Original article

Per-visit pollinator performance and regional importance of wild *Bombus* and *Andrena* (*Melandrena*) compared to the managed honey bee in New York apple orchards

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Abstract – Declines in honey bee health and increasing demand for pollination services highlight a need to optimize crop pollination by wild bees. Apple is an economically important crop in eastern North America, requires insect pollination, and is visited by a diverse bee fauna, but a direct assessment of wild bee pollination in apple orchards is lacking. We combined measurements of two facets of pollination service, per-visit efficiency (fruit and seed set) and relative abundance, to estimate orchard-level, pollinator importance of mining bees (*Andrena* subgenus *Melandrena*), bumble bees (*Bombus*), and honey bees (*Apis mellifera* L.). Average pollinator importance provided a relative measure that allowed comparison of pollination service among the three focal bees across the study region. On average, a wild bee visit resulted in higher pollen transfer to stigmas, but had the same probability of setting fruit and seed as a honey bee visit. Regionally, pollinator importance of *Melandrena* and *Bombus* were 32 and 14 % that of honey bees, respectively. Because per-visit performances were similar, such disparities in importance were based largely on differences in relative abundance. Although the summed pollinator importance of *Melandrena* and *Bombus* was less than that of the honey bee, these, and other, wild pollinators have a role to play in filling future pollination gaps, and thus, warrant further study and conservation.

native bee / *Apis mellifera* / reproductive success / crop pollination

1. INTRODUCTION

Animal pollination is essential for sexual reproduction of many wild flowering plants and agricultural crops. Apple (*Malus domestica* Borkh.) is an economically important crop that is varietally self-incompatible and requires cross-pollination by insects, mostly bees, to set a commercially viable crop (Free 1993; McGregor 1976). Apple fruit quality is also influenced by insect pollination. Inadequate pollination can cause low seed set and empty carpels resulting in small or asymmetric fruit with low market value and low mineral content which reduces shelf life (Garratt et al. 2014; Sheffield 2014). To ensure commercial quality fruit and yields, New York apple growers commonly rent honey bees (*Apis mellifera* L., hereafter referred to as *Apis*), with hive densities ranging from 0.4 to 2.8 hives per hectare in our study region, at US$65–85 per hive (Eve Consulting unpubl. data; Park et al. 2015). However, colony losses due to "Colony Collapse Disorder" in North America and competing pollination demands have fueled increased hive rental fees and supply shortages for apple growers (Oldroyd 2007; vanEngelsdorp et al. 2009). Inadequate *Apis* supplies have already been linked with sub-optimal production of highly pollinator-dependent crops, including high

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bush blueberry, gala apples, and oilseed rape (Benjamin and Winfree 2014; Breeze et al. 2014; Garratt et al. 2014). The threat of pollinator shortages due to continuing declines in *Apis* highlights a need to examine alternative pollinators for apple.

Apple is visited by a diverse wild bee fauna in central New York (Gardner and Ascher 2006; Park et al. 2015; Russo et al. 2015). Recent work showing the positive influence of wild bee species richness and functional diversity on apple production and quality indicates that wild bee communities contribute significantly to apple pollination (Mallinger and Gratton 2015; Martins et al. 2015). In terms of abundance, wild bee communities are dominated by mining bees (40 %, genus *Andrena*) and queen bumble bees (4 %, genus *Bombus*), active in spring when apple blooms (Russo et al. 2015). Among *Andrena*, species in the subgenus *Melandrena* (hereafter, referred to as *Melandrena*) seem potentially important apple pollinators due to their large body size, early spring phenology, and abundance in eastern orchards (Brittain 1933; Gardner and Ascher 2006; Park et al. 2010; Phillips 1933; Watson et al. 2011). Moreover, *Melandrena* may prefer apple flowers to co-blooming alternatives, as andrenids are found to carry large quantities of apple pollen on their bodies (Gardner and Ascher 2006; Kendall and Solomon 1973). Apple growers generally consider *Bombus* bees as good pollinators for their ability to forage in low temperatures, common during apple's spring bloom (Brittain 1935). *Bombus* bees transfer more pollen to apple stigmas than *Apis* because they frequently contact stigmas while foraging (Thomson and Goodell 2001). Similarly, andrenids contact the stigmatic surface of McIntosh apple flowers more than *Apis* (Martins et al. 2015). Additionally, andrenids store dry pollen in scopal hairs near their hind coxae, increasing the likelihood that pollen will be transferred to the stigma upon contact (Thorp 2000). In contrast, *Apis* and *Bombus* store moistened pollen in corbicula, making pollen generally unavailable for pollination (Westerkamp 1991). Despite indirect evidence that both *Melandrena* and *Bombus* are good pollinators of apple, previous studies have not documented per-visit contributions of specific

wild pollinators to apple's reproductive success nor have previous studies quantified their regional importance in apple pollination (for exception, see Brittain 1933).

To address these knowledge gaps, the goals of this study were twofold: (1) provide a reliable comparison of per-visit pollination performance among *Melandrena*, *Bombus*, and *Apis* and (2) quantitatively compare pollination services of the three focal bees in central New York apple orchards by scaling up per-visit performance to the orchard level. Aside from comparing foraging behaviors and pollen carried by pollinators (as described above), pollination ecologists rely heavily on pollen deposition as a proxy for per-visit performance of pollinators in pollination studies, including those focused on crops, due to the relative ease of collecting such data (e.g., pumpkin, Hoehn et al. 2008; blueberry, Javorek et al. 2002; watermelon, Kremen et al. 2002; Pak-choi, Rader et al. 2009; coffee, Ricketts 2004; and apple, Thomson and Goodell 2001). Unfortunately, pollen transfer does not translate completely to reproductive success (i.e., fruit set or seed set), arguably a more accurate measure of a pollinator's performance (Cane and Schiffhauer 2003). First, the relationship between pollen deposition and reproductive success likely follows a nonlinear saturation function with a maximum optimal threshold (Harder and Thomson 1989). Second, for self-incompatible plant species, like apple, the use of pollen loads is further complicated by an observer's inability to distinguish self from cross-pollen (Snow 1982). Ideally, one could measure fruit and seed set from a single or multiple visits as has been done for crops like pumpkin (Artz and Nault 2011); however, because apple produces a mass display of blossoms, the odds of a visitor landing on a single flower under observation is low, rendering this method impractical during apple's short bloom period. Counting only viable pollen grains, by assessing pollen tube growth, has been effectively used for mass-blooming almond to look at pollinator performance, but such methods require specialized equipment and skill (Brittain et al. 2013). Here, we employ an alternative method that experimentally establishes relationships between stigmatic pollen

deposition and fruiting response (Cane and Schiffhauer 2003). Ne'eman et al. (2010) distinguish a pollinator's ability to transfer pollen from its ability to initiate a fruiting response as per-visit effectiveness and efficiency, respectively. We adopt these terminologies here and, ultimately, rely on per-visit efficiency as our measure of per-visit performance.

To investigate regional pollination services of wild bees in comparison to honey bees for apple within central New York State, we scaled up per-visit efficiency to orchard-level pollinator importance. Pollinator importance is the relative contribution of a floral visitor to the pollination of a plant population (here, an orchard), and incorporates two components of pollination service: per-visit performance and relative abundance (Olsen 1996; Rader et al. 2009). Pollinator importance scales up per-visit performance by accounting for the fact that an abundant pollinator with a low per-visit impact on pollination may contribute as much, if not more, to overall pollination as a rare pollinator that has high per-visit impact. When considering how much insurance alternative pollinators could provide given future *Apis* shortages, accounting for differences in abundance provides a more informative index of pollination service than per-visit measures of performance alone.

2. MATERIAL AND METHODS

2.1. Study sites and organisms

To quantify pollinator effectiveness, we recorded rates of per-visit pollen deposition by free flying pollinators during May 2010 at Cornell University's experimental orchard (CU), Ithaca, New York (lat 42.444808°, long −76.462345°). In spring 2011, to estimate per-visit efficiency from per-visit effectiveness we developed functional relationships between pollen deposition and reproductive success at CU and at a commercial orchard near Berwick, Nova Scotia (NS, lat 44.98396, long −64.78479), using hand-applied bees (see Table I for overview of experiments conducted). To eliminate differences in pollinator behavior among apple varieties due to flower morphology, we used "Honeycrisp" throughout the study. At both orchards, experiments were conducted on two rows of

Honeycrisp trees, grown on dwarf rootstock. Tree and row spacing were similar at study orchards: experimental rows were flanked by co-blooming varieties; however, varieties of adjacent rows differed among study sites. *Apis* hives were present at both study sites, with hive densities of 0.7 and 3 hives per hectare at CU and NS, respectively. Bee surveys in 16 and 19 orchards in 2011 and 2012, respectively, throughout central New York provided relative abundance data used to scale per-visit efficiency up to pollinator importance at the orchard level.

2.2. Relative abundance

We quantified pollination services at the regional level, using pollinator importance as our framework (Olsen 1996). Here, pollinator importance is the product of (1) visitation frequency of floral visitors and (2) per-visit efficiency (Rader et al. 2009; Vázquez et al. 2005). We used relative abundance as a proxy for visitation frequency, as justified by Gallai et al. (2009). We surveyed orchards and collected apple-visiting bees during bloom in spring 2011 and 2012 throughout central New York (Park et al. 2015). All bees observed on apple blossoms were net-collected along transects that spanned both sides of two adjacent tree rows for 15 min. Collecting occurred during peak bee activity between 1000 and 1500 hours, with temperatures above 16 °C. For each bee group, we calculated average abundance per collecting event at each orchard per year. We divided the average abundance for each bee group by the total average abundance of all three bee groups included in the study to calculate relative abundances of focal bees. Due to non-normality of data, we used non-parametric Kruskall–Wallis tests to explore differences in relative abundance and non-parametric Wilcoxon rank-sum post hoc tests to further explore differences between bee groups. Experiment-wise error was controlled using a post-priori Bonferroni correction.

2.3. Free-foraging per-visit effectiveness and behavior

Following Thomson and Goodell (2001), we compared per-visit effectiveness of *Melandrena* and *Bombus* to that of *Apis*, by quantifying pollen deposition from a single visit. Prior to opening, apple flowers were emasculated and bagged to prevent contamination from self-pollen and other insects, respectively. We

Table I. Per-visit performance experiment locations and times. We provide an overview of the experiment goals and methods

		Cornell University orchard	Nova Scotia orchard
2010	Goal(s)	Measure per-visit pollen deposition and natural foraging behavior	
	Method	Interviews of free-foraging *Apis*, *Melandrena*, and *Bombus*; observations of free-foraging bees at natural flowers	NA
2011	Goal(s)	Establish relationship between per-visit pollen deposition and efficiency (fruit and seed set)	
	Method	Hand application of *Apis* and *Melandrena*	Hand application of *Apis*, *Melandrena*, and *Bombus*

"interviewed" foraging bees between 0900 and 1900 on fair days, by offering them open, viable flowers attached to the tip of a 0.5-m rod (Thomson and Goodell 2001). We used flowers that had visibly produced nectar, because it was difficult to get a bee to visit otherwise, with receptive stigmas (i.e., had not yet turned brown). A legitimate visit involved active foraging or direct contact with stigmas by the bee. Visits were timed and the following response variables recorded: visit duration, reward sought (pollen, nectar collection, or mixed), foraging approach (top, side, or mixed), and presence of pollen loads. Observing differences in foraging approach was of particular interest because side approaches, or "side-working," results in less stigmatic contact and, consequently, reduced per-visit seed set and fruit development (Robinson and Fell 1981). Side-working is a well-documented behavior for honey bees and involves bees collecting nectar through stamen filaments by standing on a petal, thereby, avoiding contact with stigmas. Both *Bombus* and andrenids have been observed to contact stigmas more frequently than *Apis*, but this has not yet been documented for *Melandrena*, per se (Martins et al. 2015; Thomson and Goodell 2001). Visited stigmas were mounted on microslides, and pollen grains were counted at ×200 magnification under a Leitz compound microscope. Because it is difficult to distinguish among species of Rosaceae based on pollen morphology alone, we categorized pollen as Rosaceae or other, with the assumption that Rosaceae pollen is largely apple since bees were foraging on apple trees and co-blooming Rosaceae were not observed adjacent to orchards. At NS apple was the only crop planted in the orchard; at CU, another Rosacea crop, beach plum (*Prunus maritima* Marshall), was in bloom at the same time in the orchard, but its pollen grains were noticeably larger and were rarely

observed on mounted stigmas. Pollen from co-blooming flowers in the orchard understory was easy to distinguish from those of apple.

Because emasculated flowers were morphologically distinct from un-manipulated apple blossoms, we assessed differences in foraging behavior among focal bee groups by observing naturally foraging bees. Each bee was followed until it flew out of the observer's sight. At CU, in 2010 and 2011, we recorded the following for each foraging "bout": bee taxonomic identity, reward sought, approach, and time at each flower. To minimize influence of external factors (e.g., time of day and temperature), we alternated our observations among bee groups. In 2010, natural foraging observations were made concurrently with interviews.

We used descriptive statistics to compare frequencies of natural and "interview" foraging behavior. For interviews, we tested fixed effects of visitor, visit duration, presence of pollen loads, foraging approach, reward sought, and their interactions, on the response variable per-visit pollen deposition in a generalized linear model (GLM). Due to non-normality of pollen deposition data, we used a negative binomial distribution and checked for overdispersion (Zuur et al. 2013). We excluded *Bombus* from the GLM given its small sample size ($n=8$). *Bombus*-included interview models kept presence of pollen load in, but removed visitor; while *Bombus*-excluded interview models kept visitor in but removed pollen load. Because there were so few mixed approaches (both top- and side-working) and rewards sought (both pollen and nectar), we reclassified them as top-working and pollen foraging, respectively, since both designations were predicted to maximize stigmatic contact and pollen deposition. Models were reduced by backwards step-wise selection: variables that were not significant ($P>0.05$) and did not improve model fit, as

determined by a log-likelihood ratio test, were removed (Zuur et al. 2013). Because the GLM excluded *Bombus*, a non-parametric Kruskall–Wallis test was used to compare pollen deposition among the three bee groups. As with all analyses in this study, the GLM was conducted in R version 3.1.2 software (R Foundation for Statistical Computing, Austria).

2.4. Manual applications of bees

To model relationships between per-visit effectiveness (pollen deposition) and efficiency (fruiting response), in May 2011, we hand-applied *Apis* and *Melandrena* treatments, as well as a positive control (100 % cross pollen) to blossoms left on the tree to develop into fruit at both study sites (Kendall and Solomon 1973). Crab apple pollen for positive controls was collected 48 h prior to application, by placing anthers under a desk lamp in an open petri dish to dehisce. Viability of this pollen was confirmed by staining with lactophenol-1 % analine blue (Kearns and Inouye 1993). At NS, we also included a negative control (no pollen), a hand-applied *Bombus* treatment, and a pollen placement treatment to see if pollen stored in scopa and on the thorax differed in viability, as scopal pollen is considered unavailable for pollination (Westerkamp 1991). As with interview flowers, we prepared virgin, Honeycrisp blossoms by bagging and emasculating them prior to opening. At CU, where poor weather conditions limited availability of viable blossoms, we randomly assigned bee and control treatments to blossoms. At NS, we performed a complete-block design where 29 trees were systematically selected from two adjacent rows. At each tree, eight flower clusters were randomly assigned a treatment (2 controls, 3 bee×2 pollen placement treatments). Each bee was collected by hand, directly from blossoms within experimental rows, with a clean, glass vial and immobilized by placing vials in ice. Using clean forceps to hold the bee, the underside of the thorax was applied gently, but directly, to stigmas for 5 seconds. The lateral, exterior edge of one scopa was similarly applied to stigmas of another flower cluster. The size of each bee's scopal pollen load was visually assessed (0=none, 1=less than 1/4 full, 2=¼–3/4 full, 3=more than 3/4 full). To control for maternal competition effects among fruits, clusters were thinned to just the one experimental blossom. All flowers were re-bagged to ensure that fertilization and seed set resulted only from treatments.

Following similar procedures to interview flowers, we recorded per-visit pollen deposition by removing stigmas from treated flowers 48 h after pollination, mounting stigmas on microslides, and counting Rosacea pollen. To allow full fruit development, we did not re-bag flowers. One week after pollination, fruit set was recorded as the proportion of flowers that had developed into fruit. Two weeks after pollination and prior to chemical thinning, apple fruitlets were collected and the following recorded per fruit: fruitlet size, number viable seeds, and number carpels with one or more viable seed. For CU fruit, we measured fruit size as the diameter with a digital caliper and identified viable seeds as those actively growing (i.e., larger and fully inflated vs. small and shriveled). We were unable to similarly process NS fruitlets, as they were held up in international customs and arrived shriveled. We therefore recorded fruit size as dry weight (g) and identified seed viability by length, measured with a millimeter ruler at ×10 on a Leitz stereoscope. A subsample of seeds was weighed, showing a strong correlation between length and mass. Seeds displayed a bimodal distribution, which guided a conservative cutoff length for viable seeds at 1.4 mm. In fall 2011, we confirmed that this was a reasonable cutoff size for seed viability, by haphazardly harvesting mature Honeycrisp apples from the CU orchard in our experimental rows and measuring aborted seeds (mean±1SD, 1.44 mm±0.79).

Due to different experimental designs, the analyses for two study sites were conducted separately. To test fixed effects of visitor and pollen load size on pollen deposition (ln-transformed) from hand-applied bees, we ran normally distributed GLM and generalized linear mixed models (GLMM), respectively. We added pollen source (thorax or scopa) as a fixed factor and tree as a random blocking variable to the NS GLMM. Both models were reduced with stepwise backward deletion as described above. To compare pollen deposition among hand-applied bee groups, we performed pairwise, post hoc, Tukey's-adjusted tests after each model.

To characterize the functional relationships between per-visit pollen deposition of the various visitors and fruit and seed set, we conducted a series of parallel linear models with fruit or seed set as the response variable and with pollen deposition (ln-transformed), visitor, and their interaction as fixed factors. A

significant interaction would indicate that the same pollen transfer by different bee groups resulted in different rates of fruit or seed set. The implication would be that bee groups vary in the quality of the pollen carried on their bodies. For CU data, we used a binomial GLM (i.e., logistic regression) to test relationships between fixed variables and fruit set; we were unable to construct a meaningful seed set model due to an inadequate sample size (n=13) and relied exclusively on NS data to explore fruit quality (described below). For NS data, we conducted a binomial GLMM to test effects of fixed variables on the response fruit set. A random term consisting of the individual bees ID nested within tree was included to account for dependence among flowers that received pollen from thorax or scopa of the same bee and for dependence of flowers developing on the same tree. A similar, but normally distributed, GLMM with seed set as the response was also conducted. All models were reduced using backwards step-wise selection as described above. We used NS data to further explore visitor effects on fruit quality. We included in a normally distributed GLMM the response fruit weight (ln-transformed) and the fixed effects visitor, pollen deposited, and their interactions, with tree as a random grouping factor. We similarly tested the effects of the same predictor variables on the response number of carpels with developing seeds in a Poisson GLMM. Mean fruit set, seed set, and fruit weight were compared using post hoc pairwise Tukey's adjusted tests.

We verified that assumptions of normality and heteroscedasticity were met, and that Poisson and negative binomial models were not overdispersed. As mentioned previously, normal and binomial GLMMs were conducted in "nlme" (Pinheiro et al. 2014) and "lme4" (Bates et al. 2011) packages in R, respectively, and their degrees of freedom were derived using Penalized Quasi-Likelihood in R package 'MASS' (Venables and Ripley 2002).

With linear models that related pollen deposition to both fruit and seed set, we then translated pollinator effectiveness to a more meaningful and accurate measure of pollinator efficiency. Specifically, we used model equations to calculate expected pollinator efficiencies from pollen deposition rates recorded during interviews. Differences in estimated fruit and seed set among focal bees and between bee pairs were compared using non-parametric Kruskall–Wallis and non-parametric Wilcoxon rank-sum post hoc tests with Bonferroni correction, respectively.

2.5. Importance

We calculated *Apis*, *Melandrena*, and *Bombus* pollinator importance at the orchard level in 2011 and 2012 by the product of a bee group's relative abundance and per-visit efficiency. We used estimated fruit set as our measure of per-visit efficiency because seed set was highly correlated and fruit set has more direct implications for production. Additionally, fruit set estimates came from the NS (but not CU) model given that at NS we had data for all three bee groups, a blocked study design, and higher sample size. Mean standard errors of importance were calculated by the delta method (Powell 2007). Statistical differences in pollinator importance among bees were tested as described above for estimated per-visit efficiencies.

3. RESULTS

3.1. Relative abundance

Study-wide, the relative abundance of bees differed significantly (Kruskall–Wallis, 2011: χ^2_2=25.63, P<0.0001; 2012: χ^2_2=44.6119, P<0.001), with *Apis* being more abundant than *Bombus* and *Melandrena* both years (Wilcoxon rank sum; all, P<0.001), and *Melandrena* more abundant than *Bombus* in 2012 (Wilcoxon rank sum, P=0.04; Figure 1a). Relative abundance of bees varied widely across orchards (Figure 1b).

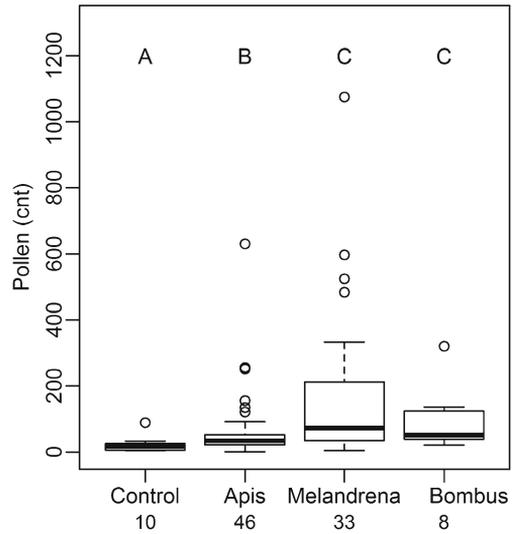### 3.2. Per-visit effectiveness and free-foraging behavior

Per-visit effectiveness varied among interviewed *Bombus*, *Melandrena*, and *Apis* (Kruskal–Wallis, χ^2_2=10.62, P=0.005). On average, *Melandrena* and *Bombus* deposited 2.5 and 1.5 times more pollen per-visit, respectively, than did *Apis* (Figure 2). Regardless of visitor identity, top-working and nectar-foraging bees deposited more pollen than side-working and pollen-foraging bees (Table II). After controlling for the influence of flower handling and reward sought, some unmeasured characteristic(s) of *Melandrena* resulted in higher pollen deposition (significant pollinator effect; Table II).

During observations of natural foraging behavior among tree rows, *Apis* side-worked apple flowers
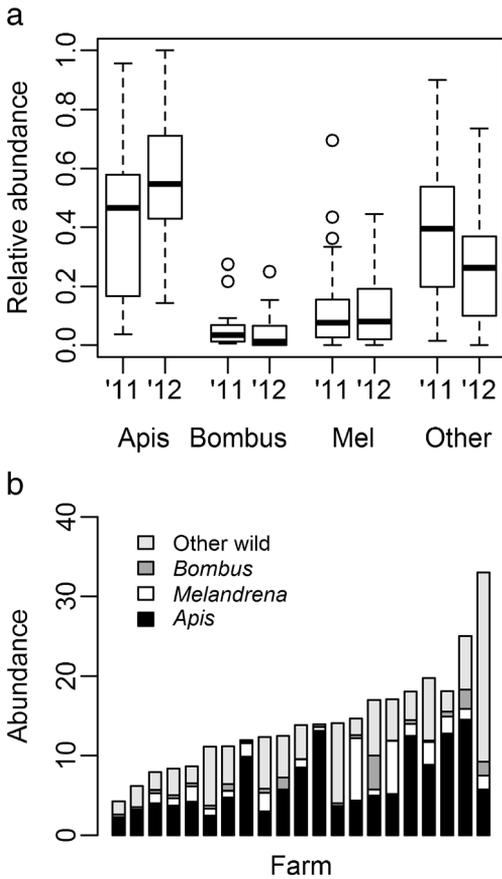
Figure 1. Relative abundance study-wide in 2011 and 2012 (**a**) and average abundance per transect per orchard across years (**b**) of *Apis mellifera*, *Melandrena* spp., *Bombus* spp., and all other wild bees.

Figure 2. Number of Rosaceae pollen grains deposited on stigma after a single visit to emasculated flowers by three bee groups studied: *Apis mellifera*, *Melandrena* spp., and *Bombus* spp. at the Cornell University study orchard. Pollen counts on negative controls are also provided. Numbers below *x*-axis labels indicate sample size. Columns labeled with the same letter are not significantly different.

Melandrena half as long, on average, at interview flowers than they did at natural flowers (Table III).

3.3. Per-visit efficiency and pollinator importance

Fruit and seed set resulting from hand-applied *Apis* did not differ significantly from those resulting from hand-applied *Melandrena* or *Bombus* (GLMM: $t_{26}=1.07$, $P=0.29$; Figure 3a, b). *Melandrena* applications, however, produced significantly larger fruitlets (*Bombus* v. *Melandrena*: 4.33 g±0.059 v. 4.56 g±0.048; GLMM: $t_{27}=3.30$, $P<0.01$) with higher seed set (*Bombus* v. *Melandrena*: 0.61±0.058 v. 0.43 ±0.081 [mean±SEM]; Tukey's adjusted: $P=0.04$; Figure 3b) than *Bombus* applications. Such differences in fruit quality mirrored differences in pollen deposition (Figure 3c) by hand-applied *Melandrena* and *Bombus* (Tukey's adjusted, $P=0.02$; Table IV). Increasing with scopal pollen load size (Table IV), pollen deposition also had a positive effect on the number of carpels with developed seeds (GLMM: $t_{77}=2.20$, $P=0.03$).

disproportionately more than *Melandrena* (Fisher's exact, 2010: $P<0.001$; Pearson's, 2011: $\chi^2_1=23.3$, $P<0.001$) and *Bombus* (Fisher's exact, $P=0.01$; see Table III for summary of all foraging data). Compared to *Apis*, *Melandrena* foraged for pollen more frequently (Fisher's exact, $P<0.001$), while *Bombus* sought pollen at similar rates (Fisher's exact, $P=1$). Visit duration of *Bombus* was half that of *Apis*, while that of *Melandrena* was twice as long (Wilcoxon rank sum, 2010: *Bombus*, $P=0.004$; *Melandrena*, $P<0.001$; Pearson's, 2011: $\chi^2_1=23.3$, $P<0.001$). As with natural visits, *Apis* side-worked interview flowers more often than *Melandrena* (Fisher's exact, $P<0.001$), but not *Bombus* (Fisher's exact, $P=0.2$). In general, more bees foraged for nectar only at interview flowers; *Apis* spent twice as long and

Table II. Significant effects of foraging behaviors and pollinator identity on per-visit pollen deposition on apple flowers from bee interviews in 2010 at Cornell University orchards. Due to low sample size for *Bombus* (n=8), only *Apis* (n=46) and *Melandrena* (n=33) were included. Approach refers to whether a bee side- or top-worked the flowers and reward refers to whether bees collected pollen or nectar. Non-significant interactions, visit duration, and presence of pollen load were excluded from final negative binomial model with df=73

Effect	Coeff. (±SE)	Z value	P value	Significant differences
Pollinator	0.99±0.26	3.854	0.00012	*Melandrena* > *Apis*
Approach	−0.78±0.26	−2.97	0.0030	Top > side
Reward	−0.87±0.29	−3.045	0.0023	Nectar > pollen

Modeling relationships between pollen deposition and fruiting response showed that both fruit and seed set were optimized by higher pollen loads on stigmas, regardless of bee or pollen placement, and followed a positive, saturating curve (GLM or GLMM, fruit set CU: Z_{43}=3.14, P<0.01; NS: Z_{62}=2.92, P<0.01; seed set NS: t_{20}=3.44, P<0.01; Figure 4). The non-significant (P>0.05) fixed effects of pollinator, pollinator×pollen deposition, and pollen placement, reduced from full fruit and seed set GLM and GLMMs through backwards deletion, indicate that (1) bees carried similar quality pollen and (2) pollen stored in the scopa was as viable as pollen from the thorax.

Using relationships between pollen deposition and fruiting response, we translated per-visit effectiveness of interviewed bees to per-visit efficiency and observed significant but less dramatic differences in per-visit pollinator performance among bee groups (Kruskal–Wallis, seed and fruit set: P<0.01; Figure 5). *Melandrena*, but not *Bombus*, was more efficient than *Apis* (Wilcoxon rank sum, seed and fruit set: P=0.007) but not by 2.5-fold as per-visit effectiveness suggested.

Orchard-level pollinator importance varied among focal bees (Kruskal–Wallis, 2011: χ^2_2=21.80, P<0.0001; 2012: χ^2_2=44.66, P<0.0001, Figure 6). *Apis* had significantly higher pollinator importance than both *Melandrena* (Wilcoxon rank sum, 2011: P<0.05; 2012: P<0.0001) and *Bombus* (Wilcoxon rank sum, 2011 and 2012: P<0.0001). *Melandrena* pollinator importance was significantly higher than that of *Bombus* in 2012 (Wilcoxon rank sum: P=0.002).

4. DISCUSSION

As honey bee declines decrease the availability and increase the cost of honey bee pollination for apple growers, the question of whether growers can rely on wild bees to fill the pollination gap becomes increasingly relevant. Per-visit, we found wild *Bombus* and *Melandrena* bees to be as efficient pollinators as *Apis*. Although *Melandrena* and *Bombus* contributed more to pollination than did *Apis* at two of our study orchards, the average importance of *Melandrena* and *Bombus* was small in comparison to *Apis* within the study region, due to the low relative abundances of these bees. Given their functional equivalence, *Melandrena* and *Bombus* have the potential to buffer some, but perhaps not all, honey bee losses, and only in orchards in which these bees are abundant.

The potential for inaccurately estimating the value of pollination in our system based on pollen transfer alone demonstrates the need to consider both pollinator efficiency and relative abundance. Based on pollen transfer alone, wild bees were more effective per-visit; however, translating pollinator effectiveness to efficiency revealed that pollinator performance was similar among our focal bees at the level of a single visit (Cane and Schiffhauer 2003). Previous work identifying *Melandrena* and *Bombus* as alternative pollinators of apple relied on pollen deposition and other proxies of pollinator efficiency: higher pollen transfer by *Bombus* compared with *Apis* (Thomson and Goodell 2001); high body counts and proportions of apple pollen found on *Bombus* and andrenids, notably *Melandrena* (Boyle and

Table III. Frequencies of foraging behaviors for free-flying *Apis mellifera*, *Melandrena* spp., and *Bombus* spp. observed in 2010 and 2011 at Cornell University orchards. Foraging data for *Bombus* at natural flowers in 2011 are not available. Data are %, means (±SEM), or medians (min–max). Statistical tests compare foraging behaviors among all bee groups available, with mixed behavior reclassified as either top work or pollen

	Apis	*Melandrena*	*Bombus*	Test (*P* value)
Natural flowers 2010, *n*	153	51	14	
Approach (%)				
Side-work	34.6	3.9	0	χ^2_2=24.2 (<0.001)
Top-work	60.1	88.2	100	
Mix	5.2	7.8	0	
Reward sought (%)				
Nectar	52.9	9.8	57.1	χ^2_2=30.2 (<0.001)
Pollen	42.5	60.8	21.4	
Mix	4.6	29.4	21.4	
Visit length (s)	4.4 (1.0–27.3)	8.2 (1.1–86.1)	2.1 (1.0–8.5)	χ^2_2=30.0 (<0.001)
Natural flowers 2011, *n*	44	43		
Approach (%)				
Side-work	61.4	16.3		χ^2_1=16.7 (<0.001)
Top-work	36.3	79.1		
Mix	2.3	4.6		
Reward sought (%)				
Nectar	70.45	51.2		χ^2_1=2.6 (0.1)
Pollen	16.0	32.6		
Mix	13.6	16.3		
Visit length (s)	8.5 (3.4–24.0)	14.1 (5.7–90.0)		χ^2_1=23.3 (<0.001)
Interview flowers, *n*	53	52	9	
Approach (%)				
Side-work	53.2	17.1	0	χ^2_2=18.0 (<0.001)
Top-work	44.7	77.1	100	
Mix	2.1	5.7	0	
Reward sought (%)				
Nectar	87.0	54.3	77.8	χ^2_2=11.0 (0.004)
Pollen	2.2	40.0	22.2	
Mix	10.9	5.7	0	
Visit length (s)	8 (0.5–48.72)	3.3 (0.39–39.8)	1.9 (1–5.90)	χ^2_2=10.9 (0.004)
Pollen load, %				
Yes	26.9	92.3	75	χ^2_2=30.2 (<0.001)
No	73.1	7.7	25	

Philogene 1983; Kendall and Solomon 1973); and higher levels of *Bombus* and andrenid activity at lower temperatures (Boyle and Philogene 1983; Boyle-Makowski 1987). Our study confirms that *Bombus* and *Melandrena* are good pollinators of apple. Compared with *Apis*, *Bombus* and *Melandrena* transferred roughly 150 to 250 % more pollen per visit, but because of a saturating relationship between pollen deposition and reproductive success, the highest rates of pollen transfer to stigmas by *Melandrena* and *Bombus* were superfluous. Per-visit efficiency for
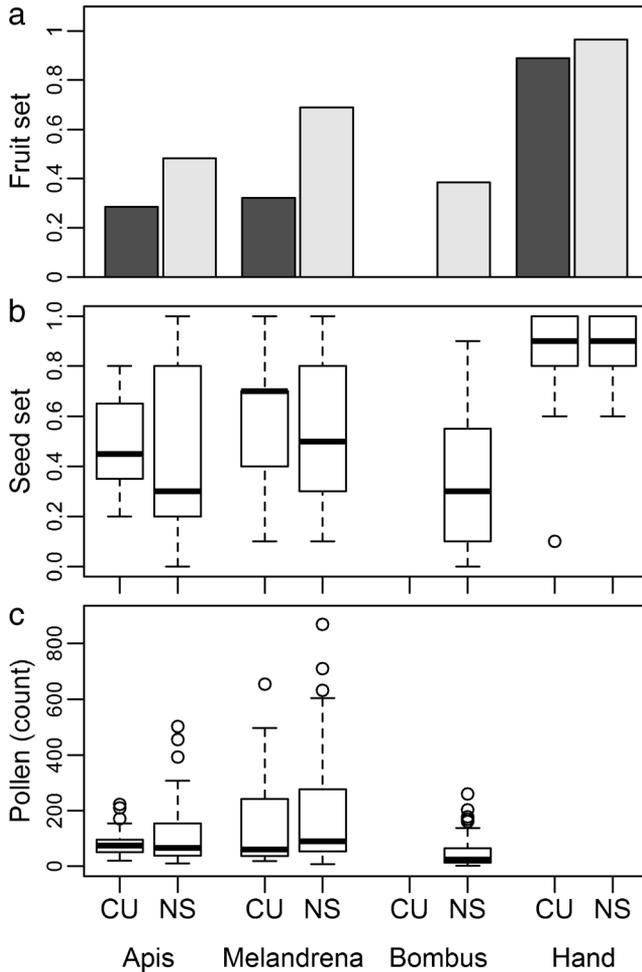
Figure 3. Proportion flowers that developed into fruit (**a**), proportion seeds that developed within a fruit (**b**), and stigmatic pollen loads (**c**) resulting from applying the underside of immobilized bees and a positive control ("Hand" applied pure cross pollen) to stigmas of experimental apple flowers at Cornell University (CU) and Nova Scotia (NS) study orchards. Note: *Bombus* were not applied to blossoms at CU. Sample size for *Apis mellifera*, *Melandrena* spp., *Bombus* spp., and positive control were as follows: CU fruit set=28, 28, NA, 27 and seed set=8, 24, 9, NA; NS fruit set=29, 29, 26, 29; and seed set=14, 19, 10, 27.

Melandrena, based on per-visit fruit and seed set estimates, was only 20 % higher than *Apis* and efficiency of *Bombus* was equivalent to that of *Apis*. Contrary to predictions, pollen quality was similar among bees, meaning bees move throughout the orchard similarly or that only recently acquired pollen is transferred to apple stigmas. Using per-visit efficiency rather than pollen deposition, per se, improved our assessment of pollinator performance among specific bee groups; however, we may still provide a simplified view

of pollination as we did not capture differences in visitation rates or in diurnal or temperature patterns of activity (Boyle and Philogene 1983; Phillips 1933).

Our results demonstrate that when assessing pollinator quality for apple, higher pollen transfer is desirable within the bounds of an upper threshold. High pollen transfer has predictable benefits for crops whose fruits require fertilization of many ovules, such as strawberry (Klatt et al. 2014). However, as has been previously found with

Table IV. Significant effects of pollinator identity and pollen load size on (ln-transformed) per-visit pollen deposition resulting from hand-applied *Apis*, *Melandrena*, and *Bombus* on apple flowers in 2011 at Cornell University (CU) and Nova Scotia (NS) orchards. At NS, tree was included as a random blocking factor. At NS, whether pollen came from the thorax or scopa was not significant and was excluded from final GLMM. Degrees of freed from CU GLM and NS GLMM were 39 and 107, respectively. Coefficients are not back-transformed

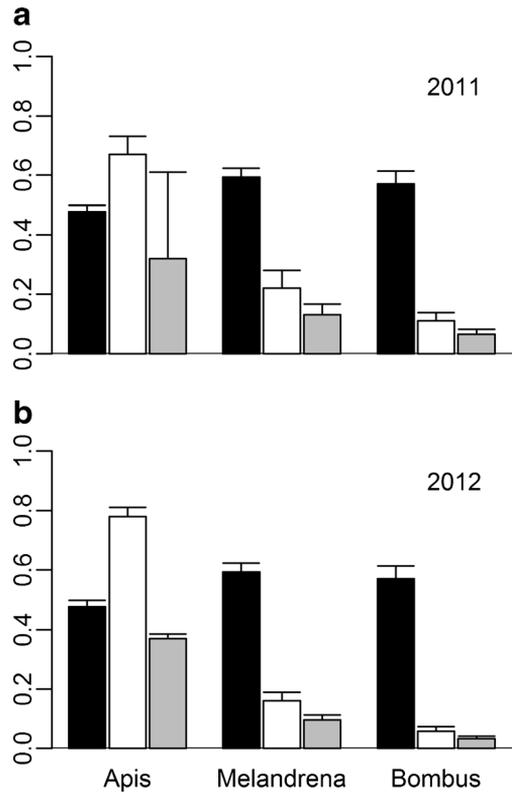| Effect	CU			NS		
	coeff. (± SE)	t-value	*P*-value	coeff. (± SE)	t-value	*P*-value
			Pollinator (ref=*Apis*)			
Melandrena	0.011±0.21	0.045	0.96	0.34±0.20	1.66	0.10
Bombus				−0.27±0.23	−1.17	0.25
			Pollen load size (ref=none)			
Small	0.33±0.28	1.17	0.24	0.74±0.31	2.39	0.019
Medium	0.90±0.30	2.99	0.0049	1.27±0.24	5.26	<0.0001
Large	1.90±0.44	4.32	0.0010	1.56±0.26	5.83	<0.0001
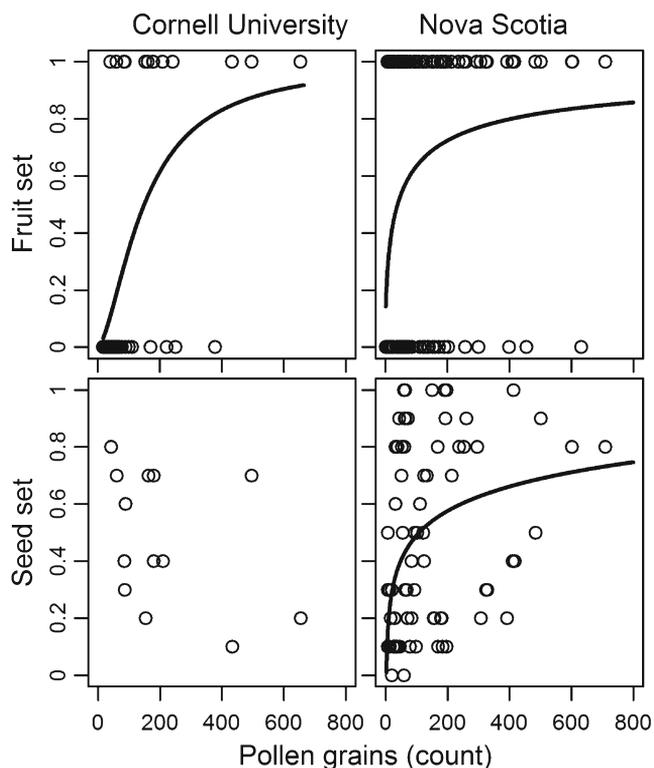
Figure 4. Relationships between stigmatic pollen loads deposited by hand-applied bees and reproductive success (both probability of fruit and seed development) at study orchards.

a

b
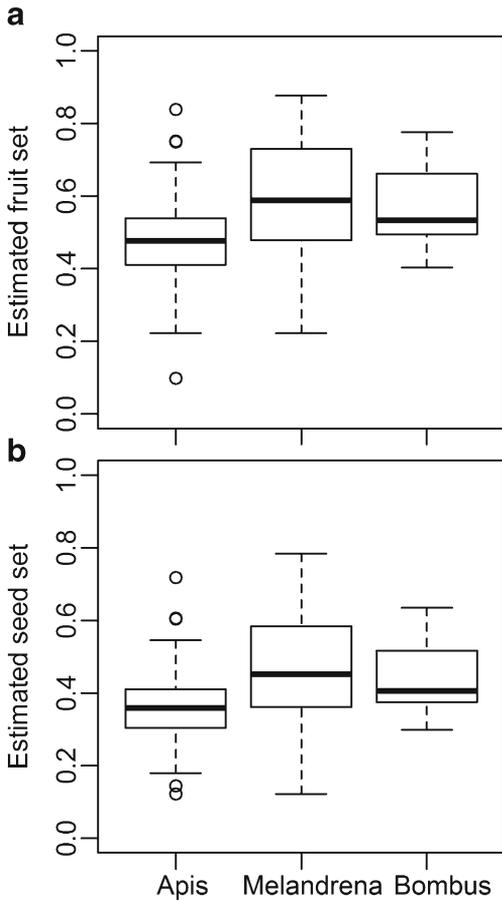
Figure 5. Estimated per-visit probabilities of fruit (**a**) and seed set (**b**) for *Apis mellifera*, *Melandrena* spp., and *Bombus* spp. based on free-flying bee pollen deposition and relationships between pollen deposition and reproductive success at NS.

a

b

Figure 6. Per-visit efficiency (i.e., estimated fruit set, *black*), relative pollinator abundance (*white*), and pollinator importance (*gray*) of three focal bees visiting apple in 2011 (**a**) and 2012 (**b**). Data are means+1SE.

cherry and almond, we found that even for apple, with only ten ovules per fruit, the amount of pollen transferred had a strong, positive influence on fruit quantity and quality (Bosch and Blas 1994; Holzschuh et al. 2012). Hand-applied gradients of cross-pollen loads to apple stigmas showed the same positive relationship between pollen load and fruit development, with optimal pollen-tube growth achieved with 40 germinating pollen grains per stigma (or 200 grains per flower; Janse and Verhaegh 1993). Mechanistically, higher loads of viable pollen could optimize reproductive success by priming stigmas (Janse and Verhaegh 1993; Visser 1981), distributing pollen among stigmas (Free 1993; Sheffield et al. 2005), and/or reducing stigmatic clogging (Shore and Barrett 1984). For crops that are self-incompatible, if similar relationships between pollen deposition and efficiency are established, further assessment of pollinator efficiency could be readily derived from pollen deposition. Even though establishing such relationships is time and labor-intensive, so is counting pollen tubes using fluorescence microscopy, the only other way to accurately estimate per-visit pollinator performance for specific pollinators (Brittain et al. 2013).

Our results validate the use of bee attributes that influence pollen transfer, specifically

handling behavior, pollen counts on bodies and pollen placement, as proxies for apple pollinator efficiency. First, as observed by Thomson and Goodell (2001), when bees top-worked Honeycrisp flowers, stigma contact increased, resulting in higher pollen deposition. Side-working, a form of nectar robbing, is a learned behavior used primarily by nectar-foraging *Apis*, which growers can manage only by introducing naive colonies to orchards sequentially (Stern et al. 2007). Solitary wild bees are less likely to side-work because they are primarily foraging for pollen and, therefore, have no reason to avoid anthers (Westerkamp 1991). Generally, pollen foragers have more pollen on their bodies and, therefore, transfer more pollen (Free 1993); however, nectar foraging resulted in higher pollen deposition among interviewed bees. We attribute this discrepancy to removal of anthers from experimental flowers, which may have altered pollen foraging behavior, or to larger quantities of nectar in virgin flowers, which encouraged *Apis* to forage longer on interview than natural flowers. Such a behavioral change among nectaring *Apis*, could have inflated pollinator effectiveness and, therefore, efficiency of this managed bee. Second, observations that pollen deposition increased with size of pollen load support the use of body pollen counts to identify, but may not be resolved enough to rank quality pollinators for apple. Scopal pollen directly applied to stigmas was as viable for fertilization as thoracic pollen in this study. For *Bombus* and *Apis*, likelihood of corbicular pollen contacting stigmas is low, therefore, pollen load size was more likely a proxy for how much pollen was on the rest of the bodies of these bees. Pollen placement is likely to be more important than load size, per se. *Melandrena* store their pollen dry in scopae near the abdomen and within the trochanteral and femoral scopa at the base of each hind leg, where pollen may more readily transfer to stigmas. Similarly, dry pollen stored by *Osmia* bees in a ventral, abdominal scopa results in high pollinator efficiency (Kuhn and Ambrose 1984; Sheffield 2014; Vicens

and Bosch 2000). Regardless of their size, bees that store pollen on their bodies in a manner that maximizes stigmatic transfer will predictably perform well, as long as they carry viable pollen. Andrenids, which comprised 40 % of the number of wild bees visiting apple and varied greatly in size, are likely efficient apple pollinators for this very reason.

We find that, at their current abundances, neither *Melandrena* nor *Bombus* would replace the level of pollination services presently provided by managed honey bees across our study region; however, several factors support the potential for growers to already rely more on wild bees and less on *Apis*. First, *Melandrena* and *Bombus* represent but a subset of more than 100 wild bee species found visiting apple in five years of survey data from central New York apple orchards (Russo et al. 2015). While these two bee groups alone may not substitute for *Apis*, because so many other wild bees visit apple (Figure 1b) further study is needed before we rule out the possibility that wild bee communities can provide all the necessary pollination even if honey bee pollination continues to decline. Second, as is the case for a suite of crops worldwide, apple production (i.e., fruit set) is positively influenced by wild bee abundance and species richness, but not *Apis* abundance (Blitzer et al. unpubl. data; Garibaldi et al. 2013; Mallinger and Gratton 2015). Such disconnect between fruit production and *Apis* implies that there may already be more *Apis* brought into orchards than is necessary due to the activity of wild pollinators. If true, then our calculations of pollinator importance, primarily influenced by relative abundances, may be skewed by widespread supplementation of honey bees within our study system. Third, apple orchards in central New York are regularly over-pollinated, as evidenced by the ubiquitous practice of thinning tree fruit load shortly after initial fruit set (Robinson et al. 2013). Such practice further supports that wild pollinators need not necessarily be as abundant as *Apis* to provide adequate pollination. Finally, wild bee abundance is not static and can be augmented. We observed high spatial and temporal variation in wild bee abundance across orchards (Figure 1b). Bee abundance is positively tied to access to natural

habitat and depressed with increasing intensity of pesticide regimes in orchards (Kennedy et al. 2013; Martins et al. 2015; Park et al. 2015; Watson et al. 2011). Therefore, growers have tools to increase wild bee abundance within their orchard, if desired.

Wild bees may also increase fruit yield in ways that cannot be captured in our study. Wild pollinators complement *Apis* pollination of apple by handling flowers differently while foraging, by visiting flowers in different parts of the tree canopy, and/or by changing *Apis* foraging behavior in a manner that improves its pollinator performance (Brittain et al. 2013; Martins et al. 2015). Boyle-Makowski (1987) found native bees, particularly *Andrena* and halictids, to be important apple pollinators during years of poor weather since honey bee visitation was low under these conditions. The value of wild pollinators compared to honey bees was similarly high on windy days, when *Apis* would not visit almond blossoms but wild bees would (Brittain et al. 2013). Optimal bee density will be context and crop specific, varying with bloom density, distance of pollen source, as well as amount of competing floral resources surrounding the focal crop (Brittain 1933). Development of protocols that monitor native bee abundance in a context-specific, reliable, and easy manner is central to providing growers with the information they need to assess native pollination services available to them.

Honey bees are important for apple production, and arguably are essential for large, intensively managed orchards with little adjacent natural habitat to support wild pollinators. Wild bees, however, are as efficient and likely contribute more to apple pollination than growers currently realize. Transitioning an orchard to rely more heavily on wild pollinators may require actions on the grower's part to increase and maintain wild bee abundance. Growers may optimize wild bee abundance by maximizing natural areas surrounding their orchards, decreasing pesticide intensity, and creating additional habitat and foraging resources for bees near orchards (Kennedy et al. 2013; Park et al. 2015; Watson et al. 2011). This study continues to build on a growing body of evidence that wild bees benefit crop production and may buffer against declines in *Apis* populations.

Performance pollinisatrice "par visite" et importance régionale des populations sauvages de *Bombus* et d'*Andrena* (*Melandrena*), comparées aux abeilles des ruchers industriels, dans les vergers de pommiers de l'Etat de New York

abeille indigène / *Apis mellifera* / succès reproducteur / pollinisation des cultures

Bestäubungsleistung pro Blütenbesuch und regionale Bedeutung von wildlebenden *Bombus* und *Andrena* (*Melandrena*) im Vergleich zu imkerlich gehaltenen Honigbienen in Apfelanlagen in New York

Einheimische Bienen / *Apis mellifera* / Reproduktionserfolg / Bestäubung

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