

1 **Pollination services for apple are dependent on diverse wild bee communities**

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21 **Abstract**

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

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37 **Keywords**

38 agroecosystem, native bees, apple production, seed set, functional group, apple orchards, pollination

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43 **1. Introduction**

44 The importance of pollinators to global agricultural stability is well documented (Klein et al.
45 2007; Garibaldi et al. 2013). Worldwide an estimated 35% of crop production, including
46 many of our most nutritious foods, benefit from insect pollination (Klein et al. 2007; Aizen et
47 al. 2008). For many crops, the most widely used pollinator is the European honey bee (*Apis*
48 *mellifera* L.). However, honey bee colonies in North America have suffered sharp declines in
49 recent decades (Holden 2006; Potts et al. 2009; Potts et al. 2010). The necessity of relying so
50 heavily on one species of managed pollinators is now being questioned (Garibaldi et al.
51 2013). Wild pollinator species can, especially in heterogeneous landscapes, provide much of
52 the pollination service needed for crop production and may enhance fruit quality regardless of
53 honey bee visitation (Garibaldi et al. 2011; Garibaldi et al. 2013).

54 Apple (*Malus domestica* Borkh.) is an economically important crop in the United States, with
55 New York State being the second largest production region in the country (USDA NASS
56 2011). Typically apple cultivars are self-incompatible and successful apple pollination
57 requires cross-pollination from a “pollinizer” variety (McGregor 1976; Free 1993; Garratt et
58 al. 2014a). Although honey bees are generally viewed as essential pollinators in apple
59 orchards, apple blossoms are also visited by a diverse community of wild pollinators
60 (Sheffield et al. 2013; Garratt et al. 2014b; Park et al. 2015; Russo et al. 2015). Because
61 honey bees are supplemented at increasing cost and effort to apple growers
62 (<http://www.ars.usda.gov>), apple provides an important test case for the efficacy of wild bee
63 pollination for sustainable crop production. Other studies have linked pollen deficits to
64 decreases in apple fruit and seed set (Garratt et al. 2014b), and calculate that pollinators in
65 UK apple orchards contribute £36.7 million per annum to apple production (Garratt et al.
66 2014a). Recent studies in apple orchards found that wild pollinators alone were able to

67 achieve comparable fruit set levels to orchards with managed honey bees (Mallinger and
68 Gratton 2014) and that functional diversity can improve pollination services in Canadian
69 orchards (Martins et al. 2015). However, more evidence linking wild pollinator biodiversity
70 and abundance to harvest level production data (i.e. seed set) in apple orchards, with direct
71 consequences for fruit quality and market value (Garratt et al. 2014b), is essential.

72 There is a growing consensus that biodiversity enhances ecosystem function in general
73 (Hooper et al. 2005) and the delivery of the ecosystem service of pollination in particular
74 (Kremen et al. 2002; Klein et al. 2003; Hoehn et al. 2008). Three main hypotheses have been
75 proposed to explain this positive diversity-pollination services relationship: 1) selection
76 effects, where diverse communities are more likely to include highly effective species
77 (Loreau and Hector 2001); 2) functional facilitation, under which some community members
78 may enhance effectiveness of other members (Cardinale et al. 2002); and 3) functional
79 complementarity where, through niche partitioning in space and time, diverse pollinator
80 communities provide more pollination services. Niche complementarity (Loreau & Hector
81 2001) is the most commonly invoked mechanism for the increase of pollination services in
82 species rich communities (Fontaine et al. 2006; Hoehn et al. 2008; Tylianakis et al. 2008).
83 However, studies which quantify the relationship between crop production and pollinator
84 species richness and functional group diversity are still quite rare (Hoehn et al. 2008;
85 Mallinger and Gratton 2014; Martins et al. 2015).

86 In this study we investigate the effects of pollinator abundance and diversity on apple
87 production at 17 farms in New York State. On each farm we quantified wild and managed
88 bee visitors to apple blossoms along with apple seed set. At a subset of 12 farms we
89 experimentally tested for pollination limitation. We asked the following questions: (1) How
90 do wild bee species richness and abundance impact apple pollination? (2) How does honey

91 bee abundance impact production? (3) Does niche complementarity, as measured by
92 functional group diversity, increase pollination in apple?

93 **2. Materials and methods**

94 2.1. Study area and site selection

95
96 This study was conducted on 17 apple orchards in three counties (Wayne, Tompkins, and
97 Seneca) in western New York State. We focused our study on two of the most common apple
98 varieties for this region: McIntosh and Golden Delicious. On the few farms which did not
99 grow Golden Delicious apples, we substituted with the Golden Delicious cross varieties
100 Jonagold or Crispin. New York State is the second largest apple producing state in the
101 country, with Wayne County being New York's top producing county. Our study farms
102 included orchards which vary widely in size (from 0.05 to 182 ha), management intensity
103 (integrated fruit management to heavy use of synthetic pesticides), and proportion of
104 surrounding natural area in a 2 km radius (from 19% semi-natural habitat to 66% semi-
105 natural habitat). In this study, we broadly defined 'natural' habitat as land that was
106 minimally managed and not cultivated for arable crops. Specifically, natural habitat included
107 forests, wooded and herbaceous wetlands, shrublands and grasslands. These farms represent
108 the variety of apple orchards typically found in New York State.

109 2.2. Wild and managed bee abundance and diversity

110 Collections of all bee visitors to apple blossoms were made during the apple bloom period
111 (May 6–17, 2013) at all 17 farms. Bees were net collected visiting apple blossoms throughout
112 the orchard along two 15-minute, standardized, 100 m transects per farm, placed within 150 m
113 of edge in rows of full bloom. Collections were made on sunny days between 10:00 and
114 15:30, when temperatures exceeded 15°C. Each farm was surveyed twice during the bloom.

115 Apple bloom was assessed at the farm level by categorizing bloom as early, peak, or past, as
116 well as at the individual transect level by counting the number of open blossoms per cluster
117 on three trees per transect. To ensure independence among farms, the minimum distance
118 between sites was 1.9 km, which is greater than the typical foraging distance of most bees
119 (Zurbuchen et al. 2010). All bees were identified to the species level using published keys
120 and comparison to voucher material in the Cornell University Insect Collection
121 (<http://cuic.entomology.cornell.edu/>). All voucher material is deposited in the Cornell
122 University Insect Collection.

123 2.3. Pollen limitation and seed set experiments

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

139 supplemented with additional Red Delicious pollen (Firman Pollen Company, Yakima,
140 Washington, USA) applied directly to the stigma.

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

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

151 2.4. Pollinator behavior functional grouping

152 To understand the mechanisms driving potential effects of bee species richness we assigned
153 all wild bee species collected from apple into functional guilds, based on differences in
154 nesting substrate, sociality and body size. We chose nesting and sociality traits as a way to
155 investigate the functional outcome (pollination services) of niche partitioning and
156 complementarity (i.e. Ground nesting bees are solitary and often more host-plant specific
157 than cavity nesters such as bumblebees.). Nest classes were assigned categorically as ground,
158 cavity/hive, or wood/stem. Species were classified as solitary, communal, cleptoparasitic, or
159 eusocial. Nest and sociality classes were based on relevant literature (reviewed in (Michener
160 2000) and extrapolations based on phylogenetic relationships (Danforth et al. 2003; Gibbs et
161 al. 2012). Body size was used as a proxy for foraging range, and classifications of small,
162 medium, large, or extra-large were assigned based on inter-tegular distance (ITD)

163 measurements made on representative male and female specimens collected at our farms over
164 a three year period (Greenleaf *et al.* 2007; Hoehn *et al.* 2008). Because quite a few of our
165 bee species are very rare we used average ITD measurements across specimens of a given
166 genus to group species into size classes. The number of specimens per genus was as follows:
167 Agapostemon 6, Andrena 75, Apis 12, Augochlorella 3, Augochloropsis 1, Augochlora 1,
168 Bombus 35, Ceratina 7, Colletes 7, Halictus 13, Lasioglossum 75, Nomada 28, Osmia 29,
169 Xylocopa 15. Our small (S) size class had an ITD range of 1.31-1.89 mm, medium (M) 2.09-
170 2.31 mm, large (L) 2.56-3.05 mm and extra-large (XL) 5.46-6.86 mm.

171 2.5. Data analysis

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

181 To explore the relationship between bee communities and pollen limitation we used linear
182 mixed effect models with pollination limitation index (PL) as the response variable. For each
183 experimental tree we calculated a pollen limitation index: $PL = 1 - (S_o/S_h)$. Where S_o number of
184 seeds per fruit on the open treatment branch and S_h the number of seeds per fruit on the hand
185 treatment branch. We conducted separate models with wild bee species richness, honey bee
186 abundance, and wild bee abundance as fixed effects and site as a random effect. In initial

187 models apple variety was also included as fixed effect, but was consistently non-significant
188 and was dropped in final models. The effect of density of flowers in bloom per transect was tested
189 against wild bee abundance and richness per transect. Sampled bees were not influenced by bloom
190 density within a transect (Park et al. 2015). All mixed effect modeling was completed in R using
191 the lme4 package (Pinheiro et al. 2014).

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

196 **3. Results**

197 3.1. Apple flower visitor community

198 Over the twelve day bloom period we conducted 93 standardized transects in 17 orchards for
199 23 hours of active net-collecting of bees visiting open blossoms. In total, we collected 1579
200 bees and 53 species. We collected similar numbers of honey bees (790 individuals) and wild
201 bees (789 individuals). The wild bee community was numerically dominated by solitary,
202 ground nesting bees in the genus *Andrena* (Andrenidae), which accounted for 62% (594
203 individuals, 18 species) of all wild bees collected (Fig. 1.). Bees in the family Halictidae
204 were the most species-rich, but individuals were rare (74 individuals, 20 species) (Fig. 1).
205 For a more complete description of the wild bee fauna of eastern NY apple orchards see
206 Russo et al. (2015).

207 3.2. Effect of species richness and abundance on pollen limitation and seed set

208 At the end of the growing season, we collected 1,461 fruit (70 ± 26 per site) (mean \pm SD)
209 from our seed set experiment branches, and 1,012 (84 ± 66 per site) fruit from our pollen

210 supplementation experiment branches. In our linear models, seed set significantly increased
211 with increasing numbers of wild bee species ($F_{1,15} = 11.49$, $p = 0.004$; Fig. 2a.) as well as
212 with increasing wild bee abundance ($F_{1,15} = 6.93$, $p = 0.018$, Fig. 2b.). In contrast, we found
213 no relationship between honey bee abundance and seed set ($F_{1,15} = 1.308$, $p = 0.271$; Fig. 2c.).
214 Similarly, pollination limitation decreased significantly (lower values of pollination limitation
215 indicate natural bee pollination closer to the maximal applied by hand) with increasing wild
216 bee species richness ($p = 0.006$; Fig. 3a.) and marginally decreased with wild bee species
217 abundance ($p = 0.073$; Fig. 3b.); but had no relationship with honey bee abundance ($p =$
218 0.394 ; Fig. 3c.).

219 3.3. Functional group effects on pollen limitation seed set

220 Using nesting, sociality, and size traits we grouped our 53 wild apple pollinator species into
221 12 functional guilds (Table 1). Increasing numbers of functional groups present at a farm led
222 to a significant increase in the number of seeds per fruit ($p = 0.0004$; Fig. 2d.), and a
223 significant decrease in pollen limitation ($p=0.007$; Fig. 3d.).

224 3.4. Functional group diversity vs species richness

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

231 **4. Discussion**

232 4.1. Functional consequences of biodiversity

233 We found that pollination services in apple increased with wild bee abundance and richness.
234 Understanding the functional consequences of biodiversity, in our case increased seed set, has
235 been a central theme of ecologists (Balvanera et al. 2006; Cardinale et al. 2006), in general,
236 and for pollination ecology in particular (Kremen 2005). In our system spatio-temporal niche
237 complementarity emerges as the most likely mechanism driving the observed patterns of
238 positive effects of pollinator communities on plant reproduction. We base this hypothesis on
239 our finding that the number of functional groups present at a site was the strongest predictor
240 of increased pollination services (Table 2). The traits (body size, nesting type, and sociality)
241 used to assign wild bee species to functional groups likely represent various combinations of
242 niche partitioning in space and time.

243 While previous studies on crop pollination relate pollinator taxonomic richness to seed or
244 fruit set, our study, along with two previous examples (Hoehn et al. 2008, Martins et al.
245 2015), also grouped bee species into functional guilds and investigated the relationship
246 between functional group richness and seed set. Although our study included a larger
247 pollinator species pool, and each study grouped bees into functional guilds based on different
248 sets of pollinator traits, all came to a similar conclusion: greater pollinator functional
249 diversity can lead to improved seed set. One disadvantage of correlative field scale studies is
250 that we are unable to disentangle the effects of abundance and richness. In a different
251 approach to testing the biodiversity-function hypothesis, pollinator species and functional
252 group richness are experimentally manipulated in controlled cage experiments, which can
253 allow one to separate the impact of abundance and diversity (Fontaine et al. 2006; Albrecht et
254 al. 2012; Fründ et al. 2013). This body of work also supports our conclusion that biodiversity
255 can enhance pollination due to functional complementarity through niche partitioning among
256 species.

257 4.2. Contribution of honey bees to apple seed set

258 Although wild bee species richness and abundance were important predictors of seed set in
259 apple, greater abundances of honey bees did not lead to an increase in the number of seeds
260 per fruit. Our results, along with studies from other crops around the globe, suggest that
261 increasing applications of honey bees will not compensate for losses of wild pollinators
262 (Garibaldi et al. 2013). In our system, two mechanisms based on honey bee foraging
263 behavior are likely to be driving this pattern. First, honey bees typically forage on flowers of
264 the same individual plant or plant variety within a site (Greenleaf and Kremen 2006;
265 Westerkamp 1991). Since apples are self-incompatible, pollen from a different variety is
266 required for successful pollination. Growers generally plant orchards with one row of cross
267 pollinizer variety for every two to three rows of the focal variety (Delaplane et al. 2000),
268 therefore honey bees which visit only one tree, or only one row, on a foraging trip will not
269 provide the cross-pollination necessary for seed set and fruit development. Second, honey
270 bee foragers in apple often specialize as nectar-gatherers; previous studies in apple show only
271 3% of honey bee workers were gathering pollen (Vicens and Bosch 2000). Nectaring honey
272 bees in our system are often observed working flowers from the side (Thomson and Goodell,
273 2001; Martins et al. 2015) limiting contact with the stigma and, therefore, may not provide
274 effective pollination services. Studies in other crops have found that wild bees alter honey
275 bee foraging behavior, improving their efficacy (Greenleaf and Kremen 2006; Brittain et al.
276 2013), but we did not explicitly test for this effect.

277 4.3. Management implications

278 Seed set is an important component of apple quality, influencing features such as fruit size
279 and shape (Brookfield et al. 1996; Volz et al. 1996; Buccheri and Di Vaio 2005; Matsumoto,
280 et al. 2012). From a methodological standpoint our study showed that simple harvest seed set

281 measurements in apple produced similar results to our controlled pollen supplementation
282 experiment. The ability to relatively easily assess seed set, and therefore a reasonable proxy
283 for fruit production, should allow future studies in orchard systems to incorporate pollination
284 efficacy into studies of pollinator communities

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

292 But how can apple growers actively maintain wild bee species richness and functional
293 diversity in their orchards? We can think of several approaches that could be combined to
294 enhance species richness as well as functional diversity. First, maintaining diverse floral
295 resources in and around orchards would help maintain both an abundant and diverse wild bee
296 fauna. Park et al. (2015) found that orchards surrounded by more natural habitat (mostly
297 forest) had a more diverse and abundant native bee fauna. We know from analyses of the
298 pollen loads carried by wild bees (Russo et al., in prep.) that early spring flowering trees
299 (such as red maple, sugar maple, and willow) are an important alternative host-plant for the
300 apple bee fauna. Hence, maintaining forest fragments within and around apple orchards
301 could have a positive impact on species richness and functional diversity. Second, given the
302 number of ground-nesting bees that comprise the apple orchard fauna, it would be advisable
303 for growers to develop strategies for providing enhanced ground-nesting bee habitat. One
304 strategy would be to till up soil in vacant areas of the orchard to a depth of 30 cm in order to

305 encourage ground nesting bee activity. Third, stem-nesters, especially *Osmia* (mason bees),
306 may be nest-site limited. Hence, installing trap nests (drilled wooden blocks or cardboard
307 straws) could be a viable strategy for enhancing the diversity and abundance of *Osmia* and
308 other stem-nesters (see Bosch and Kemp 2001). Finally, bumble bees, which comprise a
309 small but ecologically important component of the apple bee fauna, are largely above- and
310 below-ground, cavity nesting species. Bumblebee colonies can be purchased commercially
311 but an alternative strategy would be to maintain wood piles and abandoned stone walls as
312 potential nest sites for bumblebees. Together, these strategies are likely to be effective in
313 maintaining bee species richness and diversity in eastern apple orchards.

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

322

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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-tegular distance (ITD) measurements made on representative specimens collected at our farms.

Table 1

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

Species	Nest Class	Sociality Class	Size Class	Functional Guild
<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 laevissimum</i> (Smith)	ground	Eusocial	S	C
<i>Lasioglossum lineatulum</i> (Crawford)	ground	Eusocial	S	C

Species	Nest Class	Sociality Class	Size Class	Functional Guild
<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

Species	Nest Class	Sociality Class	Size Classes	Functional Guild
<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.

Table 2

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			

Figure captions

Figure 1. Wild bee community composition. Total number of wild bee species for each bee family collected.

Figure 2. 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 (d) Mean number of functional groups per 15 min. transect per farm.

Figure 3. 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 (d) Mean number of functional groups per 15 min. transect per farm.

Figure 2

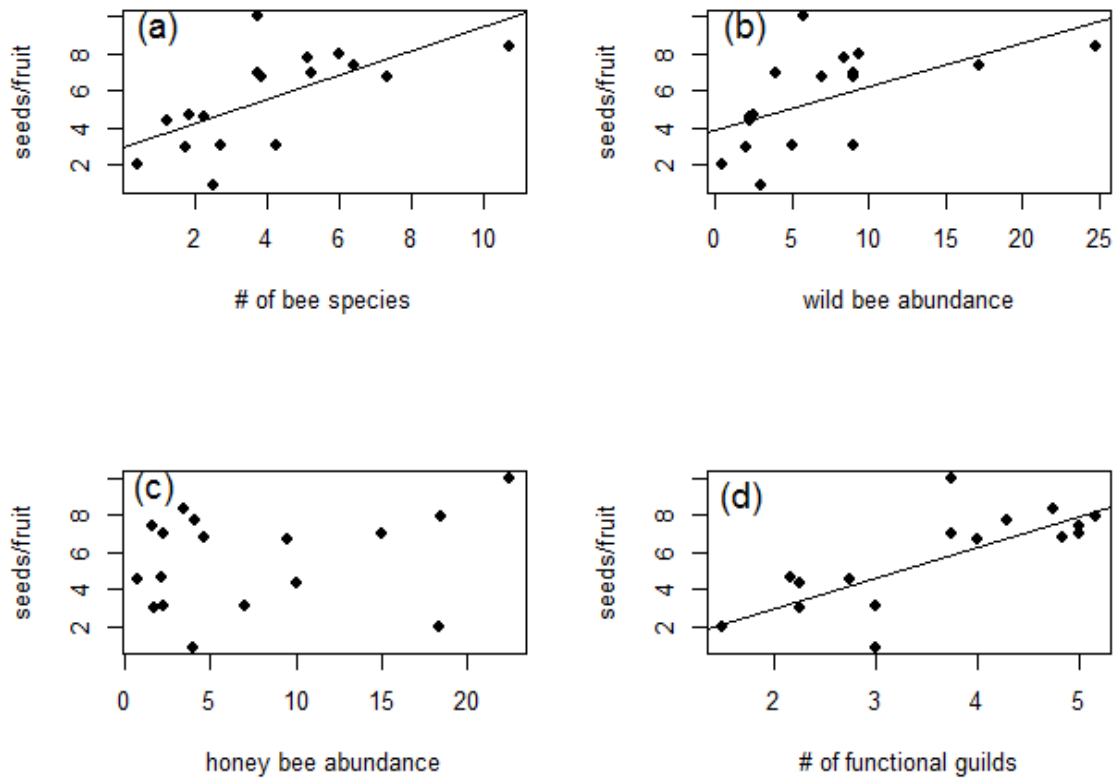


Figure 3

