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Flower handling behavior and abundance determine the relative contribution of pollinators to seed set in apple orchards

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ABSTRACT

A growing body of evidence suggests that wild bees play an important role in agricultural pollination. It is very difficult, however, to accurately quantify the contribution of wild bees relative to honeybees in most crop systems. We quantified the relative contribution of honeybees and wild bees to the pollination of an economically important, insect-pollinated crop (apple). We use an empirical dataset to identify which of three functional traits (body size, pollen load purity, and flower handling behavior) contribute significantly to seed set. We find that flower handling behavior and abundance were the only functional traits that significantly predict seed set. When we take into account flower handling behavior and abundance, wild bees contributed significantly more to seed set than honeybees in the apple orchards we surveyed. Our findings suggest that land managers may benefit from focusing on supporting communities of wild bees, rather than investing in honeybee hive rental.

1. Introduction

Pollination services provided by flower-visiting insects, especially bees, are critical to global food security (Klein et al., 2007). Moreover, a healthy human diet comprises fruits, vegetables, and oils that rely on bee pollination for their production (e.g. Eilers et al., 2011; Kant et al., 1993). While modern agriculture has traditionally used managed honeybees for pollination, global production of pollinator-dependent crops is now out-pacing world-wide production of honeybee hives (Aizen and Harder, 2009). The threat of "pollinator-deficits" is further compounded by recent honeybee declines (vanEngelsdorp and Meixner, 2010), largely due to heavy pathogen loads and exposure to pesticides (Goulson et al., 2015). Providing sustainable pollination services into the future, therefore, requires a diversification of pollination strategies, including leveraging the services provided by native and wild pollinator species.

Wild bees contribute substantially to insect-dependent crop production (Garibaldi et al., 2013; Winfree et al., 2008), particularly when wild bee communities are diverse and abundant (e.g. in strawberry (Connelly et al., 2015), watermelon (Kremen et al., 2002; Winfree et al., 2011, 2007), blueberry (Isaacs and Kirk, 2010; Javorek et al., 2002; Tuell et al., 2009), and apple (Blitzer et al., 2016; Park et al., 2015; Russo et al., 2015)). In a global study of 30 crops, wild bees provided superior pollination services (i.e. fruit set) compared to honeybees, regardless of the number of honeybees present (Garibaldi et al., 2013). Divergence in functional traits between honeybees and wild bees may explain this discrepancy in provisioned pollination service. Whereas the honeybee is a single species, wild bees comprise a diverse assemblage of species with an array of functional traits that may influence pollination services. For example, the way that bees carry pollen, their host specificity, their body size, and how they handle flowers may all play a role in pollen deposition and ultimately fruit set production and quality (Thomson and Goodell, 2001; Larsson, 2005; Martins et al., 2015; Park et al., 2015). While a positive relationship between wild bee visitation and crop pollination service is now well-described, less is known about specific functional traits of wild bee communities that afford higher quality pollination.

The relative contribution of wild bees to pollination can be estimated as the summed product of per-visit effectiveness of all species and their relative abundance (Olsen, 1996). Using this measure, Park et al. (2015) found two groups of wild pollinators to contribute less to apple pollination than honeybees due to their lower abundances. These bee groups, however, represented a small portion of the entire wild bee community. Directly comparing the pollination services of honeybees to those of the entire wild bee community is a difficult task in crop systems, like apple, which have diverse bee assemblages. Wild bees

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comprise many species, making it logistically difficult to experimentally measure the per-visit effectiveness (e.g. pollen deposition, fruit set) of every species.

Our study investigates functional traits that determine the quality of pollination services provided by wild bees for apple, *Malus domestica*. We first identify bee functional traits that predict seed set in apple orchards. We then use these functional traits as a proxy for per-visit effectiveness to estimate wild bee pollination services relative to that of honeybees at a regional scale within NY. Thus, our measure of pollinator contribution is the summed product of functional traits that predict seed set for each bee species multiplied by their relative abundance. Apple is a high-value, pollinator-dependent crop (Free, 1964; Garratt et al., 2014a) and an ideal system in which to explore the role of functional traits in crop pollination. Wild bees visiting apple blossoms are abundant and diverse (Gardner and Ascher, 2006; Sheffield et al., 2013; Russo et al., 2015; Kammerer et al., 2015), and apple fruit and seed set increase directly with wild bee abundance but not with honeybee abundance; (Martins et al., 2015; Mallinger and Gratton, 2015; Joshi et al., 2015; Blitzer et al., 2016). Indeed functional diversity is a strong predictor of pollination service (i.e. fruit and seed set) in apple orchards (Martins et al., 2015; Mallinger and Gratton, 2015; Blitzer et al., 2016). While these studies document benefits of functional diversity for apple pollination, they included a variety of traits, including some that were not likely to have a direct effect on pollination, such as sociality. Our study identifies specific functional traits that may directly affect pollinator effectiveness and have not been accounted for together in previous studies: flower handling, body size, and the composition of pollen carried by different bee species.

In this manuscript, we combine data from several studies. We identify functional traits that predict seed set, a direct correlate to fruit quality and value (Garratt et al., 2014b), and then quantify the relative pollinator contribution of bee species detected in NY apple orchards. We compare contributions of wild bees relative to managed honeybees based on the functional traits we identified as significant predictors of seed set. Our results indicate that wild bees, especially ground-nesting bees, provide the bulk of pollination services in the majority of surveyed orchards. Thus, we find that wild bees are not only a good insurance policy against honeybee declines, but also a major contributor to commercial NY apple production − both because of their abundance in NY apple orchards and their high propensity to make direct contact with a flower's anthers and stigma. Moreover, our results show that wild bees contribute significantly more to seed set relative to honeybees on average across the apple orchards we surveyed.

2. Methods

To quantitatively compare pollination services of wild bees to that of honeybees in NY apple orchards, we calculated the summed contribution to seed set of the entire wild bee community relative to that of the honeybee. There are two fundamental components to estimating the contribution of a pollinator or group of pollinators to seed set: (1) *abundance* (visitation rate) and (2) *per-visit effectiveness* (Ne'eman et al., 2010; Olsen, 1996). Abundance is relatively easy to measure even when the pollinator fauna is as diverse as that in apples. Measuring per-visit effectiveness of each species, however, poses significant challenges when pollinator diversity is high. Per-visit pollinator effectiveness is often quantified as the number of pollen grains deposited on a previously unvisited flower in a single visit (Ne'eman et al., 2010Park et al., 2015). This can be obtained by attaching a flower to a stick and "interviewing" free-foraging bees. Measures of per-visit pollen deposition have been obtained for a small fraction of the bee diversity in apple orchards. Thomson and Goodell (2001) compared bumblebees (*Bombus*) to honeybees using this method, and Park et al. (2015) compared bumblebees, honeybees, and members of the *Andrena* subgenus *Melandrena*. The interview method can only yield sufficient sample sizes for common species slow enough to place interview flowers in their foraging path.

We first identified functional traits of bees that directly influence per-visit effectiveness and could be applied to all species detected to date in New York apple orchards. Specifically, we used model selection to identify functional traits that significantly predict seed set. These significant functional traits were then used to quantify the summed pollination contribution of wild bees and honeybees. This contribution was calculated as per-visit effectiveness multiplied by abundance for each species; we used functional traits as a proxy for per-visit effectiveness and then multiplied these trait values by the abundance of the bees. Rather than correlating abundance of wild bees and honeybees to seed set (see Mallinger and Gratton 2015; Martins et al., 2015; Blitzer et al., 2016), we directly quantified their relative contribution to seed set and tested whether this contribution was significantly different.

2.1. Abundance

We used a subset of the abundance data collated by Russo et al. (2015) for the visitation rate component of the pollinator contribution equation (Ne eman et al., 2010Ne'eman et al., 2010). Bees were net collected in apple orchards during bloom at 28 orchards from 2008 to 2013 (see Russo et al., 2015 for a full description). Over 100 wild bee species were detected in these orchards, but a relatively small number of species made up the vast majority of the abundance. To compare relative pollinator contributions to seed set, we exclusively used abundance data from 2013 bee surveys of orchards (53 species, 99 15-min transects) where seed set monitoring occurred that same year (Blitzer et al., 2016). Once we identified functional traits that contributed measurably to seed set, we compared relative pollinator contribution across orchards (Figs. 1 and 2), using abundance data from 15 min standardized transects (Russo et al., 2015) surveyed in 2011–2013 (78 bee species, 363 transects) because sampling was most consistent during these years. Thus, all abundance data used in this study are from 15-min standardized net collections in NY apple orchards.

Species were assigned to functional groups based on close taxonomic relatedness and similar size and behavior patterns. These functional group classifications allowed us to include the entire wild bee community in our investigation because we could measure functional traits on a representative species from each functional group, and then assume these functional traits were similar across the group. Many bee species were represented by a small number of individuals; ignoring these rare species would have underestimated the bee community's contribution to pollination. We therefore assigned rare species to functional groups that were defined by closely related, abundant species, on which we are able to measure functional traits in a replicated fashion. When placed into functional groups, 14 species represented 99% of total functional group diversity (see Table S1 for functional group classification). Below, we describe these measurable functional traits in more detail. In the analyses reported in the main body of this paper, we use these functional group classifications. To ensure that we have not biased our findings by doing so, we repeat all of our analyses, in the supplemental materials, with a more conservative model where we only include species on which we directly measured functional traits.

2.2. Behavior

Bees that visit flowers specifically for nectar can bypass the reproductive parts of the flower (anthers and stigma) by nectar robbing (Inouye, 1983). In open flowers, such as apple and other Rosaceae, floral visitors have been observed to visit flowers in two different ways. "Side-working" bees are those that land on the petals and probe the base of the anther column without contacting the anthers or stigma (http://tinyurl.com/grvavv3), whereas "top-working" bees actively gather pollen and contact both anthers and stigma (http://tinyurl.com/

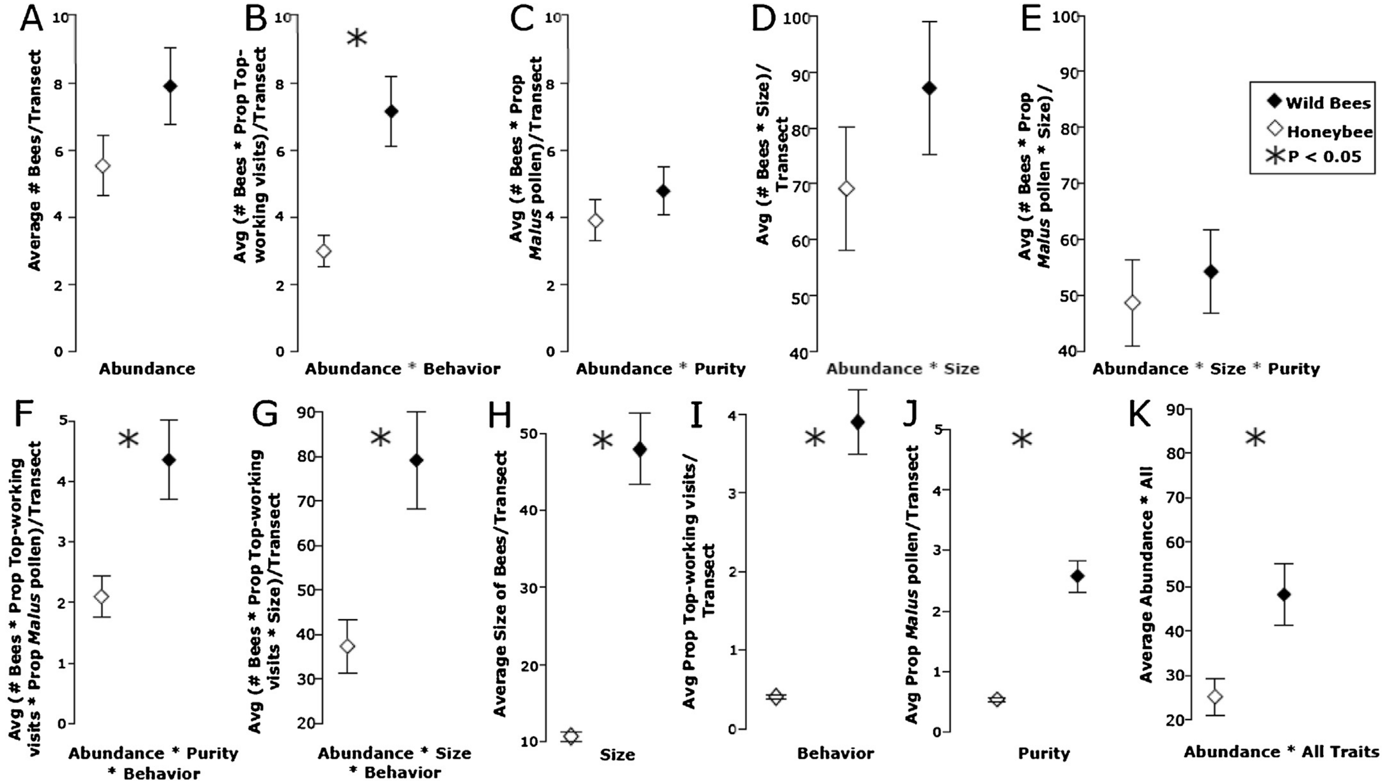

Fig. 1. Visualizations of pollinator contribution models of honeybees (white) and wild bees (grey) in apple orchards. All functional traits are averaged across bees collected during 15-min transects in 23 apple orchards from 2011 to 2013. Abundance (A) is the basic model. All other functional traits here (B-G) are multiplied by abundance. (H-J) represent the functional traits directly compared between wild bees and honeybees. (K) compares abundance multiplied by all the functional traits to represent the full model from Table 2. The model testing in Table 2 suggests that abundance and flower handling behavior (B) are significant predictors of seed set. Significant differences ($P < 0.05$) are marked by an asterisk (*); all other comparisons are not statistically significant ($P > 0.05$).

zju8v65) (Thomson and Goodell, 2001; Park et al., 2015).

Bees that visit apple flowers for nectar only tend to approach from the side (side-working) and do not contact stigmas, while bees visiting apple flowers for pollen tend to approach from the top (top-working) and, as a result, contact the stigmas (Martins et al., 2015). Studies by Park et al. (2015) and Martins et al. (2015) agreed qualitatively on the flower handling behavior exhibited by specific bee taxa, and where they disagreed quantitatively (e.g. on proportion of top-working visits), we averaged the values (Table S1). Martins et al. (2015) visually classified bees into seven categories: (1) honeybees, (2) bumblebees, (3) metallic

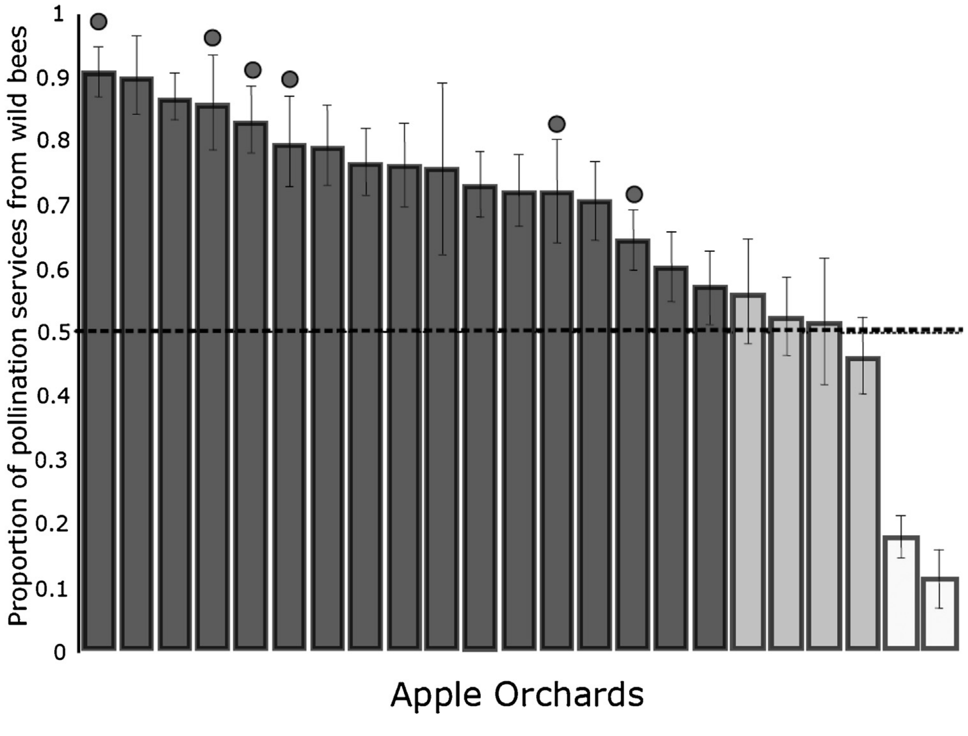

Fig. 2. The relative contribution to seed set of wild bees compared to honeybees in 23 orchards (columns). The contribution in this case is defined as the abundance of each bee species multiplied by the proportion of flower visits during which it contacts the anthers and stigma (top-working). For each orchard, this value is summed for all bee species in a given 15-min transect and then averaged across transects. The grey circles above the columns denote orchards that did not rent honeybee hives for the duration of the study. Dark grey columns denote orchards where wild bees contribute more than honeybees, light grey columns where they contribute an equal amount, and white columns where the honeybee contributes more to seed set.

green bees, (4) large *Andrena*, (5) *Osmia*, (6) small *Andrena*, and (7) small black bees (see Martins et al., 2015 for further explanation). Park et al. (2015) observed the flower handling behavior of bees classified in three categories (1) honeybees, (2) bumblebees, and (3) large *Andrena* (subgenus *Melandrena*) (see Park et al., 2015 for further explanation). We then applied these classifications of flower handling to bees collected in our apple orchards.

The proportion of side-working vs. top-working visits by different bee species could be a reasonable correlate of per-visit pollen deposition. We hypothesized that top-working bees are more effective pollinators on a per-visit basis than those that side-work. To determine whether this is true, we tested whether the proportion of flower visits where the bee contacts the anther and stigma (top-working visits) of the species collected is a significant predictor of apple seed set. We used an empirical dataset on seed set collected in the same year and orchards (Blitzer et al., 2016) as our response variable (see Statistical analyses below).

Using data on flower handling behavior collected by Park et al. (2015) and Martins et al. (2015), we quantified the proportion of time spent top-working relative to side-working for approximately 82% of the bee species in our study; species not represented were in low abundances, including *Nomada*, Augochlorini, *Agapostemon*, and *Osmia*. As with our other functional traits, some species that were not directly observed in the field were assumed to have similar behavior to bees in the same functional group (Table S1). The purpose of the functional group classifications was to better describe the behavior of the whole wild bee community, without ignoring uncommon species that were difficult to measure reliably. To verify that our functional groupings did not bias our results, we repeated our analyses with only the species whose traits were directly measured (see supplemental materials).

2.3. Other functional traits

In addition to floral handling, we tested two other functional traits: pollen purity and bee body size (Fig. 1). We define pollen purity as the proportion of the pollen load consisting of apple pollen relative to pollen of other species. The pollen counts were conducted on field-collected specimens from surveyed apple orchards by the authors for the purposes of this study. Our hypothesis was that pollen purity is positively correlated with legitimate pollen deposition (Larsson, 2005). We quantified the proportion of *Malus* pollen carried by 170 bees of 14 species representing 99% of total functional group diversity (Table S1). We identified the species composition of the pollen, calculated the proportion of *Malus* pollen, and tested whether this was a significant predictor of orchard level seed set (see statistical analyses below). A full description of the pollen purity analysis is in the supplemental materials.

We also hypothesized that larger bees, because of their larger surface area, will have a higher per-visit effectiveness than smaller bees. We collected data from the literature on body length of each bee species (Mitchell, 1960) and measured the intertegular distances of the field-collected bees for the purposes of this study. As intertegular distances in this case were highly correlated with body length values (see supplemental materials), we found little difference in the analyses resulting from these two measures. As a result, we used body length for the final models reported in this manuscript. The intertegular distances are reported in the supplemental materials. We test whether body size is a significant predictor of seed set in the apple orchards (see statistical analyses below).

2.4. Statistical analyses

To test which bee functional traits have a meaningful relationship with the economic value of pollination service, we used seed set as our response variable (Blitzer et al., 2016). Blitzer et al. (2016) monitored fruit and seed set on 6 trees of several different varieties at a subset (15 of 23) of orchards surveyed for bee species richness in Russo et al. (2015). We used generalized linear mixed effects models R package lmer (R Core Team, 2013) to conduct model comparisons with seed set in the surveyed apple orchards as the response variable. We used apple variety and orchard location as random effects and kept these random effects constant for all model comparisons. We based all model comparisons off of a basic model from Blitzer et al. (2016), which found a significant positive correlation between seed set and both species richness and abundance of wild bees, but not abundance of honeybees. For our model, we used predictors of honeybee abundance and wild bee abundance. We compared models composed of the abundance of honeybees and wild bees, plus functional traits of these species. Then we compared every model combination of honeybee abundance, wild bee abundance, flower handling behavior (proportion of top working visits), pollen purity (proportion of *Malus* pollen), and body size (listed explicitly in Table 2). We used AIC values and percent variation explained to identify the best fit model for this comparison, where the best fit model had the lowest AIC value and the highest percent variation. We divide percent variation explained into marginal R^2 and conditional R^2, where the marginal R^2 shows the variation explained by the fixed effects alone and the conditional R^2 shows the variation explained by both the fixed and random effects (Johnson, 2014; Nakagawa and Schielzeth, 2013). The model variations we explored, their AIC values, and the percent variation they explain are presented in Table 2.

The fixed effects of our best model as determined by our model selection process were then considered to be significant contributors to seed set. We directly compared the contributions of wild bees and honeybees to seed set according to these functional traits (significant fixed effects) by treating significant fixed effects as proxies for per-visit effectiveness and multiplying them by species abundance to calculate pollinator contribution. We used abundance data from 2011 to 2013 and included all species represented by a functional group (Table S1).

3. Results

3.1. Abundance

There was no significant difference in the abundance of honeybees and wild bees across study orchards (Fig. 1A, $P = 0.08$). Wild bees were equally abundant despite the fact that, of the 23 orchards evaluated, only six did not rent honeybee hives for the duration of the study. There was no significant effect of honeybee abundance or hive density on wild bee abundance or species richness ($P > 0.05$, Russo et al., 2015).

3.2. Behavior

The foraging behavior (proportion of top-working flower handling) of all but 14 of 78 species was represented by functional groups observed in the field by Martins et al. (2015) and Park et al. (2015). For groups where Martins et al. (2015) and Park et al. (2015) overlapped, we averaged the reported values, which were very similar (Table S1). This proportion varied between 0.54 and 1.00, with honeybees being the least likely to top-work flowers (Table 1). Bees with the highest proportion of top-working individuals (100%) included *Bombus*, large *Andrena*, and *Colletes inaequalis*.

The basic model explaining seed set at the orchard level had the fixed effects of honeybee abundance (estimate 0.09, $P < 0.05$) and wild bee abundance (0.17, $P < 0.001$) and random effects of orchard identity and apple variety. The generalized linear mixed effects model with the lowest AIC value, which also explained the most variation, included honeybee abundance, wild bee abundance, and flower handling behavior as fixed effects and orchard identity and apple variety as random effects (Table 2). This model explained 28% of the marginal variation and 67% of the conditional variation in seed set at the orchard level (Table 2). The relative contributions of the different fixed effects

Table 1
Functional traits including flower handling behavior (proportion of time spent top-working, or contacting stigma (data from Martins et al., 2015)), percent *Malus* pollen (data collected for this study from field-collected specimens, pollen purity, n = 10), and body length (data collected for each species from Mitchell, 1960).

	Flower Handling	Pollen Purity	Body Length (mm)
Female			
Andrena crataegi	1.00	0.48 ± 0.10	11.5
Andrena hippotes	0.97	0.51 ± 0.11	9.5
Andrena miserabilis	0.97	0.80 ± 0.07	8.2
Andrena nasonii	0.97	0.68 ± 0.08	8.0
Andrena regularis	0.81	0.74 ± 0.08	12.0
Andrena vicina	0.81	0.70 ± 0.11	12.5
Andrena (*Melandrena*)*	0.81	0.72 ± 0.10	12.3
Apis mellifera	0.54	0.70 ± 0.09	12.5
Augochlora pura	–	0.45 ± 0.12	8.0
Bombus impatiens	1.00	0.61 ± 0.11	19.0
Colletes inaequalis	1.00	0.54 ± 0.10	12.5
Halictus rubicundus	0.95	0.65 ± 0.11	10.5
Lasioglossum hitchensi	0.95	0.28 ± 0.14	5.2
Osmia cornifrons	–	0.76 ± 0.10	13.5
Xylocopa virginica	0.82	0.61 ± 0.11	21.0
Male			
Andrena crataegi	1.00	0.70 ± 0.06	10.5
Xylocopa virginica	0.82	0.66 ± 0.05	19.0

* Averaged between *Andrena regularis/vicina*.

Table 2
Models of the relationship between seed set and different ways of measuring pollinator contribution in apple orchards, compared to a basic abundance model. The only model that improves the variation explained and model fit is a model that includes honeybee abundance, wild bee abundance, and flower handling behavior. All models have random effects of orchard identity and apple variety. Significance at the P < 0.05 level is indicated by an asterisk.

Model Description	Marginal	Conditional	AIC	Sig.
Basic Model (Honeybee abundance + wild bee abundance)	0.21	0.66	771.5	
Basic Model + Size	0.24	0.67	773.4	
Basic Model + Pollen Purity	0.23	0.67	773.8	
Basic Model + Flower Handling Behavior	0.28	0.67	769.9	*
Basic Model + Size + Pollen Purity	0.20	0.66	772.7	*
Basic Model + Size + Pollen Purity + Flower Handling Behavior	0.27	0.67	770.8	*
Basic Model + Size + Flower Handling Behavior	0.22	0.69	777.9	
Basic Model + Pollen Purity + Flower Handling Behavior	0.29	0.68	772.6	*
Pollen Purity	0.17	0.66	774.5	
Size	0.05	0.67	781.6	
Flower Handling Behavior	0.11	0.67	778.6	*

were: honeybee abundance (estimate 0.12, $P < 0.01$), wild bee abundance (0.12, $P < 0.05$), and flower handling behavior (5.73, $P < 0.01$).

When we measured pollinator contribution as a combination of abundance and proportion of time that species contacted the stigma of the flower (i.e. proportion top-working visits), wild bees were found to contribute, on average, significantly more to seed set than honeybees across the orchards ($P < 0.01$, t stat = 3.2, Fig. 1B). We also found that wild bees, as a community, contributed more to seed set than honeybees at 17 of 23 orchards (Fig. 2). At an additional four orchards, they had equal contribution to the honeybee.

3.3. Other functional traits

Compared to honeybees, wild bees carried proportionately more apple pollen and were bigger, on average, per transect across orchards ($P < 0.01$ for both, purity t stat = 7.6, size t stat = 8.2, Fig. 1J, H). Neither purity of pollen loads or body size, however, significantly contributed to seed set at the orchard level (Table 2). Compared to the basic model, models containing size alone, purity alone, or the basic model variables (i.e. abundance) with size or purity alone were not significantly different from the basic model alone (Table 2). The basic model with purity and size was significantly worse than the basic model alone (Table 2). A full model containing all three functional traits and abundance performed significantly better than the basic model alone, but this full model explained less variation and had a higher AIC value than the basic model with flower handling behavior alone (Table 2). Excluding bees represented by functional groups did not significantly change our results (see supplemental materials).

4. Discussion

Our study demonstrates that the best predictors of seed set in NY apple orchards are abundance and flower handling behavior of the bee community. Using these functional traits, we quantified the relative contribution of wild bees relative to honeybees and show that wild bees contribute significantly more than honeybees to seed set across the study area. Here we provide a comprehensive view of mechanisms driving the increased contribution of wild pollinators to seed set in apple orchards, as well as potential insight into the role of wild pollinators in other crops. Our study is in agreement with other empirical studies, showing bee abundance (Olsen, 1996; Winfree et al., 2015) and flower handling behavior (Park et al., 2015) are important factors in seed set. Because apple orchards are a mass blooming crop with a large number of flowers, it is no surprise that pollinator abundance is a key driver of pollinator contribution to seed set. Theory also supports the importance of abundance in dictating pollinator contributions both in agricultural and natural systems (Ne eman et al., 2010Ne'eman et al., 2010). We have further shown that we can strengthen our understanding of the mechanisms driving the contributions of wild bees to seed set by combining information about flower handling behavior with abundance.

The functional traits of pollen purity and body size were not significant predictors of seed set at the orchard level, though both may influence pollen deposition (see supplemental materials). This may be because at the scale of the orchard, with many thousands of flowers, the abundance of a given pollinator and whether or not it contacts the reproductive parts of the flower are more essential for pollination efficacy. On the other hand, this lack of significance may relate to the fact that the majority of the abundant bees collected in apple orchards were relatively similar in size and carried a similar proportion of *Malus* pollen. Andrenids were the most abundant wild bees in our study, while these bees vary in size, many are similar in size to a honeybee worker (Table S1). Honeybees and the most abundant *Andrena* species in our study orchards also carried similarly high proportions of *Malus* pollen (Fig. S1).

The importance of a particular functional trait for crop pollination may change over space and time. The seed set data used in this study were collected over the course of one year (Blitzer et al., 2016). Because we surveyed the bee communities in these same orchards that year, we were able to directly compare the composition of the bee community with the ultimate seed set. However, the abundance and composition of the bee community fluctuates greatly from year to year (Russo et al., 2015). Thus, it is possible that other functional traits of these pollinators will contribute more to seed set in other years. For example, though body size was not a significant predictor of seed set in our study, this trait may become important in years where the community composition of bees significantly shifts toward larger or smaller bees. Likewise, the majority of bees in our study carried relatively high proportions of *Malus* pollen. If the composition of the bee community shifts toward bees that rarely visit *Malus*, pollen purity may become a much more significant trait in determining seed set. For example, Park et al. (2015) showed that the relationship between pollen grains deposited and likelihood of fruit set was a saturating curve. Other factors not measured in this study (e.g., visitation rate of different bee species) may also play a role in pollination contribution and are potential avenues for future research.

Honeybees have an unusually high propensity to side-work flowers in comparison to wild bees and the main effect of this behavior was to reduce the contribution of honeybees. Honeybees have greater nectar requirements to build honey stores; as a result, honeybee workers may specialize on nectar rewards and use side-working as an efficient method of floral handling. The values describing the flower handling behavior of bees observed visiting apple flowers were limited; most wild bees exhibited a high proportion of top-working visits, while honeybees only contacted the reproductive parts of 50% of flowers visited (Park et al., 2015; Martins et al., 2015). In spite of this limitation, flower handling behavior was a significant predictor of seed set in apple orchards (Table 2). This suggests that bees that do not contact the stigma of the flower directly are unlikely to transfer enough viable pollen for fertilization to occur (but see Degrandi-Hoffman et al., 1985). This may explain why Blitzer et al. (2016) found no correlation between honeybee abundance and seed set at the orchard level. Flower handling is also important for the pollination of buzz-pollinated crops, such as tomatoes (Banda and Paxton, 1990) and blueberries (Javorek et al., 2002). However, in crops with very small flowers in which most floral visitors always make contact with the anthers and stigma, flower handling may be irrelevant to pollinator effectiveness.

Our study provides some insights into quantifying the seed set contribution of a community of wild bees relative to that of the honeybee. While per-visit pollen deposition is often thought to be the most accurate measure of per-visit effectiveness, we find the flower handling behavior (proportion of top-working visits) of bees was a significant predictor of seed set in apples. Future studies of pollinator contribution in crops with a diverse wild bee fauna might focus on quantifying flower handling behavior as a potential proxy for per-visit effectiveness, given the challenges of obtaining per-visit pollen deposition data for large numbers of species. On the other hand, the labor intensive process of identifying the composition of pollen loads carried by bees may not be worthwhile for quantifying pollinator contributions to crops. While increased pollen purity did increase seed set at the scale of an individual apple flower (Park et al., 2015), it was not a significant factor at the scale of the orchard. This may be due to the fact that orchards in full bloom can have trillions of flowers and, at this scale, the sheer quantity of visits is more important than the quality of any individual visit.

Finally, no matter how we quantify pollinator contribution, unmanaged bees, especially of the genus *Andrena*, are providing critical pollination services in New York apple orchards. When we quantify the contribution of pollinators to seed set as flower handling behavior and abundance, wild bees contribute more than honeybees in 17 of 23 orchards and an equal amount in an additional 4 orchards, despite the fact that only 6 of the orchards did not rent honeybee hives during the study (Fig. 2). When we quantify pollinator contribution in this way, wild bees are more than twice as important in apple orchards as honeybees (Fig. 1B).

5. Conclusion

Our findings support the use of pollinator abundance as a proxy for pollinator contribution to crop yield (e.g. Garibaldi et al., 2013; Vazquez et al., 2005), but demonstrate flower handling behavior is also an important component of pollinator services. Understanding per-visit pollen deposition, or the purity of pollen loads carried by bees might be less important than bee flower handling behavior and abundance for agricultural pollination. The importance of flower handling behavior has been shown in crops that must be buzz-pollinated, such as blueberries (Javorek et al., 2002), and where flowers are difficult for bees to handle, such as alfalfa (Cane, 2002). In apples, this means the visitation rate of honeybees is effectively cut in half, as they only contact the stigma and anthers of flowers approximately half of the time. Wild bees in apple orchards are more likely to contact the reproductive parts of the flower on each visit, and thus contribute more in terms of pollination services where they are abundant. Such trends are likely to be found in other crop systems where the flower morphology facilitates honeybee side-working (e.g. peaches, plums, cherries, apricots, and almonds). Our study helps explain recent research demonstrating a strong relationship between yield and wild bee abundance, but not honeybee abundance (e.g. Garibaldi et al., 2013; Mallinger and Gratton, 2015). Ultimately, understanding the mechanisms driving specific pollinator contributions to crop yield can help us manage for more effective pollination services. In the case of New York apples, given the efficacy of the wild bees, it might be more cost-effective for some apple growers to develop strategies to support a healthy wild bee community than to rent additional honeybee hives.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.05.033.

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