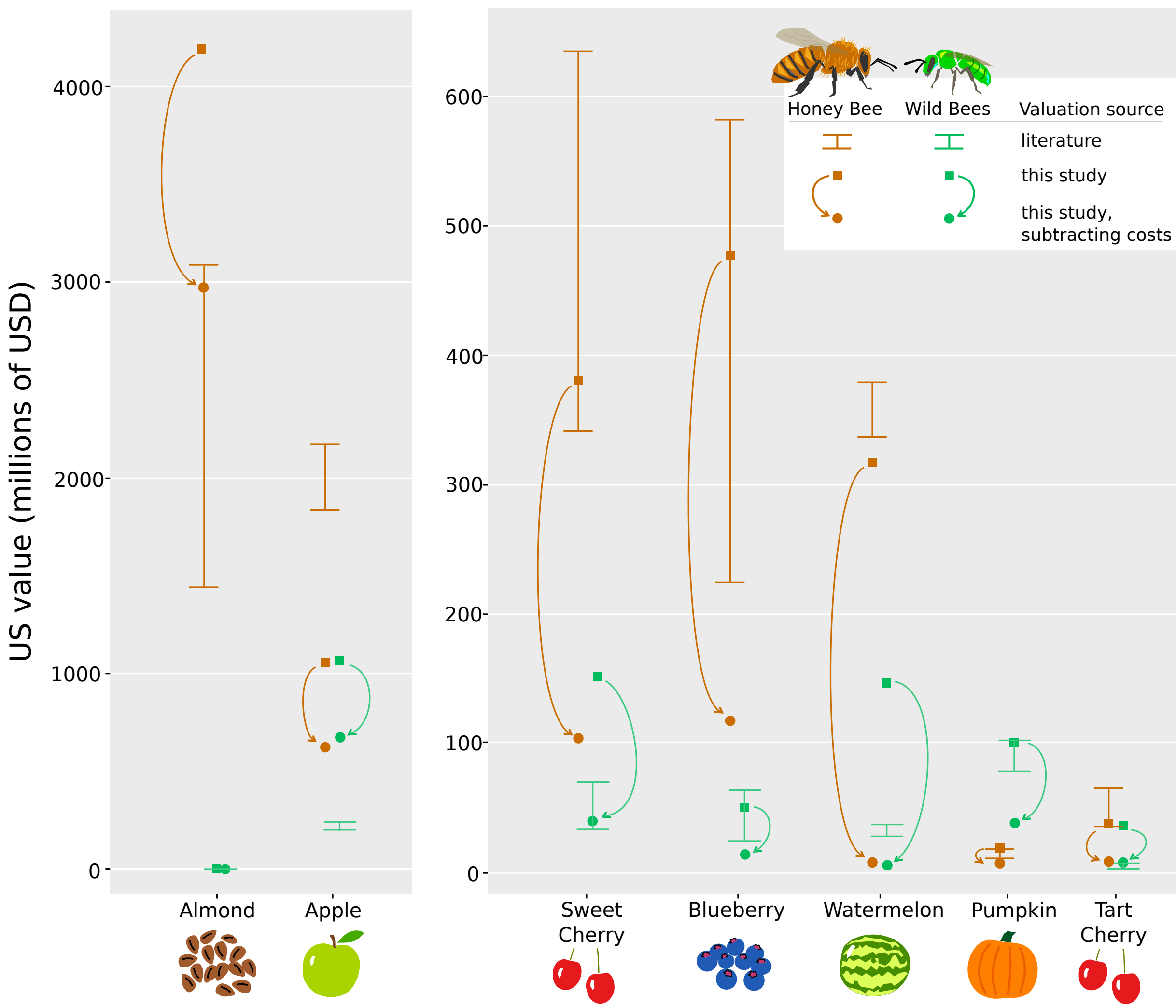

Figure S5. Comparison of valuations before and after subtracting variablecosts of production. Points represent value estimates for honey bee (orange) and wild bees (green), extrapolated to the level of the United States. Bars encompass the range of estimates in the published literature (Losey and Vaughn 2006 and Calderone 2012). Square points show total value estimates, equivalent to those shown in Fig. 4 of the main text. Circle points show net value estimates, following the methods in this supplementary analysis. Arrows are included to indicate the magnitude and direction of value change as a result of subtracting variable costs. All values have been adjusted to 2015 dollars.

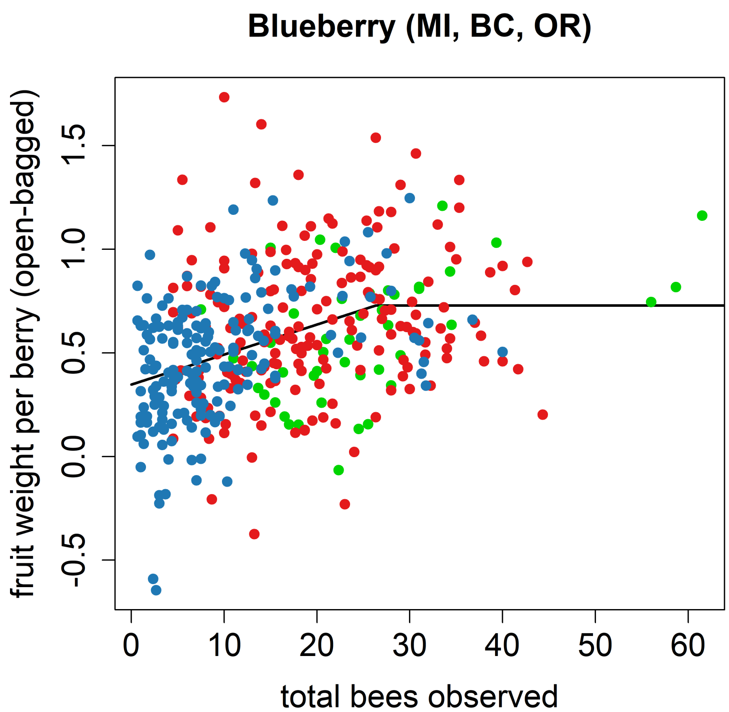

Figure S6. Plot of the relationship between visits and crop production for each northern highbush blueberry site (in MI, BC, and OR) showing how the distribution of bee visitation values differs across region. Note that more of the transects with low visitation occur in the British Columbia data (blue), than in the Michigan (red) or Oregon (green) data. For reference, the segmented model relationship as selected in Fig. S2 is plotted in black.

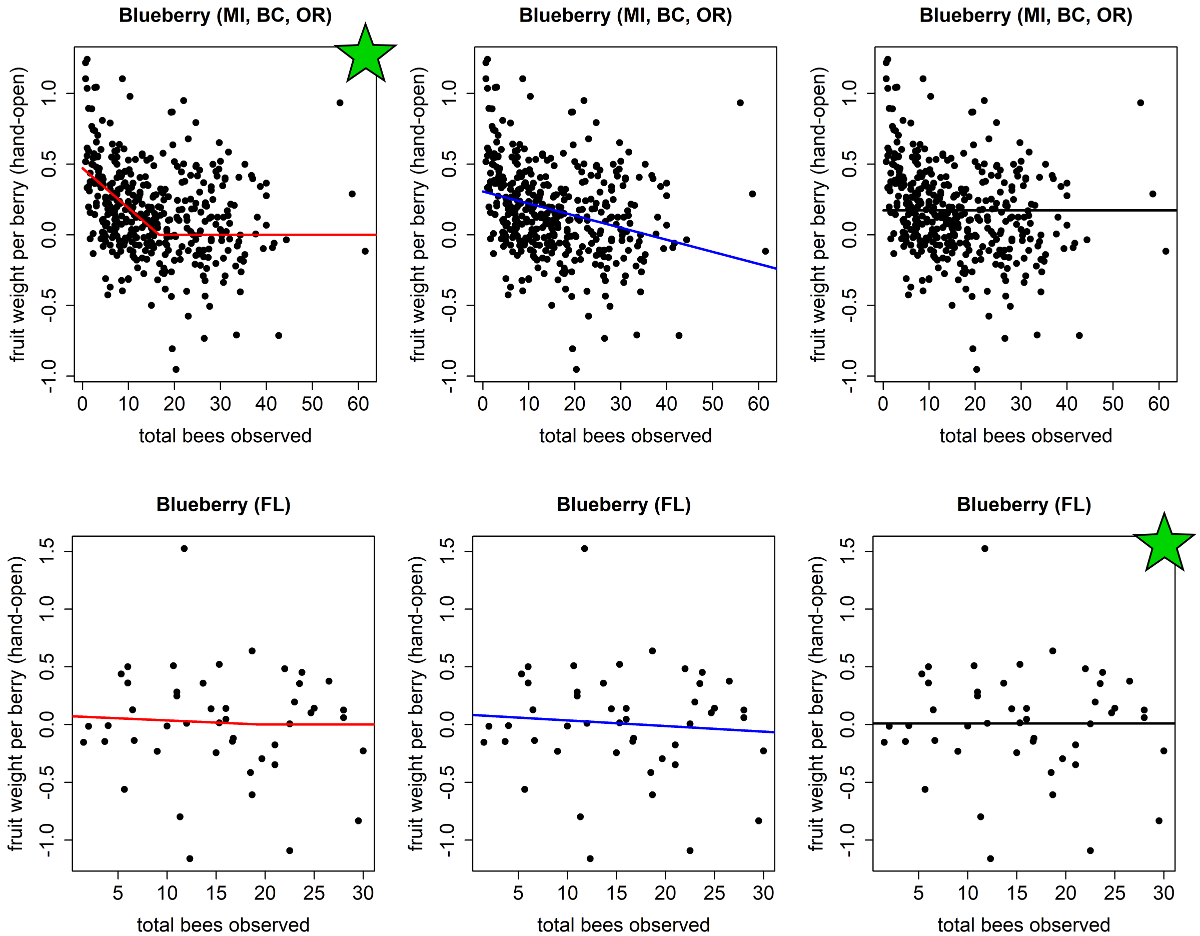

Figure S7. Plots of different potential relationships between visits and the effect of hand-pollination for blueberry. In these plots, a larger y-axis value corresponds to more pollen limitation, thus a negative slope indicates pollenlimitation across transects (the opposite of Fig. S2). The first row of plots correspond to modelsfor northern highbush blueberryof a) a segmented relationship between visits and the effect of hand pollination where there is initially a negative relationship, but after an estimated breakpoint there is no relationship, b) a linear relationship between visits and the effect of hand pollination across all sampled locations and c) no relationship. The second row shows the results of the same models for southern highbush blueberry (Florida). AIC model selection was used to select the best model of the three. The green star in the corner denotes which model was selected.

Table S2. Relative visit rates (% of total visits) by each species group from our study, pollen deposition per visit (PPV) estimates collected from the literature for each species group, and PPV values relative to that of the honey bee (PPV of species group divided by PPV of honey bee).

species_group	**crop_state**	**visits (%)**	**PPV (pollen grains)**	**relative PPV**	**PPV reference (state)**	**reference species group (PPV sample size)**
honey_bee	watermelon_fl	56.1	40	1.0	Winfree et al. 2007 (NJ)	honey_bee (44)
tiny_bee	watermelon_fl	28.7	49	1.2	Winfree et al. 2015 (NJ)	tiny_dark_bee (33)
green_bee	watermelon_fl	10.2	43	1.1	Winfree et al. 2015 (NJ)	mean of small_green_bee and large_green_bee (54)
Bombus	watermelon_fl	2.9	142	3.6	Winfree et al. 2015 (NJ)	Bombus (79)
large_bee	watermelon_fl	1.0	37	0.9	Winfree et al. 2015 (NJ)	large_dark_striped_bee (6)
small_bee	watermelon_fl	0.9	79	2.0	Winfree et al. 2015 (NJ)	small_dark_bee (67)
Xylocopa	watermelon_fl	0.2	479	12.1	Winfree et al. 2015 (NJ)	Xylocopa (1)
megachilid	watermelon_fl	0.04	56	1.4	Winfree et al. 2015 (CA)	Melissodes_megachile_dia dasia (56)
honey_bee	watermelon_ca	90.9	40	1.0	Winfree et al. 2007 (NJ)	honey_bee (44)
Dialictus_Hylaeus	watermelon_ca	6.5	19	0.5	Winfree et al. 2015 (CA)	Lasioglossum_dialictus_hyl aeus (66)
Halictus_tripartitus	watermelon_ca	1.9	46	1.2	Winfree et al. 2015 (CA)	Halictus tripartitus (61)
Halictus_ligatus	watermelon_ca	0.5	73	1.8	Winfree et al. 2015 (CA)	Halictus ligatus (30)
Anthophora	watermelon_ca	0.1	275	6.9	Winfree et al. 2015 (CA)	Anthophora urbana (22)
Peponapis	watermelon_ca	0.04	54	1.4	Winfree et al. 2015 (CA)	Peponapis (39)
Melissodes	watermelon_ca	0.03	56	1.4	Winfree et al. 2015 (CA)	Melissodes_megachile_dia dasia (56)
Tripeolus	watermelon_ca	0.02	3	0.1	Winfree et al. 2015 (CA)	Triepeolus (4)
other_bee	watermelon_ca	0.02	185	4.6	Winfree et al. 2015 (CA)	mean of Lasioglossum_large and Agapostemon (41)
Bombus	pumpkin_pa	53.5	170	2.5	Artz and Nault 2011 (NY)	Bombus impatiens (20)
honey_bee	pumpkin_pa	25.4	68	1.0	Artz and Nault 2011 (NY)	Apis mellifera (20)
squash_bee	pumpkin_pa	17.7	63	0.9	Artz and Nault 2011 (NY)	Peponapis pruinosa (20)

small_dark_bee	pumpkin_pa	2.0	NA	1.0	no data	
green_bee	pumpkin_pa	1.2	NA	1.0	no data	
small_striped_bee	pumpkin_pa	0.3	NA	1.0	no data	
large_dark_bee	pumpkin_pa	0.04	NA	1.0	no data	
honey_bee	cherry_pa	67.7	15 (num fruit)	1.0	Eeraerts et al 2019 (sweet cherry, Belgium)	Apis mellifera (179)
other_bee	cherry_pa	27.5	58 (num fruit)	3.0	Eeraerts et al 2019 (sweet cherry, Belgium)	solitary and mason bees (231)
Bombus	cherry_pa	4.8	0 (num fruit)	0	Eeraerts et al 2019 (sweet cherry, Belgium)	Bombus (30)
honey_bee	cherry_mi	62.9	15 (num fruit)	1.0	Eeraerts et al 2019 (sweet cherry, Belgium)	Apis mellifera (179)
other_bee	cherry_mi	34.1	58 (num fruit)	3.0	Eeraerts et al 2019 (sweet cherry, Belgium)	solitary and mason bees (231)
Bombus	cherry_mi	3.0	0 (num fruit)	0	Eeraerts et al 2019 (sweet cherry, Belgium)	Bombus (30)
honey_bee	sweet_cherry_wa	56.5	15 (num fruit)	1.0	Eeraerts et al 2019 (sweet cherry, Belgium)	Apis (179)
Bombus	sweet_cherry_wa	42.6	58 (num fruit)	3.0	Eeraerts et al 2019 (sweet cherry, Belgium)	solitary and mason bees (231)
other_bee	sweet_cherry_wa	0.8	0 (num fruit)	0	Eeraerts et al 2019 (sweet cherry, Belgium)	Melandrena (30)
honey_bee	blueberry_or	97.1	12	1.0	Javorek et al. 2002 (NS)	Apis mellifera (10)
other_bee	blueberry_or	1.5	11	0.9	Benjamin et al. 2014 (NJ)	mean of large and medium Andrena (83)
Bombus	blueberry_or	1.3	24	2.0	Benjamin et al. 2014 (NJ)	Bombus (queen) (80)

honey_bee	blueberry_mi	94.9	12	1.0	Javorek et al. 2002 (NS)	Apis mellifera (10)
other_bee	blueberry_mi	3.4	11	0.9	Benjamin et al. 2014 (NJ)	mean of large and medium Andrena (83)
Bombus	blueberry_mi	1.4	24	2.0	Benjamin et al. 2014 (NJ)	Bombus (queen) (80)
Xylocopa	blueberry_mi	0.2	3	0.3	Benjamin et al. 2014 (NJ)	Xylocopa virginica (34)
honey_bee	blueberry_fl	82.4	12	1.0	Javorek et al. 2002 (NS)	Apis mellifera (10)
Habropoda	blueberry_fl	8.4	28	2.3	Benjamin et al. 2014 (NJ)	Habropoda laboriosa (38)
Bombus	blueberry_fl	7.3	24	2.0	Benjamin et al. 2014 (NJ)	Bombus (queen) (80)
other_bee	blueberry_fl	1.2	11	0.9	Benjamin et al. 2014 (NJ)	mean of large and medium Andrena (83)
Xylocopa	blueberry_fl	0.8	3	0.3	Benjamin et al. 2014 (NJ)	Xylocopa virginica (34)
honey_bee	blueberry_bc	90.1	12	1.0	Javorek et al. 2002 (NS)	Apis mellifera (10)
Bombus	blueberry_bc	8.9	24	2.0	Benjamin et al. 2014 (NJ)	Bombus (queen) (80)
other_bee	blueberry_bc	1.0	11	0.9	Benjamin et al. 2014 (NJ)	mean of large and medium Andrena (83)
honey_bee	apple_pa	70.2	34	1.0	Park et al. 2016 (NY)	Apis (46)
other_bee	apple_pa	25.3	73	2.5	Park et al. 2016 (NY)	Melandrena (33)
Bombus	apple_pa	4.4	51	1.5	Park et al. 2016 (NY)	Bombus (8)
honey_bee	apple_mi	64.0	34	1.0	Park et al. 2016 (NY)	Apis (46)
other_bee	apple_mi	31.8	73	2.5	Park et al. 2016 (NY)	Melandrena (33)
Bombus	apple_mi	4.2	51	1.5	Park et al. 2016 (NY)	Bombus (8)
honey_bee	almond_ca	100	18	1.0	Thomson & Goodell 2001 (CA)	Apis mellifera (16)

Table S3. Methods details for bee observations on each crop.

crop	state	years	sites	transects	bee obs dates per year	bee obs times per day	bee obs replicate unit
almond	CA	2013, 2014	6	35	1	1	6.7 min (20 sec x 4 areas per tree x 5 trees). The four areas observed on each tree were bottom exterior, bottom interior, top exterior, and top interior.
apple	MI	2013, 2014, 2015	5	57	1	1	10 min (60 sec per tree x 10 trees). Approximately equal time was spent on both sides of the tree.
apple	PA	2013, 2014	5	32	1	1	10 min (60 sec per tree x 10 trees). Approximately equal time was spent on both sides of the tree.
blueberry	BC	2013, 2014, 2015	17	177	3	1	10 min (20 bushes along transect, 1 side each). Observers walked along the row, observing only the facing half of each bush.
blueberry	MI	2013, 2014, 2015	17	188	3	1	10 min (20 bushes along transect, 1 side each). Observers walked along the row, observing only the facing half of each bush.
blueberry	OR	2014, 2015	6	45	3	1	10 min (20 bushes along transect, 1 side each). Observers walked along the row, observing only the facing half of each bush.
blueberry	FL	2014, 2015	12	47	3	1	10 min (20 bushes along transect, 1 side each). Observers walked along the row, observing only the facing half of each bush.
tart cherry	MI	2013, 2014, 2015	5	58	1	1	10 min (60 sec per tree x 10 trees). Approximately equal time was spent on both sides of the tree.
tart cherry	PA	2015	4	16	1	1	10 min (60 sec per tree x 10 trees). Approximately equal time was spent on both sides of the tree.
sweet cherry	WA	2013, 2014, 2015	11	56	3	1	10 min (60 sec per tree x 10 trees). Approximately equal time was spent on both sides of the tree.
pumpkin	PA	2013, 2014, 2015	13	49	3	2	22.5 min (45 sec x 30 replicates per transect). Each replicate was a patch of flowers small enough to be observed from one location.
watermelon	CA	2013, 2014, 2015	17	68	2	2	16.7 min (25 sec x 40 replicates per transect). Each replicate was a patch of flowers small enough to be observed from one location.
watermelon	FL	2013, 2014, 2015	19	80	2	2	16.7 min (25 sec x 40 replicates per transect). Each replicate was a patch of flowers small enough to be observed from one location.

Table S4. Methods details for yield or production measurements of each crop.

crop	state	crop production variable	replicate unit
almond	CA	number of fruit per flower	5 trees sampled per transect
apple	MI	number of fruit per branch*	10 trees per transect (1 branch sampled per tree)
apple	PA	number of fruit per branch*	2-50 (mean 16) trees per transect (1 branch sampled per tree)
blueberry	BC	fruit weight (per berry, open-bagged)	10 bushes per transect (1 bagged and unbagged branch sampled per bush)
blueberry	MI	fruit weight (per berry, open-bagged)	10 bushes per transect (1 bagged and unbagged branch sampled per bush)
blueberry	OR	fruit weight (per berry, open-bagged)	10 bushes per transect (1 bagged and unbagged branch sampled per bush)
blueberry	FL	fruit weight (per berry, open-bagged)	10 bushes per transect (1 bagged and unbagged branch sampled per bush)
tart cherry	MI	number of fruit per flower	10 trees per transect (1 branch sampled per tree)
tart cherry	PA	number of fruit per flower	10 trees per transect (1 branch sampled per tree)
sweet cherry	WA	fruit weight per branch	10 trees per transect (1 branch sampled per tree)
pumpkin	PA	fruit weight per area	5 (2013), 20 (2014-15) quadrats per transect (1 sq m each)
watermelon	CA	fruit weight per area	20 quadrats per transect (2.25 sq m each)
watermelon	FL	fruit weight per area	10 (2013), 20 (2014-15) quadrats per transect (2.25 sq m each)

*Note: for apple, we additionally explored models that included branch cross -sectional area to control for the possibility that larger branches could produce more fruit. However, the orchards we sampled were of similar cross - sectional area, thus the additional variable was not retained by AIC selection.

Table S5. Percent of national gross production value represented by the states sampled in this study (average of 2013-2015 production values). States that are often the top state in terms of national value are marked with an asterisk. In the case of apple, our data rely on estimates from Michigan and Pennsylvania, which both contain important apple producing regions (see Fig. S1), but sum to only about 10% of national value. However our estimates of honey bee and wild bee visitation rates for apple match very well with literature estimates from New York, which is a higher-value state (Park et al. 2016). Similarly, pumpkin is grown widely across the USA, while our data for this crop come only from Pennsylvania. Although it is reasonable to expect that there may be regional differences in pollination that our analysis will not incorporate, our data nevertheless represent the best information currently available.

Crop	States sampled	Percent of National Value
Almond	California*	100.0
Tart Cherry	Michigan*, Pennsylvania	67.0
Sweet Cherry	Washington*	57.6
Blueberry	Florida, Michigan*, Oregon	48.2
Watermelon	Florida*, California	39.7
Pumpkin	Pennsylvania	12.0
Apple	Michigan, Pennsylvania	10.2

Table S6. Pollinator limitation analysis model results (part 1). Yield or crop production variables used in the models, best model as chosen by AIC, breakpoint (if segmented model was chosen), and estimated percent of transects that were pollination limited are listed for each model.

crop	state	variable	best model	segmented breakpoint	percent limited
almond	CA	number of fruit per flower	linear negative	NA	0
apple	MI	number of fruit per branch	linear positive	NA	100
apple	PA	number of fruit per branch	linear positive	NA	100
blueberry	BC	fruit weight per berry (open-bagged)	segmented	26.3	94
blueberry	MI	fruit weight per berry (open-bagged)	segmented	26.3	72
blueberry	OR	fruit weight per berry (open-bagged)	segmented	26.3	64
blueberry	FL	fruit weight per berry (open-bagged)	flat	NA	0
tart cherry	MI	number of fruit per flower	segmented	131.0	72
tart cherry	PA	number of fruit per flower	NA	NA	NA
sweet cherry	WA	fruit weight per branch	segmented	7.3	74
pumpkin	PA	fruit weight per area	flat	NA	0
watermelon	CA	fruit weight per area	segmented	0.3	9
watermelon	FL	fruit weight per area	linear negative	NA	0

Table S7. Pollinator limitation analysis model results (part 2). AIC values, delta AIC values, and Akaike weights are listed for each model, and the best model for each crop state combination is marked in bold.

crop	states	model	AIC	ΔAIC	*w*
almond	CA	flat model	-31.4	1.7	0.30
almond	**CA**	**linear model (neg)**	**-33.1**	**0**	**0.70**
almond	CA	segmented model	NA	NA	NA
apple	MI	flat model	350.5	5.5	0.06
apple	**MI**	**linear model (pos)**	**345**	**0**	**0.91**
apple	MI	segmented model	351.9	6.9	0.03
apple	PA	flat model	232.7	8.4	0.01
apple	**PA**	**linear model (pos)**	**224.3**	**0**	**0.59**
apple	PA	segmented model	225.1	0.8	0.40
blueberry	MI, OR, BC	flat model	264.7	56.3	0.00
blueberry	MI, OR, BC	linear model (pos)	211.1	2.7	0.21
blueberry	**MI, OR, BC**	**segmented model**	**208.4**	**0**	**0.79**
blueberry	**FL**	**flat model**	**39.2**	**0**	**0.68**
blueberry	FL	linear model (neg)	40.7	1.5	0.32
blueberry	FL	segmented model	NA	NA	NA
tart cherry	MI	flat model	-86.1	4.8	0.05
tart cherry	MI	linear model (pos)	-90.5	0.4	0.43
tart cherry	**MI**	**segmented model**	**-90.9**	**0**	**0.52**
sweet cherry	WA	flat model	353.6	8.7	0.01
sweet cherry	WA	linear model (pos)	354.6	9.7	0.01
sweet cherry	**WA**	**segmented model**	**344.9**	**0**	**0.98**
pumpkin	**PA**	**flat model**	**352.3**	**0**	**0.48**
pumpkin	PA	linear model (pos)	352.7	0.4	0.39
pumpkin	PA	segmented model	354.9	2.6	0.13
watermelon	CA	flat model	432.6	1.7	0.27
watermelon	CA	linear model (pos)	434.3	3.4	0.11
watermelon	**CA**	**segmented model**	**430.9**	**0**	**0.62**
watermelon	FL	flat model	338.3	6.2	0.00
watermelon	**FL**	**linear model (neg)**	**332.1**	**0**	**1.00**
watermelon	FL	segmented model	NA	NA	NA

Table S8. Variable input costs per acre (in USD) for each crop-state used in our value analysis, and reference for best-available local extension publication from which cost estimates were calculated.

crop	state	Variable input cost per acre (USD)	reference	notes	% of gross production value
cherry_tart	MI	$2080	Penn State Cooperative Extension (2014)	variable costs	88%
cherry_tart	PA	$2080	Penn State Cooperative Extension (2014)	variable costs	73%
cherry_sweet	WA	$6495	Washington State University Extension (2007)		49%
watermelon	CA	$6885	University of California Cooperative Extension (2004)	all costs minus land prep	86%
watermelon	FL	$2759	Clemson University Extension (2009)	variable costs	51%
blueberry	MI	$7420	Penn State Cooperative Extension (2014)	variable costs	86%
blueberry	OR	$6052	Oregon State University Extension Service (2011)	variable costs for machine harvest	43%
blueberry	FL	$8017	University of Georgia Cooperative Extension (2004)	total variable + harvesting and marketing	45%
apple	MI	$3794	Penn State Cooperative Extension (2014)	60 40 processing vs fresh market (different input costs)	56%
apple	PA	$3794	Penn State Cooperative Extension (2014)	60 40 processing vs fresh market (different input costs)	82%
almond	CA	$2151	University of California Cooperative Extension (2011)	total operating costs	29%
pumpkin	PA	$1672	Penn State Cooperative Extension (2000)		62%

Table S9. A comparison of the fraction of blueberry transects below the estimated breakpoint for pollinator/pollen limitation in the main analysis and hand-pollination analysis (see Supplementary analysis 2). For Florida blueberry, the no relationship model was preferred by AIC, so we do not apply the breakpoint model and therefore estimate 0% (i.e. no limitation).

blueberry region	main analysis (open-bagged)	hand analysis (hand-open)
British Columbia	0.94	0.88
Michigan	0.72	0.42
Oregon	0.64	0.22
Florida	0 / NA	0 / NA

Table S10. Percentages of agricultural and natural landcover within various radii of the study farms. Within each crop system, values are mean percentages across study farms calculated using the 2016 National Landcover Dataset (Homer et al. 2020).

	percent agriculture				percent natural			
crop	1 km	3 km	5 km	10 km	1 km	3 km	5 km	10 km
almond_ca	80	80	73	67	16	17	22	26
apple_mi	67	61	55	49	29	34	38	43
apple_pa	45	35	35	32	47	58	57	60
blueberry_fl	35	25	21	21	60	69	73	71
blueberry_mi	41	30	29	32	48	55	54	50
blueberry_or	84	77	75	71	9	14	13	13
cherry_sweet_wa	13	18	14	10	81	74	78	76
cherry_tart_mi	66	56	50	45	28	36	42	47
cherry_tart_pa	64	55	50	40	24	34	40	51
pumpkin_pa	52	44	44	41	39	47	47	49
watermelon_ca	92	84	81	72	3	9	13	20
watermelon_fl	58	50	46	39	36	41	46	52

Table S11. (separate .xlsx file) Economic value estimates associated with Analysis 3 and Supplementary analysis 1. Quantities referenced by each equation (equations S3-S8) within the economic value analyses are listed with their associated crop and state. These estimates were used to produce Fig. 4 and Fig. S5.