



Pollination services for apple are dependent on diverse wild bee communities



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ARTICLE INFO

Article history:

Received 14 May 2015

Received in revised form 16 December 2015

Accepted 2 January 2016

Available online xxx

Keywords:

Agroecosystem
Native bees
Apple production
Seed set
Functional group
Apple orchards
Pollination

ABSTRACT

Understanding the importance of biodiversity in applied settings is a central theme for ecologists. Pollination is an essential ecosystem service, which may rely on biodiversity for effectiveness and stability. Empirical examples which link functional outcomes of increased biodiversity to pollination services are rare. To investigate the importance of wild and managed pollinator communities to apple production, we assessed the effect of wild and managed bee abundance and diversity on pollen limitation and seed set on commercial farms in New York State. Seed set increased and pollen limitation decreased with increasing wild bee species richness, functional group diversity (based on nesting, sociality, and size traits), and abundance, but not with honey bee abundance. Functional group diversity explained more variation in apple seed set than species richness. Our findings demonstrate the important role of functional complementarity of wild bees, defined here as functional group diversity, to crop pollination even in the presence of large populations of managed honey bees. Therefore, our results suggest that management of diverse pollinator communities may decrease reliance on managed honey bees for pollination services and enhance crop yields.

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1. Introduction

The importance of pollinators to global agricultural stability is well documented (Klein et al., 2007; Garibaldi et al., 2013). Worldwide an estimated 35% of crop production, including many of our most nutritious foods, benefit from insect pollination (Klein et al., 2007; Aizen et al., 2008). For many crops, the most widely used pollinator is the European honey bee (*Apis mellifera* L.). However, honey bee colonies in North America have suffered sharp declines in recent decades (Holden, 2006; Potts et al., 2009, 2010). The necessity of relying so heavily on one species of managed pollinators is now being questioned (Garibaldi et al., 2013). Wild pollinator species can, especially in heterogeneous landscapes, provide much of the pollination service needed for crop production and may enhance fruit quality regardless of honey bee visitation (Garibaldi et al., 2011, 2013).

Apple (*Malus domestica* Borkh.) is an economically important crop in the United States, with New York State being the second largest production region in the country (USDA NASS 2011). Typically apple cultivars are self-incompatible and successful apple pollination requires cross-pollination from a “pollinizer” variety (McGregor, 1976; Free, 1993; Garratt et al., 2014a). Although honey bees are generally viewed as essential pollinators in apple orchards, apple blossoms are also visited by a diverse community of wild pollinators (Sheffield et al., 2013; Garratt et al., 2014b; Park et al., 2015; Russo et al., 2015). Because honey bees are supplemented at increasing cost and effort to apple growers (<http://www.ars.usda.gov>), apple provides an important test case for the efficacy of wild bee pollination for sustainable crop production. Other studies have linked pollen deficits to decreases in apple fruit and seed set (Garratt et al., 2014b), and calculate that pollinators in UK apple orchards contribute £36.7 million per annum to apple production (Garratt et al., 2014a). Recent studies in apple orchards found that wild pollinators alone were able to achieve comparable fruit set levels to orchards with managed honey bees (Mallinger and Gratton, 2014) and that functional diversity can improve pollination services in Canadian orchards (Martins et al., 2015). However, more evidence linking wild pollinator biodiversity and abundance to harvest level production data (i.e., seed set) in apple orchards, with direct consequences for fruit quality and market value (Garratt et al., 2014b), is essential.

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There is a growing consensus that biodiversity enhances ecosystem function in general (Hooper et al., 2005) and the delivery of the ecosystem service of pollination in particular (Kremen et al., 2002; Klein et al., 2003; Hoehn et al., 2008). Three main hypotheses have been proposed to explain this positive diversity-pollination services relationship: (1) selection effects, where diverse communities are more likely to include highly effective species (Loreau and Hector, 2001); (2) functional facilitation, under which some community members may enhance effectiveness of other members (Cardinale et al., 2002); and (3) functional complementarity where, through niche partitioning in space and time, diverse pollinator communities provide more pollination services. Niche complementarity (Loreau and Hector, 2001) is the most commonly invoked mechanism for the increase of pollination services in species rich communities (Fontaine et al., 2006; Hoehn et al., 2008; Tylianakis et al., 2008). However, studies which quantify the relationship between crop production and pollinator species richness and functional group diversity are still quite rare (Hoehn et al., 2008; Mallinger and Gratton, 2014; Martins et al., 2015).

In this study we investigate the effects of pollinator abundance and diversity on apple production at 17 farms in New York State. On each farm we quantified wild and managed bee visitors to apple blossoms along with apple seed set. At a subset of 12 farms we experimentally tested for pollination limitation. We asked the following questions: (1) How do wild bee species richness and abundance impact apple pollination? (2) How does honey bee abundance impact production? (3) Does niche complementarity, as measured by functional group diversity, increase pollination in apple?

2. Materials and methods

2.1. Study area and site selection

This study was conducted on 17 apple orchards in three counties (Wayne, Tompkins, and Seneca) in western New York State. We focused our study on two of the most common apple varieties for this region: McIntosh and Golden Delicious. On the few farms which did not grow Golden Delicious apples, we substituted with the Golden Delicious cross varieties Jonagold or Crispin. New York State is the second largest apple producing state in the country, with Wayne County being New York's top producing county. Our study farms included orchards which vary widely in size (from 0.05 to 182 ha), management intensity (integrated fruit management to heavy use of synthetic pesticides), and proportion of surrounding natural area in a 2 km radius (from 19% semi-natural habitat to 66% semi-natural habitat). In this study, we broadly defined 'natural' habitat as land that was minimally managed and not cultivated for arable crops. Specifically, natural habitat included forests, wooded and herbaceous wetlands, shrublands and grasslands. These farms represent the variety of apple orchards typically found in New York State.

2.2. Wild and managed bee abundance and diversity

Collections of all bee visitors to apple blossoms were made during the apple bloom period (May 6–17, 2013) at all 17 farms. Bees were net collected visiting apple blossoms throughout the orchard along two 15-min, standardized, 100 m transects per farm, placed within 150 m of edge in rows of full bloom. Collections were made on sunny days between 10:00 and 15:30, when temperatures exceeded 15 °C. Each farm was surveyed twice during the bloom. Apple bloom was assessed at the farm level by categorizing bloom as early, peak, or past, as well as at the individual transect level by counting the number of open blossoms per cluster on three trees

per transect. To ensure independence among farms, the minimum distance between sites was 1.9 km, which is greater than the typical foraging distance of most bees (Zurbuchen et al., 2010). All bees were identified to the species level using published keys and comparison to voucher material in the Cornell University Insect Collection (<http://cuic.entomology.cornell.edu/>). All voucher material is deposited in the Cornell University Insect Collection.

2.3. Pollen limitation and seed set experiments

To study the impact of wild and managed bee communities on apple yield we used two methods: pollen supplementation experiments and seed set measurements. Pollen supplementation experiments test for pollen limitation by comparing the fruit or seed set of plants given supplemental pollen to the fruit/seed set of control plants which receive ambient pollen loads (Knight et al., 2006). Comparing pollen limitation values allows for a measure of pollination services which control for variation within and between sites. On a subset of 12 of our 17 study orchards we set up a pollen supplementation experiment. At each farm we selected twelve experimental trees, six each of McIntosh and Golden Delicious varieties. Before the apple bloom period (early May 2013), we chose two branches of approximately equal diameter and location within the tree to reduce any potential horticultural effects on seed set. We returned to each farm during peak apple bloom (May 13–23, 2013) and first removed all nonviable (damaged, unopened, or past receptivity) blossoms. Branches were then randomly assigned to either an "open" or "hand" pollination treatment. The open-pollination treatment received natural pollination from managed and wild bees. The hand-pollination treatment also received natural pollination, but all blossoms were hand-supplemented with additional Red Delicious pollen (Firman Pollen Company, Yakima, Washington, USA) applied directly to the stigma.

To expand our apple yield experiments to include all 17 farms surveyed for bees we also set up a more simple measurement of apple pollination without pollen supplementation controls. We selected a set of six Golden Delicious or closely related (Jonagold or Crispin varieties) trees per farm. At peak apple bloom we chose one branch of similar diameter and location per tree and counted all blossoms along a 1 m segment of each branch.

For both experiments we recorded data on early season (pre thinning) fruit set when apple fruitlets were 5–10 mm and on mature fruit from experimental branches prior to fall harvest. For all mature fruit we counted all developed seeds per fruit. In our final analysis we used number of seeds per fruit as our measure of apple pollination. Seeds per fruit is correlated with apple weight, and is a more direct measure of pollination efficacy (Hoehn et al., 2008).

2.4. Pollinator behavior functional grouping

To understand the mechanisms driving potential effects of bee species richness we assigned all wild bee species collected from apple into functional guilds, based on differences in nesting substrate, sociality and body size. We chose nesting and sociality traits as a way to investigate the functional outcome (pollination services) of niche partitioning and complementarity (i.e., Ground nesting bees are solitary and often more host-plant specific than cavity nesters such as bumblebees.). Nest classes were assigned categorically as ground, cavity/hive, or wood/stem. Species were classified as solitary, communal, cleptoparasitic, or eusocial. Nest and sociality classes were based on relevant literature (reviewed in (Michener, 2000) and extrapolations based on phylogenetic relationships (Danforth et al., 2003; Gibbs et al., 2012). Body size was used as a proxy for foraging range, and classifications of small,

medium, large, or extra-large were assigned based on inter-tegular distance (ITD) measurements made on representative male and female specimens collected at our farms over a three year period (Greenleaf et al., 2007; Hoehn et al., 2008). Because quite a few of our bee species are very rare we used average ITD measurements across specimens of a given genus to group species into size classes. The number of specimens per genus was as follows: *Agapostemon* 6, *Andrena* 75, *Apis* 12, *Augochlorella* 3, *Augochloropsis* 1, *Augochlora* 1, *Bombus* 35, *Ceratina* 7, *Colletes* 7, *Halictus* 13, *Lasioglossum* 75, *Nomada* 28, *Osmia* 29, *Xylocopa* 15. Our small (S) size class had an ITD range of 1.31–1.89 mm, medium (M) 2.09–2.31 mm, large (L) 2.56–3.05 mm and extra-large (XL) 5.46–6.86 mm.

2.5. Data analysis

We explored the relationship between bee community variables and seed set using linear models with seeds per fruit as the response variable. Because of co-linearity, we conducted separate models with wild bee species richness, honey bee abundance, and wild bee abundance as continuous predictors. For each model we looked for statistically significant ($p < 0.05$) relationships between seed set and bee community data which would indicate a unique effect of each type of bee community on seed set data. Mean values of bee community data were used because seed set experiment data were collected at the farm level. Residuals in all models were tested for a normal distribution. All statistical analyses were completed with the R statistical computing program (R Development Core Team, 2014).

To explore the relationship between bee communities and pollen limitation we used linear mixed effect models with pollination limitation index (PL) as the response variable. For each experimental tree we calculated a pollen limitation index: $PL = 1 - (S_o/S_h)$. Where S_o number of seeds per fruit on the open treatment branch and S_h the number of seeds per fruit on the hand treatment branch. We conducted separate models with wild bee species richness, honey bee abundance, and wild bee abundance as fixed effects and site as a random effect. In initial models apple variety was also included as fixed effect, but was consistently non-significant and was dropped in final models. The effect of density of

flowers in bloom per transect was tested against wild bee abundance and richness per transect. Sampled bees were not influenced by bloom density within a transect (Park et al., 2015). All mixed effect modeling was completed in R using the lme4 package (Pinheiro et al., 2014).

To test species richness versus functional group diversity as predictors of seeds per fruit we ran two sequential multiple regression models with the order of the explanatory variables reversed. By comparing the ANOVA tables of these two sequential models we can examine the unique effects of each variable (Hector et al., 2010).

3. Results

3.1. Apple flower visitor community

Over the twelve day bloom period we conducted 93 standardized transects in 17 orchards for 23 h of active net-collecting of bees visiting open blossoms. In total, we collected 1579 bees and 53 species. We collected similar numbers of honey bees (790 individuals) and wild bees (789 individuals). The wild bee community was numerically dominated by solitary, ground nesting bees in the genus *Andrena* (Andrenidae), which accounted for 62% (594 individuals, 18 species) of all wild bees collected. Bees in the family Halictidae were the most species-rich, but individuals were rare (74 individuals, 20 species). For a more complete description of the wild bee fauna of eastern NY apple orchards see Russo et al. (2015).

3.2. Effect of species richness and abundance on pollen limitation and seed set

At the end of the growing season, we collected 1,461 fruit (70 ± 26 per site) (mean \pm SD) from our seed set experiment branches, and 1012 (84 ± 66 per site) fruit from our pollen supplementation experiment branches. In our linear models, seed set significantly increased with increasing numbers of wild bee species ($F_{1,15} = 11.49$, $p = 0.004$; Fig. 1(a)) as well as with increasing wild bee abundance ($F_{1,15} = 6.93$, $p = 0.018$, Fig. 1(b)). In contrast, we found no relationship between honey bee abundance and seed set

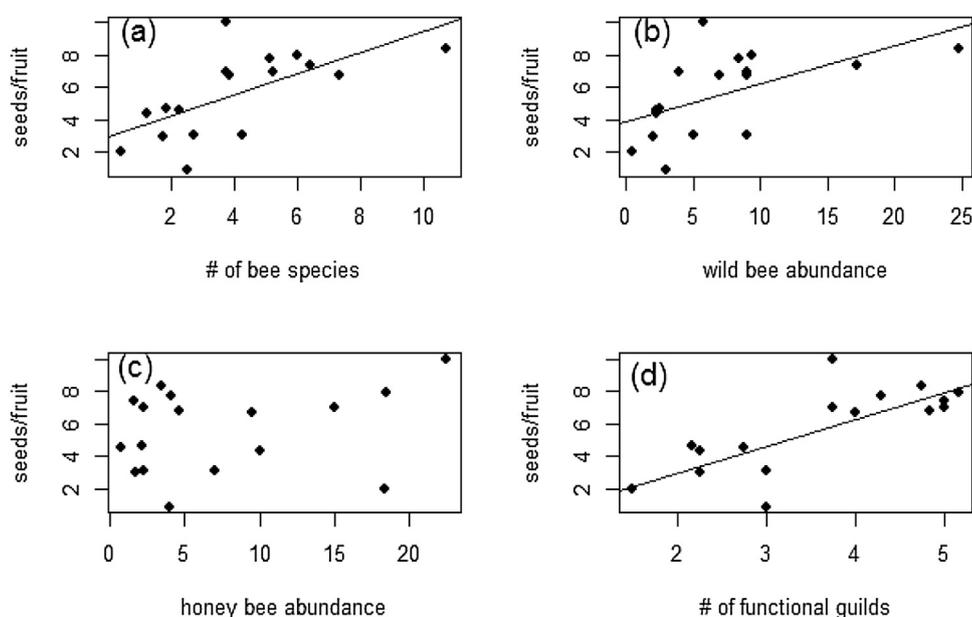


Fig. 1. Mean number of seeds per fruit per farm in relation to (a) mean number of bee species per 15 min transect per farm, (b) mean number of wild bee individuals per 15 min transect per farm, (c) mean number of honey bee individuals per 15 min transect per farm, and (d) mean number of functional groups per 15 min transect per farm.

($F_{1,15} = 1.308$, $p = 0.271$; Fig. 1(c)). Similarly, pollination limitation decreased significantly (lower values of pollination limitation indicate natural bee pollination closer to the maximal applied by hand) with increasing wild bee species richness ($p = 0.006$; Fig. 2(a)) and marginally decreased with wild bee species abundance ($p = 0.073$; Fig. 2(b)); but had no relationship with honey bee abundance ($p = 0.394$; Fig. 2(c)).

3.3. Functional group effects on pollen limitation seed set

Using nesting, sociality, and size traits we grouped our 53 wild apple pollinator species into 12 functional guilds (Table 1). Increasing numbers of functional groups present at a farm led to a significant increase in the number of seeds per fruit ($p = 0.0004$; Fig. 1(d)), and a significant decrease in pollen limitation ($p = 0.007$; Fig. 2(d)).

3.4. Functional group diversity vs species richness

Functional group diversity explained more variation in apple seed set than species richness (Table 2). In the model with bee species richness included first, both species richness and functional group diversity were significant, indicating that even when all of the overlapping variation was attributed to species richness, functional group diversity still explained a significant amount of the variation in seeds per fruit. However, when functional group was included first, species richness was non-significant (Table 2).

4. Discussion

4.1. Functional consequences of biodiversity

We found that pollination services in apple increased with wild bee abundance and richness. Understanding the functional consequences of biodiversity, in our case increased seed set, has been a central theme of ecologists (Balvanera et al., 2006; Cardinale et al., 2006), in general, and for pollination ecology in particular (Kremen, 2005). In our system spatio-temporal niche

complementarity emerges as the most likely mechanism driving the observed patterns of positive effects of pollinator communities on plant reproduction. We base this hypothesis on our finding that the number of functional groups present at a site was the strongest predictor of increased pollination services (Table 2). The traits (body size, nesting type, and sociality) used to assign wild bee species to functional groups likely represent various combinations of niche partitioning in space and time.

While previous studies on crop pollination relate pollinator taxonomic richness to seed or fruit set, our study, along with two previous examples (Hoehn et al., 2008; Martins et al., 2015), also grouped bee species into functional guilds and investigated the relationship between functional group richness and seed set. Although our study included a larger pollinator species pool, and each study grouped bees into functional guilds based on different sets of pollinator traits, all came to a similar conclusion: greater pollinator functional diversity can lead to improved seed set. One disadvantage of correlative field scale studies is that we are unable to disentangle the effects of abundance and richness. In a different approach to testing the biodiversity–function hypothesis, pollinator species and functional group richness are experimentally manipulated in controlled cage experiments, which can allow one to separate the impact of abundance and diversity (Fontaine et al., 2006; Albrecht et al., 2012; Fründ et al., 2013). This body of work also supports our conclusion that biodiversity can enhance pollination due to functional complementarity through niche partitioning among species.

4.2. Contribution of honey bees to apple seed set

Although wild bee species richness and abundance were important predictors of seed set in apple, greater abundances of honey bees did not lead to an increase in the number of seeds per fruit. Our results, along with studies from other crops around the globe, suggest that increasing applications of honey bees will not compensate for losses of wild pollinators (Garibaldi et al., 2013). In our system, two mechanisms based on honey bee foraging behavior are likely to be driving this pattern. First, honey bees typically forage on flowers of the same individual plant or plant

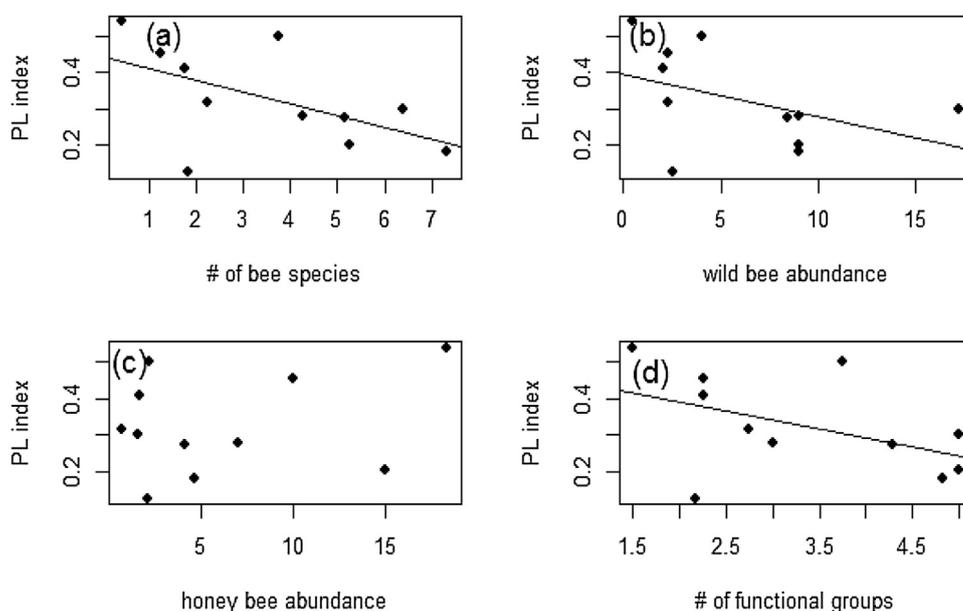


Fig. 2. Mean value of pollen limitation index: $PL = 1 - (S_o/S_h)$. Where S_o number of seeds per fruit on the open treatment branch and S_h the number of seeds per fruit on the hand treatment branch seeds per fruit per farm in relation to (a) mean number of bee species per 15 min transect per farm, (b) mean number of wild bee individuals per 15 min transect per farm, (c) mean number of honey bee individuals per 15 min transect per farm, and (d) mean number of functional groups per 15 min transect per farm.

Table 1

Nest, sociality, and size class of all bee species, resulting in classification into 12 functional guilds (from A to L). Nest and sociality classes were based on relevant literature and extrapolations based on phylogenetic relationships. Body size classifications of small, medium, large, or extra-large were assigned based on inter-tetragonal distance (ITD) measurements made on representative specimens collected at our farms.

Species	Nest class	Sociality class	Size class	Functional guild
<i>Agapostemon sericeus</i> (Förster)	Ground	Solitary	M	A
<i>Andrena carlini</i> Cockerell	Ground	Solitary	M	A
<i>Andrena erythronii</i> Robertson	Ground	Solitary	M	A
<i>Andrena hippotes</i> Robertson	Ground	Solitary	M	A
<i>Andrena mandibularis</i> Robertson	Ground	Solitary	M	A
<i>Andrena milwaukeensis</i> Graenicher	Ground	Solitary	M	A
<i>Andrena perplexa</i> Smith	Ground	Solitary	M	A
<i>Andrena pruni</i> Robertson	Ground	Solitary	M	A
<i>Andrena regularis</i> Malloch	Ground	Solitary	M	A
<i>Andrena rugosa</i> Robertson	Ground	Solitary	M	A
<i>Andrena vicina</i> Smith	Ground	Solitary	M	A
<i>Andrena w-scripta</i> Viereck	Ground	Solitary	M	A
<i>Augochloropsis metallica</i> Fabricius	Ground	Solitary	M	A
<i>Colletes inaequalis</i> Say	Ground	Solitary	M	A
<i>Lasioglossum zonulum</i> (Smith)	Ground	Solitary	M	A
<i>Apis mellifera</i> L.	Cavity/hive	Eusocial	M	B
<i>Augochlorella aurata</i> (Smith)	Ground	Eusocial	S	C
<i>Lasioglossum abanci</i> (Crawford)	Ground?	Eusocial	S	C
<i>Lasioglossum cinctipes</i> (Provancher)	Ground	Eusocial	S	C
<i>Lasioglossum heterognathum</i> (Mitchell)	Ground	Eusocial	S	C
<i>Lasioglossum hitchensi</i> Gibbs	Ground	Eusocial	S	C
<i>Lasioglossum laevisimum</i> (Smith)	Ground	Eusocial	S	C
<i>Lasioglossum lineatulum</i> (Crawford)	Ground	Eusocial	S	C
<i>Lasioglossum paradmirationum</i> (Knerer & Atwood)	Ground	Eusocial	S	C
<i>Lasioglossum truncatum</i> (Robertson)	Ground	Eusocial	S	C
<i>Lasioglossum versatum</i> (Robertson)	Ground	Eusocial	S	C
<i>Augochlora pura</i> (Say)	Wood/stem	Solitary	S	D
<i>Ceratina calcarata</i> Robertson	Wood/stem	Solitary	S	D
<i>Bombus bimaculatus</i> Cresson	Cavity	Eusocial	L	E
<i>Bombus borealis</i> Kirby	Cavity	Eusocial	L	E
<i>Bombus griseocollis</i> (DeGeer)	Cavity	Eusocial	L	E
<i>Bombus impatiens</i> Cresson	cavity	Eusocial	L	E
<i>Bombus ternarius</i> Say	Cavity	Eusocial	L	E
<i>Lasioglossum cressonii</i> (Robertson)	Wood/stem	Eusocial	S	F
<i>Nomada cressonii</i> Robertson	Cleptoparasitic	Cleptoparasitic	S	G
<i>Nomada sp. 1</i>	Cleptoparasitic	Cleptoparasitic	S	G
<i>Osmia bucephala</i> Cresson	Wood/stem	Solitary	M	H
<i>Osmia cornifrons</i> (Radoszkowski)	Wood/stem	Solitary	M	H
<i>Osmia lignaria</i> Say	Wood/stem	Solitary	M	H
<i>Osmia pumila</i> Cresson	Wood/stem	Solitary	S	H
<i>Xylocopa virginica</i> (L.)	Wood/stem	Solitary	XI	I
<i>Andrena barbilabris</i> (Kirby)	Ground	Solitary	S	J
<i>Andrena cressonii</i> Robertson	Ground	Solitary	S	J
<i>Andrena forbesii</i> Robertson	Ground	Solitary	S	J
<i>Andrena imitatrix</i> Cresson	Ground	Solitary	S	J
<i>Andrena miserabilis</i> Cresson	Ground	Solitary	S	J
<i>Andrena nasonii</i> Robertson	Ground	Solitary	S	J
<i>Lasioglossum foxii</i> (Robertson)	Ground	Solitary	S	J
<i>Lasioglossum pectorale</i> (Smith)	Ground	Solitary	S	J
<i>Lasioglossum quebecense</i> (Crawford)	Ground	Solitary	S	J
<i>Andrena crataegi</i> Robertson	Ground	Communal	M	K
<i>Halictus confusus</i> Smith	Ground	Eusocial	M	L
<i>Halictus rubicundus</i> (Christ)	Ground	Eusocial	M	L

Table 2

Results of sequential multiple regression models to compare effects of species richness vs functional group richness.

Source	d.f.	SS	MS	F	P
(a)					
Number of bee species	1	45.765	45.765	14.361	0.002
Number of functional groups	1	15.118	15.118	4.744	0.047
Residual	14	44.614	3.187		
Total	16	105.497			
(b)					
Number of functional groups	1	60.852	60.852	19.010	0.0006
Number of bee species	1	0.032	0.032	0.010	0.921
Residual	14	44.614	3.187		
Total	16	105.497			

variety within a site (Greenleaf and Kremen, 2006; Westerkamp, 1991). Since apples are self-incompatible, pollen from a different variety is required for successful pollination. Growers generally plant orchards with one row of cross pollinizer variety for every two to three rows of the focal variety (Delaplane et al., 2000), therefore honey bees which visit only one tree, or only one row, on a foraging trip will not provide the cross-pollination necessary for seed set and fruit development. Second, honey bee foragers in apple often specialize as nectar-gatherers; previous studies in apple show only 3% of honey bee workers were gathering pollen (Vicens and Bosch, 2000). Nectaring honey bees in our system are often observed working flowers from the side (Thomson and Goodell, 2001; Martins et al., 2015) limiting contact with the stigma and, therefore, may not provide effective pollination services. Studies in other crops have found that wild bees alter

honey bee foraging behavior, improving their efficacy (Greenleaf and Kremen, 2006; Brittain et al., 2013), but we did not explicitly test for this effect.

4.3. Management implications

Seed set is an important component of apple quality, influencing features such as fruit size and shape (Brookfield et al., 1996; Volz et al., 1996; Buccheri and Di Vaio, 2005; Matsumoto et al., 2012). From a methodological standpoint our study showed that simple harvest seed set measurements in apple produced similar results to our controlled pollen supplementation experiment. The ability to relatively easily assess seed set, and therefore a reasonable proxy for fruit production, should allow future studies in orchard systems to incorporate pollination efficacy into studies of pollinator communities.

We found that diverse and abundant communities of wild bees in apple orchards are likely contributing essential pollination services that have been long attributed to managed honey bees. Our results show that seed set nearly triples (from 20% to 60%) when the number of functional groups present at a site increases from less than two to more than four. These findings suggest that in order to optimize pollination services by wild bees, management programs that maintain high functional diversity are required and strategies focused on one or two effective species are not enough.

But how can apple growers actively maintain wild bee species richness and functional diversity in their orchards? We can think of several approaches that could be combined to enhance species richness as well as functional diversity. First, maintaining diverse floral resources in and around orchards would help maintain both an abundant and diverse wild bee fauna. Park et al. (2015) found that orchards surrounded by more natural habitat (mostly forest) had a more diverse and abundant native bee fauna. We know from analyses of the pollen loads carried by wild bees (Russo et al., in prep.) that early spring flowering trees (such as red maple, sugar maple, and willow) are an important alternative host-plant for the apple bee fauna. Hence, maintaining forest fragments within and around apple orchards could have a positive impact on species richness and functional diversity. Second, given the number of ground-nesting bees that comprise the apple orchard fauna, it would be advisable for growers to develop strategies for providing enhanced ground-nesting bee habitat. One strategy would be to till up soil in vacant areas of the orchard to a depth of 30 cm in order to encourage ground nesting bee activity. Third, stem-nesters, especially *Osmia* (mason bees), may be nest-site limited. Hence, installing trap nests (drilled wooden blocks or cardboard straws) could be a viable strategy for enhancing the diversity and abundance of *Osmia* and other stem-nesters (see Bosch and Kemp (2001)). Finally, bumble bees, which comprise a small but ecologically important component of the apple bee fauna, are largely above- and below-ground, cavity nesting species. Bumble-bee colonies can be purchased commercially but an alternative strategy would be to maintain wood piles and abandoned stone walls as potential nest sites for bumblebees. Together, these strategies are likely to be effective in maintaining bee species richness and diversity in eastern apple orchards.

Finally, our results support the view that wild bees are likely contributing essential pollination services that have been long attributed to managed honey bees. Prior to the appearance of CCD in 2008 there was very little incentive to quantify the relative contribution of wild and managed bees to crop pollination. Honey bees were widely cited as essential pollinators for apples based on limited quantitative data on their actual contribution (McGregor, 1976). However, with honey bees increasingly costly to rent and, for some crops, increasingly difficult to obtain, it is critical that we

have a better understanding of the actual contribution of honey bees and wild (native) bees in pollinator-dependent crop systems.

Acknowledgments

We thank collaborating apple growers and managers for permission to survey orchards. We especially thank J. Eve for facilitating grower contacts and providing expertise. Art Agnello, I. Merwin, H. Reissig provided additional expertise and guidance. We are grateful to Justin Cappadonna and Sally Hartwick for their hard work in the field and laboratory. This project was supported by Smith Lever and Hatch Funds administered by Cornell University Agricultural Experiment Station and by a USDA-AFRI grant [USDA 2010-03689, B.N. Danforth, PI].

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