

# Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop

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## Summary

1. Native, wild bees are important pollinators for both crop and wild plants. With concerns over the availability and cost of managed honeybees, attention has turned to native, wild bees as crop pollinators. However, the ability of native, wild bees to provide sufficient pollination may depend on their populations at local scales.

2. Therefore, at the farm scale, we examined the pollination contribution of both native, wild bees and managed honeybees to apples and assessed the relative importance of bee abundance vs. species richness. Over three growing seasons, apple fruit set, bee abundance and bee species richness were measured at orchards in Wisconsin, half of which used managed honeybees, thus allowing us to independently examine the contribution of native, wild bees to fruit set. We additionally conducted observations of honeybees and wild bees foraging on apple blossoms in order to examine functional complementarity.

3. We found that apples are highly dependent on animal pollinators. However, fruit set was not significantly higher at orchards with managed honeybees, nor did it increase with the number of honeybees per orchard. Instead, fruit set significantly increased with the species richness of native, wild bees during bloom.

4. Honeybees and wild bees showed different foraging preferences: honeybees more frequently visited apple flowers on densely blooming trees, while wild bees showed no preference for floral density, thereby evenly visiting trees throughout the orchard.

5. *Synthesis and applications.* Our results show that native, wild bees play a significant and unique role in apple pollination within our region and cannot therefore be replaced by managed bees. Moreover, our findings suggest that bee conservation efforts should focus specifically on maintaining or increasing bee species richness in order to improve pollination and crop yields.

**Key-words:** Agroecosystems, *Apis mellifera*, apple, bee conservation, diversity–function, functional complementarity, native bee, orchards, pollination, yield

## Introduction

Animal-mediated pollination is important for more than half of the agricultural crops grown world-wide for direct human consumption (Klein *et al.* 2007), including crops that provide essential human nutrients (Eilers *et al.* 2011). The European or western honeybee *Apis mellifera* L. is the most common managed pollinator world-wide. But as demand for pollinator-dependent crops increases, honeybees may not be able to meet pollination requirements (Aizen & Harder 2009; Breeze *et al.* 2014). Thus, increased

attention has been placed on wild bees as alternative pollinators. Wild bees currently play a significant role in crop pollination and are estimated to provide \$150 billion in pollination services globally (Gallai *et al.* 2009). Wild bees can offer insurance against changes in the availability of managed bees. For many crops, wild bees are also better pollinators compared to honeybees (Garibaldi *et al.* 2013; Woodcock *et al.* 2013). However, farmers may be hesitant to rely solely on wild bees as bee abundance and diversity vary across regions and growing seasons, resulting in unreliable pollination services. Therefore, it is important to examine how variability in wild bee populations affects pollination rates and the relative contribution of wild bees to crop yields. Understanding native, wild

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bees' role in crop pollination can motivate bee conservation efforts and inform agricultural management.

Wild bees have been shown to significantly affect the yields of many crops, though their ability to provide full pollination services is dependent on their population sizes and the pollination requirements of the crop. A meta-analysis of 29 studies conducted around the world found that fruit set significantly increased with visitation rates and species richness of wild pollinators (Garibaldi *et al.* 2013). Visits by wild pollinators increased fruit set even where substantial quantities of managed bees were present, suggesting that the pollination contribution of wild bees is unique and additive to that of managed bees (Carvalho *et al.* 2010). In agroecosystems where populations of wild bees were large, these unmanaged insects were estimated to fully pollinate crops (Kremen, Williams & Thorp 2002; Winfree *et al.* 2007; Rader *et al.* 2012). But, in regions where wild bee abundance or diversity was low, the estimated pollination by wild bees was insufficient to achieve an acceptable crop yield without managed bees (Scott-Dupree & Winston 1987; Kremen, Williams & Thorp 2002). Thus, whether or not wild bees alone can meet the pollination requirements of a crop is context dependent and is largely unknown or inferred for most agroecosystems. Predicting the contribution of wild bees to crop pollination will require knowledge of the spatial and temporal variability in wild bee communities, as well as an understanding of the relative effects of bee abundance vs. diversity on pollination rates.

The abundance of bees is expected to influence pollination primarily through increasing floral visitation rates, while bee diversity or species richness may influence pollination through many possible mechanisms. Multiple species of bees may directly interact with one another and affect each other's foraging behaviours in ways that enhance the quality or quantity of pollen deposition (facilitation). For example, in sunflowers, wild bees facilitated the movement of honeybees across rows of male and female plants, thereby increasing fertilization (Greenleaf & Kremen 2006). Furthermore, a diverse guild of bees can exhibit temporal complementarity, as emergence dates and foraging periods vary. Wild bees also show spatial complementarity through different preferences for plant species, varieties or foraging locations (Hoehn *et al.* 2008; Brittain, Kremen & Klein 2013). Agroecosystems with more species of wild bees may also be more likely to contain the most effective pollinator species. Bees vary in pollen load, pollen deposition rates and in floral constancy, all of which determine a pollinator's efficacy (Delaplane & Mayer 2000). Finally, greater wild bee diversity may result in redundancy that provides stability in climatic or human-induced disturbances (Winfree & Kremen 2009; Bartomeus *et al.* 2013). Through any of these mechanisms, wild bee diversity or species richness, in addition to wild bee abundance, may significantly affect pollination rates.

Apples are one of many crops requiring insect-mediated pollination. Pollen not only needs to be moved among flowers, but needs to be transferred among different varieties in order to achieve optimal fertilization (Delaplane & Mayer 2000; Schneider, Stern & Goldway 2005; Klein *et al.* 2007). Historically many growers have relied on honeybees for apple pollination (Parker, Batra & Tepedino 1987). However, certain wild bee species have characteristics that make them better pollinators for apples. For example, large-bodied mining bees *Andrena* spp. and bumblebees *Bombus* spp. carry and deposit more apple pollen compared to honeybees (Kendall & Solomon 1973; Thomson & Goodell 2001). Furthermore, some wild bees including bumblebees have a higher tolerance for cool or inclement weather, which commonly occurs during the springtime bloom of apples (Boyle & Philogène 1983; Vicens & Bosch 2000). In northern Wisconsin and New York, at least 30 wild bee species were recorded visiting apple flowers, and additional species were found foraging in the orchard (Gardner & Ascher 2006; Watson, Wolf & Ascher 2011). These observations suggest that a diverse wild bee community is attracted to apples and has the potential to provide significant pollination services.

In this study, we quantified the role of both wild bees and managed bees in pollinating apples of southern Wisconsin and examined the relative importance of bee abundance and species richness for pollination. Specifically, we addressed whether or not wild bees could provide adequate pollination services in the absence of managed honeybees. Apple orchards in southern Wisconsin vary in size, management intensity and in landscape context, which results in large gradients in both the use of managed honeybees and in wild bee populations. We hypothesized that apple fruit set would be positively related to wild bee abundance and species richness regardless of the use of managed honeybees. We also hypothesized that average fruit set would be higher, and be less variable across sites, at orchards with managed honeybees. Our study aimed to understand the contribution of wild bees, and the relative importance of bee abundance and species richness, to crop pollination.

## Materials and methods

### STUDY SITES

Prior to apple bloom in each of 3 years, we identified apple growers that planned to have honeybees on the farm or would not have honeybees and were unaware of any neighbouring hives. In 2011, we sampled five orchards with and six orchards without honeybees, in 2012, we sampled nine orchards with and eight orchards without honeybees, and in 2013, we sampled 12 orchards with and seven orchards without honeybees for a total of 26 samples from orchards with honeybees and 21 samples from orchards without honeybees (see Table S1, Supporting Information).

We collected data from a total of 21 orchards, and while we sampled some orchards in multiple years, an orchard's use of honeybees was not necessarily consistent across years (Table S1, Supporting Information). Orchard study sites were located in southern Wisconsin, USA (between 42.5°N–43.75°N and 87.75°W–91.5°W), and were at least 5 km from any other study site in order to ensure independence of measurements.

Orchard study sites varied in the surrounding landscape structure, but there was no difference in the amount of intensive agricultural habitat or natural habitat (non-agricultural, non-developed land) at a 1-km radius surrounding orchards with and without honeybees ( $t_{45} = -0.41$ ,  $P = 0.68$ ;  $t_{45} = 0.35$ ,  $P = 0.73$ , respectively), as analysed using remotely sensed land-cover data (National Agricultural Statistics Service Cropland Data Layer) in ArcMap 9.2 (ESRI 2009). In other words, farmers' decisions to use managed honeybees did not appear to be correlated with their landscape context. Twelve orchards practiced conventional pest management, while nine orchards used only USDA-certified organic inputs or no chemical inputs (Table S1, Supporting Information). There was no difference in the use of managed honeybees between conventional orchards and organic/no-input orchards ( $\chi^2 = 0.73$ , d.f. = 1,  $P = 0.39$ ). Orchards with honeybees were significantly larger than those without honeybees ( $t_{45} = 2.76$ ,  $P = 0.01$ ), though both groups showed variation in orchard size (Table S1, Supporting Information).

#### MEASURING FRUIT SET

We measured fruit set at all orchards as the proportion of flowers that became fruit on each of 10 trees per orchard. The number of flowers examined per tree, *c.* 500, was kept relatively constant in order to avoid differences in subsampling despite variations in the number of flowers per tree. In early spring, when flowers were in the 'pink tip' (pink flower buds) or 'popcorn' (loose petal clusters) stage, we counted the exact number of flowers on a marked section of outer branches in the lower half of each tree, 1.5–2 m above-ground. Then, 3–4 weeks after petal fall and during the calyx stage of development, we counted the number of fruits resulting from the *c.* 500 marked flowers. Fruit set at this stage is the best indication of pollination as most unfertilized or inadequately fertilized ovaries would have fallen, and additional fruit drop due to competition, weather, injury or over ripening (i.e. non-pollination-dependent factors) is unlikely to have occurred (Bekey, Burgett & Fisher 1981; McCartney *et al.* 2004). No chemical thinning was done prior to fruit counts at any orchard, and any hand thinning avoided our marked branches. The 10 trees utilized at each orchard were mature, blooming trees, representing at least two different self-incompatible varieties, and were all located within a 1-ha area of the orchard.

Additionally, in order to assess the dependence of apples on animal pollinators, we measured fruit set within fine mesh bags made from bridal veil, which is impermeable to even the smallest insects. On each of the 10 trees per orchard, we covered one branch with *c.* 30 flowers. We covered branches at the pink tip or popcorn stage and counted the exact number of flower buds prior to bagging. Observations made during bloom confirmed that flowers inside the mesh bag had fully opened. At petal fall, we removed bags in order to avoid any effects of the bags on fruit development and marked the branches with flagging tape. Approximately 3–4 weeks after petal fall, we counted the fruit on

these marked branches. Fruit set on closed branches was calculated for each orchard using the proportion of flowers that became fruit across all ten trees.

In 2012, severe frosts in late spring affected fruit set in most of the orchard study sites. To account for the effects of frost on fruit set, we measured frost damage at each site after temperatures below freezing occurred throughout southern Wisconsin. These frost events occurred when most apple varieties were in the 'popcorn' stage through full bloom stage. At each orchard, on each of the same 10 trees measured for fruit set, we opened 20 flower pistils located on outer branches at *c.* 1.5–2 m above-ground to check for noticeable discoloration and/or wrinkling (Longstroth 2005; Larsen 2010). We recorded the percentage of discoloured pistils (out of the 200 examined) for each orchard study site.

#### BEE SAMPLING AND OBSERVATIONS

We sampled bees during the apple bloom period in 2012, for two consecutive weeks, and 2013, for 1 week, using bee traps at each study site. Bee traps were 355-ml white plastic cups (Solo Cup Co., Urbana, IL) painted fluorescent blue, fluorescent yellow, or left white, and filled up to 2 cm from the top with a soapy solution containing *c.* 1-ml unscented dish soap per litre of water. At each site, we hung ten traps of alternating colours from stakes 1.5 m above-ground, approximately mid-canopy height, so as to sample wild bees that are flying in the apple canopy and likely to be contributing to apple pollination. We placed stakes 5 m apart from one another within two interior tree rows where fruit set was counted, at least 10 m from the orchard edge but within 100 m of a non-orchard habitat. At sites with honeybees, stakes were located at least 30 m away from, but within 200 m of, any honeybee hive(s). After 1 week in the field, we emptied the contents of bee traps and added new soap solution for each consecutive week of sampling. All bees were stored in alcohol until processed and identified with the assistance of expert taxonomists.

We also observed bee visits to apple blossoms during bloom in 2012 and 2013 to assess differences in wild and honeybee foraging behaviours. We conducted all observations at the Peninsula Agricultural Research Station (44.88°N, 87.34°W) in Door County, Wisconsin, which maintains several blocks of apple trees varying in planting design, size and variety, and all located within a 49-ha area. Honeybees are managed at the station. In both years, we observed bee visits to apple flowers over 2 or 3 days during bloom in six different orchard blocks, each *c.* 0.5 ha and 20–50 m away from any other block. The trees within and across blocks varied considerably in the number of flowers per tree due to biennial bearing, tree age and size, and other possible factors. In each block, we randomly selected approximately six trees to be observed for 10-min period and estimated the number of open flowers on each tree, which varied from 100 to 5000. Then, we selected a group of 50 flowers on outer branches in the lower half of the tree, 1.5–2 m above-ground, for observation. The number of flowers observed was kept constant across all trees in order to analyse visits per flower as a function of floral density per tree (Essenberg 2012). We recorded the number of bee visits and the morphospecies identity of bee visitors during each 10-min period, with 42 ten-minute observations in 2012, and 28 ten-minute observations in 2013. All observations were done in sunny, mild weather with temperatures above 15 °C and between 10 am and 4 pm.

## STATISTICAL ANALYSES

To determine the effect of animal pollinators on apple fruit set, we compared the average fruit set on open branches to the average fruit set on closed branches using a mixed effects model on combined data from 2011 to 2013. In addition, to assess the effect of honeybees on fruit set, we compared average fruit set on open branches between sites with and without honeybees using a mixed effects model on data from 2011 to 2013. To determine whether the use of honeybees was correlated with wild bee populations, we compared abundance and species richness of wild bees at sites with and without honeybees using a mixed effects model, and additionally correlated the number of honeybees captured in traps with wild bee abundance and species richness using simple linear regression on combined data from 2012 to 2013. All mixed effects models included year as an additional fixed effect and site as a random effect. To examine the hypothesis that managed honeybees reduce variability in fruit set, we used a Levene's test to compare variance in fruit set between orchards with and without honeybees. We additionally used a Levene's test to compare variance in fruit set among years and among orchards that were sampled repeatedly (Levene 1960).

We then examined the relationship between apple fruit set and six independent variables: the number of wild bees captured, wild bee species richness, orchard size, number of honeybees captured, frost damage and year using a backwards, stepwise model selection with a  $P$ -value threshold of  $P = 0.10$  to determine the best-fit model. Two separate models were run using total wild bee abundance captured per bloom period, or wild bee abundance per week, as the variable 'bee abundance', in order to account for differences in the length of the bloom period between years. Models combined data from 2012 to 2013. The best-fit model was then modified to include site as a random factor in order to account for the repeated sampling of study sites across study years.

To assess whether wild bees or honeybees showed significant foraging preferences based on floral density per tree, we used generalized linear models with Poisson distributions corrected for overdispersion. We ran two separate models comparing the number of honeybee visits, or the number of wild bee visits, per tree as a function of the number of flowers per tree. Data were combined across 2012 and 2013. Due to the relatively low number of visits in 2013, we did not have enough data to split wild bees into separate morphospecies groups. All data analyses were conducted in JMP 10.0 (SAS Institute Inc., Cary, NC, USA).

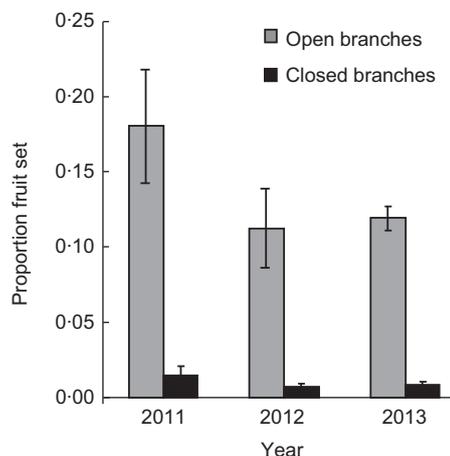
## Results

### FRUIT SET ON OPEN AND CLOSED BRANCHES

Average proportion fruit set on open branches was highest in 2011 at 0.18, and lowest in 2012 at 0.11 due to significant frost damage (Fig. 1). Average fruit set on closed branches ( $0.01 \pm 0.01$ ) was significantly lower than average fruit set on open branches ( $0.14 \pm 0.01$ ) ( $F_{1,73} = 83.5$ ,  $P < 0.0001$ ).

### BEE ABUNDANCE AND SPECIES RICHNESS

Total wild bee abundance per orchard during bloom averaged 112 individuals in 2012 (range 14–330) and was



**Fig. 1.** The average proportion of apple flowers that set fruit within open and closed treatments across apple orchards from 2011 to 2013. 'Open branches' were open to all pollinators while 'Closed branches' were covered with a fine mesh to exclude flying pollinators.

significantly lower in 2013 with an average of 24 individuals (range 7–62) ( $F_{1,21} = 16.2$ ,  $P < 0.001$ ). Across the entire study period, 78 different species of wild bees were found in apple orchards during bloom. Species richness per site in a given year ranged from 5 to 23 and was significantly higher in 2012 compared to 2013 ( $F_{1,19} = 10.5$ ,  $P = 0.004$ ). Wild bee abundance and species richness were not significantly related to the number of honeybees captured in traps ( $R^2 = 0.08$ ,  $P = 0.11$ ;  $R^2 = 0.01$ ,  $P = 0.51$ , respectively). Furthermore, wild bee abundance was not significantly different at orchards with honeybees ( $76 \pm 18$  individuals orchard<sup>-1</sup>) or without honeybees ( $55 \pm 21$  individuals orchard<sup>-1</sup>,  $F_{1,24.0} = 1.57$ ,  $P = 0.22$ ), and there was no difference in wild bee species richness at orchards with honeybees ( $10.95 \pm 1.02$  species orchard<sup>-1</sup>) or without honeybees ( $10.33 \pm 1.2$  species orchard<sup>-1</sup>,  $F_{1,23.3} = 0.51$ ,  $P = 0.48$ ). Honeybees were found in bee bowl traps at 86% of orchards that had honeybees hives on their property. Of the orchards that did not manage or rent honeybees in either year, only two (6%) had honeybees found in traps, presumably from nearby managed or wild hives. These data suggest that whether or not growers had managed honeybees on their property is in fact a strong indicator of honeybee activity within their orchards.

### EFFECTS OF MANAGED AND WILD BEES ON FRUIT SET

Average fruit set was not significantly different between orchards that used managed honeybees ( $12.5 \pm 0.02$ ) vs. those that did not have honeybees ( $13.8 \pm 0.02$ ) ( $F_{1,28} = 0.09$ ,  $P = 0.77$ ). The best-fit multiple regression model ( $R^2 = 0.38$ ) found that proportion fruit set was significantly affected by only two measured variables: frost damage significantly decreased fruit set ( $b = -0.18 \pm$

0.05,  $P = 0.001$ ) and wild bee species richness significantly increased fruit set ( $b = 0.008 \pm 0.002$ ,  $P = 0.003$ , Fig. 2). No other factors significantly affected fruit set including the abundance of honeybees ( $P = 0.13$ ), the abundance of wild bees (per week:  $P = 0.30$  or per bloom period:  $P = 0.46$ ), orchard size ( $P = 0.47$ ) or year ( $P = 0.52$ ).

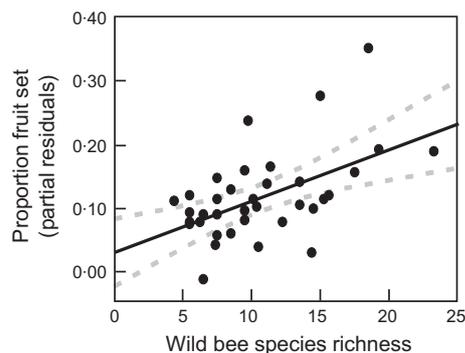
Furthermore, the variance in fruit set was not significantly higher at orchards without honeybees compared to orchards with honeybees (Levene's test,  $F_{1,45} = 1.68$ ,  $P = 0.20$ ). Though we did find that within-year variability in fruit set was significantly different across years (Fig. 1), and within-orchard variability for those that were sampled repeatedly was significantly different among orchards (Levene's test,  $F_{2,44} = 5.18$ ,  $P = 0.01$ ;  $F_{15,26} = 4.15$ ,  $P = 0.001$ , respectively), likely because of the differential effects of frost and weather during bloom.

#### FORAGING BEHAVIOURS OF WILD BEES AND HONEYBEES

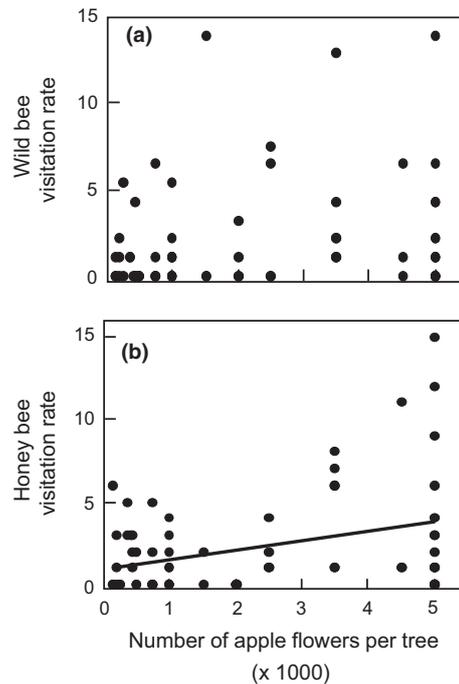
At the agriculture research station where observations were conducted, the most frequent visitors to apple flowers were honeybees and mining bees *Andrena* spp. Wild bees as a group showed no preference for floral density; that is the number of wild bee visits per flower did not significantly differ among trees with varying number of apple flowers ( $\chi^2 = 2.02$ , d.f. = 1,  $P = 0.16$ , Fig. 3a). Honeybees, however, showed higher visitation rates per flower on trees with a greater number of flowers ( $\chi^2 = 10.31$ , d.f. = 1,  $P = 0.001$ , Fig. 3b).

#### Discussion

As the demand for managed bees increases faster than global supply (Breeze *et al.* 2014), greater attention is being given to the pollination potential of wild bees. In apples, a highly pollinator-dependent crop, we found that wild bees alone were able to achieve an adequate fruit set comparable to that at orchards with managed bees. Surprisingly, the use of managed honeybees in southern Wisconsin did not result in greater apple fruit set, and



**Fig. 2.** The effect of wild bee species richness on proportion fruit set after accounting for frost damage in a multiple regression model using data from 2012 to 2013.



**Fig. 3.** The number of visits made by (a) wild bees and (b) honeybees to a cluster of 50 apple blossoms per 10-min observation period on trees with varying total numbers of apple flowers (varying floral density) in Door County, WI, in 2012 and 2013.

nor did it significantly reduce the variability in fruit set as we had hypothesized. The only measured factors that were related to fruit set were frost damage and the species richness of wild bees during crop bloom. Our results highlight the critical role that wild bees play in apple pollination and show that bee species richness is important for crop productivity.

While we did not directly measure apple pollination done by bees (i.e. the quantity and quality of pollen deposited by bees), fruit set during the calyx stage of development is a strong indication of successful pollination. At this stage, trees have dropped most inadequately pollinated ovaries, while final yield may be determined by additional non-pollination-dependent factors such as extreme weather, and pest and disease damage. Furthermore, we found very low fruit set within closed branches inaccessible to animal pollinators, suggesting that our measurements of fruit set are strongly linked to pollinator visitations. As bees are the most effective group of animal pollinators for apples (Delaplane & Mayer 2000), differences in fruit set at this stage are therefore likely to be caused by differences in bee pollination.

#### ROLE OF MANAGED AND WILD BEES IN APPLE POLLINATION

Although honeybees were relatively abundant and active within orchards that used managed bees, they did not increase apple fruit set compared to orchards without honeybees. Honeybees comprised *c.* 11 % of the bee

community found in bee traps over both years and made up 51% of all visits to apple flowers during observations, suggesting that honeybees were present in the study orchards and attracted to apple flowers. One possible explanation for the limited role of honeybees in apple pollination is that honeybees are inefficient pollinators due to their foraging behaviours. Honeybees will often selectively forage for nectar, avoiding contact with the stigmas and therefore carry less pollen on their bodies (Kendall & Solomon 1973; Woodcock *et al.* 2013). Furthermore, honeybees were found to move primarily within apple varieties during a single foraging trip, resulting in lower cross-pollination compared to bees that move more freely among varieties (Kendall & Smith 1975). Additionally, recent studies have shown that honeybee foraging activity declines significantly with wind, which is common during apple bloom (Brittain, Kremen & Klein 2013). Therefore, the amount and quality of pollen deposited by honeybees, and the breadth of conditions under which they forage, may reduce their pollination contribution despite their high abundances and activity levels at many orchards.

We additionally found that honeybees prefer to forage on trees with a large number of blossoms, which could result in selective pollination to trees with dense floral displays. In contrast, the wild bee community showed more random visitation patterns with respect to floral density. Other studies have also found that honeybees show preferences for dense floral displays or large plant populations, exhibiting a concentration effect, while wild bees display a dilution effect (Conner & Neumeier 1995; Jha & Vandermeer 2009a). Honeybees also tend to prefer the upper canopy of blooming trees (Brittain, Kremen & Klein 2013), which could further contribute to selective pollination. These preferences may be driven by honeybees' foraging range and by social recruitment to flowers. Relatively large, social bees such as honeybees can forage at great distances from their hive and are therefore not restricted to foraging options near their nests (Steffan-Dewenter & Kuhn 2003; Greenleaf *et al.* 2007). Honeybees may thus be more selective when choosing foraging sites. They can also recruit one another to mass flowering resources (Conner & Neumeier 1995; Jha & Vandermeer 2009b). Thus, due to their foraging preferences, honeybees alone may not be able to fully pollinate a crop. In contrast, a diverse wild bee community may ensure a greater, and more even, fruit set throughout the orchard.

Another possible reason why managed honeybees did not increase apple fruit set is that in our study system, fruit set may not have been limited by pollinator abundance. In other words, if wild bee populations are large, adding one managed bee species may have little effect on fruit set unless it fills a unique pollination niche or increases facilitation. Furthermore, apple fruit set may have been limited by factors other than pollinator abundance including frosts, nutrient availability, tree stress and overall tree health. A recent study showed that even with hand pollination, which ensures adequate pollen

deposition, proportion of apple fruit set varied from branch to branch, but was always <0.3 due to non-pollination factors (Garratt *et al.* 2014). Therefore, differences in honeybee abundance may be inconsequential if pollinator abundance is relatively high overall, and other limiting factors control fruit set.

In fact, we found that fruit set varied due to both frost damage and wild bee species richness and that these two factors were more important than bee abundance. After accounting for frost damage, each additional wild bee species resulted in a 0.8% increase in proportion fruit set. An increase of nearly 1% per species is economically significant considering that growers typically aim for a proportion fruit set of around 10% (Bekey, Burgett & Fisher 1981). Other studies have also found that pollinator diversity and/or identity is more important for pollination than the sheer number of pollinators (Klein, Steffan-Dewenter & Tschardt 2003; Hoehn *et al.* 2008; Gómez *et al.* 2010). However, in some contexts, pollinator abundance does affect pollination rates, suggesting that the factors limiting fruit set will vary by crop and region (Steffan-Dewenter & Tschardt 1999; Kremen, Williams & Thorp 2002). While we were unable to determine the exact mechanism for the relationship between bee species richness and apple fruit set, other studies have found facilitation, niche partitioning and redundancy among pollinators to increase crop yields (Greenleaf & Kremen 2006; Bartomeus *et al.* 2013; Brittain, Kremen & Klein 2013; Brittain *et al.* 2013; Brosi & Briggs 2013; Fruend *et al.* 2013). Niche partitioning or complementarity can occur both spatially and temporally as bee species forage at different times during the growing season and/or on different flowers. Alternatively, our results may be due to a sampling effect whereby the best pollinator species is more likely to be found in a species-rich bee community.

#### IMPLICATIONS FOR FARM MANAGEMENT AND CONSERVATION

In this study, we assessed the ability of wild bees to adequately pollinate apples in the absence of honeybees, but we were unable to measure the pollination contribution of honeybees in the absence of wild bees. If wild bees had been excluded from orchards, honeybees would likely contribute to fruit set as they can pollinate apple flowers (Degrandi-Hoffman, Hoopingarner & Klomparens 1986; Parker, Batra & Tepedino 1987; Delaplane & Mayer 2000). Given the wild bee community in our study region, though, the addition of managed honeybees did not increase fruit set. Furthermore, after accounting for frost damage, the majority of orchards, including those without honeybees, received a proportion fruit set of 10% or greater. This proportion fruit set is the upper threshold commonly cited as adequate pollination for apples (Bekey, Burgett & Fisher 1981). Our results therefore suggest that the wild bee community in southern Wisconsin is sufficient enough to achieve acceptable crop yields without the help of managed honeybees.

Availability of honeybees is decreasing and rental costs are increasing in North America and Europe (vanEngelsdorp & Meixner 2010); therefore, apple farmers could see economic benefits in relying on wild bees for pollination. At farms with sufficient wild bee populations, farmers could redirect costs associated with managing or renting honeybees towards the conservation of wild bees. A leading hypothesis for declines in wild bee populations is anthropogenic land-use change and subsequent loss of floral and nesting resources (National Research Council 2007; Potts *et al.* 2010; Burkle, Marlin & Knight 2013). In our study region, we previously found that a high diversity of habitats surrounding an orchard, including a mixture of woodlands, open grasslands, diverse crop fields and urban development, increased wild bee species richness within the orchard (R.E. Mallinger unpublished data). To enhance pollination services, farmers could create or maintain diverse habitats on their property to support a species-rich wild bee community. Farmers located in homogeneous landscapes, particularly ones dominated by intensive agriculture, may have reduced wild bee species richness and therefore pollination services. Conservation programs established to help farmers install diverse floral plantings and nest sites where they do not occur naturally (Wratten *et al.* 2012) may have a measurable effect on crop yield by increasing wild bee species richness.

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## Data accessibility

Site characteristics: uploaded as online supplementary material.

Input data for all analyses and a complete bee species list: DRYAD entry: <http://dx.doi.org/10.5061/dryad.t75c4> (Mallinger & Gratton 2014).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Table S1.** Study site characteristics.