

Characterization of wild bee communities in apple and blueberry orchards

Sabine S. Nooten^{*†} , Katherine Odanaka^{*‡} and Sandra M. Rehan^{*‡} 

^{*}Department of Biological Sciences, University of New Hampshire, Durham, NH, U.S.A., [†]School of Biological Sciences, The University of Hong Kong, Pok Fu Lam Road, Hong Kong, Hong Kong and [‡]Department of Biology, York University, Toronto, ON, Canada

- Abstract**
- 1 Wild bees provide invaluable ecosystem services in agricultural landscapes such as pollination. However, in recent decades, pollinator biodiversity, especially in wild bees, is declining on a global scale, with potentially far-reaching consequences for crop production. Thus, there is an urgent need to determine whether wild bees are present in agricultural systems, such as fruit orchards.
 - 2 In the present study, we examined the wild bee fauna at species and community levels during the period of bee activity (May to August) in apple and high-bush blueberry orchards in New England.
 - 3 Bee communities are crop-specific and dominated by very few species, which fluctuate according to crop and season. The blueberry associated bee fauna was more diverse. In apple, communities were phylogenetically clustered at the genus level and dominated by solitary ground nesting bees within the genus *Andrena*. Species fluctuated widely in presence and abundance throughout the season, leading to differences in community composition and functional trait structure.
 - 4 The results obtained in the present study show that apple and blueberry harbour a distinct and diverse bee fauna that performs vital pollination services in orchards. Our results provide essential baseline data for wild bees in blueberry and apple orchards and this can be used to improve management and conservation strategies for wild bee preservation in these crops.

Keywords Community composition, functional traits, native bees, network, phenology, phylogenetic diversity.

Introduction

Pollinators perform vital ecosystem services for native and agricultural plants (Klein *et al.*, 2007; Kremen *et al.*, 2007; Ollerton *et al.*, 2011). In agricultural systems, crop production is greatly enhanced by pollination services worth \$200 billion dollars worldwide annually (Klein *et al.*, 2007; Kleijn *et al.*, 2015). With the rise of agricultural intensification, services provided by managed bees, such as the domesticated honey bee (*Apis mellifera*) and, to a lesser degree, bumble or mason bees (e.g. *Bombus*, *Megachile* and *Osmia*) are most heavily relied upon because these can be readily deployed in the agricultural landscape to accommodate pollination during crop flowering time (Klein *et al.*, 2007; Potts *et al.*, 2010). Because domesticated bee colonies have shown drastic reductions in

numbers and performance in recent decades, as a result of stress, diseases and parasites (van Engelsdorp *et al.*, 2008; Potts *et al.*, 2010; Goulson *et al.*, 2015; Brown *et al.*, 2016), they cannot solely be relied upon for these vital crop pollination services. This sparked increased interest in assessing the crop-associated wild pollinator fauna in farms and orchards.

Wild insects, especially bees, perform pollination services for a multitude of crops, ranging from sunflower and rapeseed to multiple vegetable and fruit crops (Klein *et al.*, 2007; Winfree *et al.*, 2008; Garibaldi *et al.*, 2013). A diverse and locally distinct wild bee fauna is associated with apple orchards throughout north-eastern U.S.A. and Europe (Gardner & Ascher, 2006; Sheffield *et al.*, 2013; Russo *et al.*, 2015; Gibbs *et al.*, 2017) and with blueberry farms (Tuell *et al.*, 2009; Bushmann & Drummond, 2015). In orchards, flower visitations by wild bees are beneficial because wild bees can pollinate some crops (e.g. berries and almonds) more efficiently than domesticated bees (Garibaldi *et al.*, 2013). Crop productivity, measured as fruit size and/or

Correspondence: Sandra Rehan. Tel.: +1 416 736 2100; e-mail: sanrehan@yorku.ca

seed set, has been linked to the presence of a diverse wild bee fauna, in terms of species richness (Klein *et al.*, 2012; Rogers *et al.*, 2014; Campbell *et al.*, 2017), abundance (Isaacs & Kirk, 2010), phylogenetic diversity (Grab *et al.*, 2019) and functional group diversity based on traits, such as body size, nesting habits and/or sociality (Blitzer *et al.*, 2016; Woodcock *et al.*, 2019); but see Ratti *et al.* (2008). However, positive relationships of biodiversity and ecosystem services might not be generalizable across all agricultural systems because the abundance of a few dominant wild bee species in the community deliver the majority of the pollination services in a variety of crops, including watermelon, cranberry and blueberry (Winfree *et al.*, 2015). This suggests that wild bee surveys describing common and rare species are invaluable for crop-associated pollinator assessments. Based on these multifaceted ecological relationships and the difficulties in discerning generalizable patterns, the diversity and function of wild bees in many agricultural systems and geographical regions remains elusive. Although some regions are well documented (e.g. New York, Michigan, California), less information exists about the crop-associated wild bee fauna in fruit orchards in New Hampshire.

In New Hampshire, apple (*Malus domestica* Borkh.) and high-bush blueberry (*Vaccinium corymbosum* L.) are locally important crops (USDA NASS, 2011). Apple belongs to the plant family Rosacea; five white petals shape a relatively flat or shallowly cup-shaped flower, with conspicuous stigma and whorls of stamens (Pratt, 1988). They are self-incompatible and insect mediated pollination services are essential for successful fruit production (Free, 1964; Garratt *et al.*, 2014). As such, apple orchards associated with a diverse wild bee fauna show greatly enhanced fruit productivity (Garratt *et al.*, 2014; Blitzer *et al.*, 2016; Grab *et al.*, 2019). Recently, wild bee surveys across several apple orchards in the eastern U.S.A. have shown that dominant bees in the community vary among orchards; they included species within the genera *Andrena*, *Lasioglossum* and *Ceratina* (Sheffield *et al.*, 2013; Russo *et al.*, 2015; Kammerer *et al.*, 2016) and perhaps apple orchards in New Hampshire show a similar pattern.

Blueberry is part of the Ericaceae; its flowers comprise a bell-shaped whitish-pink corolla, with stamen and anthers inside and the stigma protruding through the opening of the corolla (Arrington & DeVetter, 2018). They are mainly bee pollinated and require sonication (i.e. buzz pollination) for adequate release and transfer of pollen between flowers (Javorek *et al.*, 2002; Benjamin & Winfree, 2014). Because domesticated bees are not able to buzz pollinate, this crop is particularly dependent on the presence of buzz pollination capable native bees, which include species in the genera *Bombus*, *Andrena*, *Osmia* and *Lasioglossum* (Javorek *et al.*, 2002; Ratti *et al.*, 2008). Similar to apple orchards, wild bee surveys in blueberry orchards in northeastern U.S.A. revealed that dominant genera in the community varied with geographical location. These included *Ceratina*, *Andrena*, *Lasioglossum* and *Augochlorella* in Michigan (Tuell *et al.*, 2009), *Andrena* in North Carolina (Rogers *et al.*, 2014), and *Bombus* in Maine (Bushmann & Drummond, 2015). With New Hampshire being geographically close to Maine, we anticipate *Bombus* to be abundant in the blueberry associated bee community. To date, the wild bee fauna associated with apple and blueberry orchards in New Hampshire has not been described.

Such baseline data provides invaluable information for farmers regarding orchard-based wild bee management and sustainable practices.

The present study characterizes the wild bee fauna associated with two locally dominant fruit crops in New England: apple and high-bush blueberry. Bees are compared between crops at the species level in terms of richness and diversity, as well as at the community level, including community composition, phylogenetic diversity and functional trait structure. We further compare the phenology of these communities in correspondence with crop bloom periods and throughout the period of bee activity.

Based on previous wild bee surveys, we hypothesize that the bee communities in apple and blueberry will be distinct, with the former being dominated by the genus *Andrena* and the latter *Bombus*. We further expect that bees will be most abundant during bloom period.

Materials and methods

Study area

Two replicate orchards, growing predominantly northern high-bush blueberry (*Vaccinium corymbosum*) and apple (*Malus pumila*), were chosen in Strafford County, New Hampshire, U.S.A. (43.2383°N, 71.0236°W). Orchards were located 17 km apart and similar in size with 10.4 ha (orchard 1) and 8.7 ha (orchard 2), featuring large stands of blueberry and apple crops. Both orchards grew multiple cultivars: for example, blueberry cultivars at orchard 1 were patriot and bluecrop, and blueray, nelson and liberty at orchard 2; apple cultivars were honey crisp and cortland at both orchards. To characterize the wild bee fauna in apple and blueberry crops, three replicate 100-m transects per crop were selected in each orchard ($2 \times 3 \times 2 = 12$ transects). Transects between crop types were approximately 500 m apart.

Bee sampling

Bees were collected from May to August 2018 using pan traps in accordance with procedures described in Tucker & Rehan (2016). In each transect, nine pan traps with alternating colours (blue, yellow and white) were filled with soapy water and placed on the ground from 08.00 h and 16.00 h on low wind sunny days. To retrieve the pan traps, the contents of the nine pans per transect were strained together and transferred into a jar filled with 70% ethanol. During bloom period (May to early June), bees were collected on a weekly base, after bloom, from mid-June onwards, bees were collected on a bi-weekly base. Eleven sampling events were carried out per orchard, resulting in 108 pan trap samples ($n = 55$ in orchard 1 and $n = 53$ in orchard 2). Monitoring bees in this fashion may introduce some bias, with effects being positive – affected by flower density (Wood *et al.*, 2015), negative – collecting fewer species (Cane *et al.*, 2000; O'Connor *et al.*, 2019) or neutral (Rhoades *et al.*, 2017).

During the blooming period, pan trap sampling was supplemented with sweep netting in the same transects, in accordance with the protocol described in Tucker & Rehan (2016). However this method accounted for <5% of individuals and <3% of

species (see Supporting information, Table S1), yielded very few common and new species, and was therefore excluded.

Bee processing, identification and functional traits

Bees were processed in accordance with procedures described in Droege (2015); specimens were washed, dried, mounted and stored in the laboratory of Sandra M. Rehan at York University. Bees were identified to species level using the interactive guide Discover Life (www.DiscoverLife.org) and taxonomic literature (Mitchell, 1960; Mitchell, 1962; Michener *et al.*, 1994; Gibbs, 2011; Rehan & Sheffield, 2011; Gibbs *et al.*, 2013; Williams *et al.*, 2014).

Bee functional trait classification occurred on species level according to their (i) nesting habit and (ii) social behaviour based on published literature (Giles & Ascher, 2006; Cane *et al.*, 2007; Michener, 2007; Matteson *et al.*, 2008; Wolf & Ascher, 2008; Rehan & Sheffield, 2011; Ascher *et al.*, 2014; Sheffield *et al.*, 2014; Selfridge *et al.*, 2017). Bees were classified into ground or stem nesting depending on the substrate used: wood or pithy stems versus soil. We categorized bees into four behaviour types according to the degree of sociality: solitary (bees living solitary or loosely communal), subsocial bees known to have prolonged parental care and mother-offspring interaction (e.g. small carpenter bees), social were all primitively and advanced eusocial bees (*Apis*, *Bombus* and some Halictidae) and parasitic for those with a cleptoparasitic lifestyle.

Statistical analysis

Data from all sampling events ($n = 11$) were pooled to compare species richness and diversity and assess adequacy of sampling for each crop type. We calculated the Chao-1 index (Chao, 1984) as an estimator for species richness, Simpson's invert ($1/D$) as diversity index (Simpson, 1949; Magurran, 2004) and generated species accumulation curves (Gotelli & Colwell, 2001) in ESTIMATES, version 8.2 (Colwell, 2013).

Statistical analyses were conducted in R (R Development Core Team, 2017). To compare the bee fauna between crop type (apple versus blueberry), differences in bee species and abundance were analyzed using a mixed model design 'glmer.nb' in *lme4* (Bates *et al.*, 2015), analysing crop as fixed and orchard as random factor (Zuur *et al.*, 2009). Relationships between bee communities and crop types were analyzed in three ways: (i) community composition; (ii) functional trait structure; and (iii) phylogenetic community structure. Community composition was compared between crops using the multivariate extension of generalized linear models 'manyglm' based on negative binomial distribution (Warton *et al.*, 2012) in *mvabund* (Wang *et al.*, 2012). The block function was used to account for the nested design of crops in farms (crops = fixed effect, farms = random effect) and the multivariate Wald χ^2 test statistic was used to evaluate compositional differences. Differences in bee functional traits in terms of nesting habit and social behaviour between crops were analyzed using the same approach as described for community composition.

Phylogenetic community structure was compared between crop types, using a published phylogenetic tree, based on

protein-coding nuclear gene DNA sequence data, covering > 13 000 wasp and bee species from Hedtke *et al.* (2013), as a baseline for further modification. Species collected during this study but not contained in the tree were added using 'add.species.to.genus' in *Phytools* (Revell, 2012). Surplus species were removed using 'drop.tip' in *Ape* (Paradis & Schliep, 2018). The resulting modified tree contained 78 species from 18 genera across five families. Phylogenetic diversity of each community was assessed using *Picante* (Kembel *et al.*, 2010); we used 'ses.mpd' to calculate mean pairwise distance (MPD), a measure of average branch length of each species in the community; we used 'ses.mntd' for mean nearest taxon difference (MNTD), which is a measure for the mean distance that separates each species in a community from its closest relative (Webb, 2000; Webb *et al.*, 2002). Both measures (MPD and MNTD) detect phylogenetic over-dispersion or clustering in a community. Expected MPD and MNTD were calculated by community randomization (999 permutations), and their standardized effect sizes (SES) were calculated by comparing the observed communities to the randomized ones (= null model). Negative SES values indicate phylogenetic clustering (i.e. species are closer related than expected) and positive SES values indicate evenness (i.e. species are spread randomly across the phylogeny).

To investigate phenology (i.e. seasonal variation of the bee fauna in regard to species richness, abundance and community), we categorized the sampling time into three periods in relation to the apple and blueberry bloom period. Both crops bloomed at the same time in spring for 2 weeks, from 17 to 31 May 2018. Thus, seasons were classified as 'pre-bloom' before 17 May, 'bloom' (17–31 May) and 'post-bloom' from June onwards. Differences in species numbers and abundances were analyzed using 'glmer.nb' in *lme4* (Bates *et al.*, 2015), and seasons were analyzed as fixed and orchards as random factors. Seasonal effects on species composition were analyzed using 'manyglm' (Warton *et al.*, 2012) in *mvabund* (Wang *et al.*, 2012), with season as fixed effect and orchards as random effect. Plant–pollinator network plots, reflecting crop-bee associations, were constructed using 'plotweb' with bee abundance data in the package *bipartite* (Dormann *et al.*, 2008). We used 'networklevel' to calculate estimates of stability and robustness of the crop–pollinator association (Dormann *et al.*, 2009), and 'specieslevel' for measures of individual bee contributions, as well as to identify the most influential and rare bees in the crop–pollinator association (Dormann, 2011). At bee species level, we calculated the number of floral hosts (i.e. if a bee species was associated with both or only one crop), and pollination service index (PSI) as a measure of relative importance of each bee species in the community, where values range from 0–1, with 1 indicating that the bee performs essential pollinator services (Dormann, 2011). At the community level, we calculated the absolute and relative number of bee species associated with each crop. Weighted nestedness was calculated as an estimate of association structure, with 1 being completely nested (i.e. interactions of generalists and specialists overlap) and 0 being chaotic with no overlap (Galeano *et al.*, 2009). Connectance was calculated as an estimate for complexity and resilience of a community to species loss by calculating the proportion of achieved versus possible interactions, where 1 indicates robustness and 0 weakness to species loss (Dunne *et al.*, 2002).

Results

In total, 1115 individual bees belonging to 76 species were collected using pan traps across all sites (see Supporting information, Fig. S1 and Table S1). The most abundant family was Andrenidae ($n = 435$; 39% of the total), followed by Halictidae ($n = 306$; 27%) and then Apidae ($n = 247$; 22%). The most species rich family was Halictidae ($n = 24$; 32%) then Apidae and Andrenidae (each $n = 21$; 28%). The most abundant genus was *Andrena* ($n = 503$; 38%), second was *Lasioglossum* ($n = 205$; 18%) and third was *Ceratina* ($n = 137$; 12%). The most species rich genera were *Andrena* ($n = 20$; 26%), *Lasioglossum* ($n = 14$; 18%) and *Nomada* ($n = 9$; 12%). The most abundant bee species collected was *Andrena crataegi* ($n = 194$; 16% of all individuals), followed by *Lasioglossum tegulare* ($n = 120$; 11%) and *Ceratina calcarata* ($n = 109$; 10%). Most frequent (i.e. collected in all 12 transects) were *Andrena carlini* and *Halictus ligatus*; in more than 90% of transects were *Agapostemon virescens*, *C. calcarata*, *Lasioglossum tegulare* and *Osmia atriventris*. Rare species were 37% ($n = 29$), collected only with one individual ($n = 20$; 25%) or with two ($n = 10$; 13%).

Species level comparisons between crop types

Species richness, based on rarefied number of individuals ($n = 369$), was similar for both crops ($n = 49$) (see Supporting information, Fig. S2A). The blueberry associated bee fauna was slightly more diverse [Simpson's invert ($1/D$) = 15.69] than the apple associated fauna ($1/D = 13.53$). Sampling adequacy was comparable between the two crop types (78% in blueberry and 72% in apple) shown by the non-asymptotic behaviour of the species accumulation curves (see Supporting information, Fig. S2B), indicating that three quarters of the crop-associated species pool has been collected. Twice as many bees were collected from apple than from blueberry, whereas numbers of species were comparable (Fig. 1). Most abundant in both crops were the genera *Andrena*, *Lasioglossum*, *Ceratina* and *Osmia*, each collected with > 100 individuals, and together comprising 79% of the collected bees in this study (Table 1); particularly, many individuals from the genus *Andrena* were collected from apple; the most abundant species was *A. crataegi*, followed by *L. tegulare*, *C. calcarata* and *A. carlini*, comprising 44% of the collected bees (Table 1). In apple, there were also more *Nomada*, the only cleptoparasitic genus collected in this study, and *Eucera pruinosa*, *A. virescens* and *O. atriventris* (Table 1, see also Supporting information, Table S1). On average, significantly more bees were collected from apple than blueberry transects in terms of species (Wald $\chi^2_1 = 4.749$, $P = 0.03$, d.f. = 107,1) (Fig. 2A and Table 2) and individuals (Wald $\chi^2_1 = 16.767$, $P < 0.0001$, d.f. = 107,1) (Fig. 2B and Table 2).

Community level comparisons between crops

At the community level, a distinct bee fauna was associated with apple and blueberry crops. Species composition was significantly different between apple and blueberry (Wald $\chi^2 = 7.87$, $P = 0.024$, d.f. = 107.1). Differences were largely

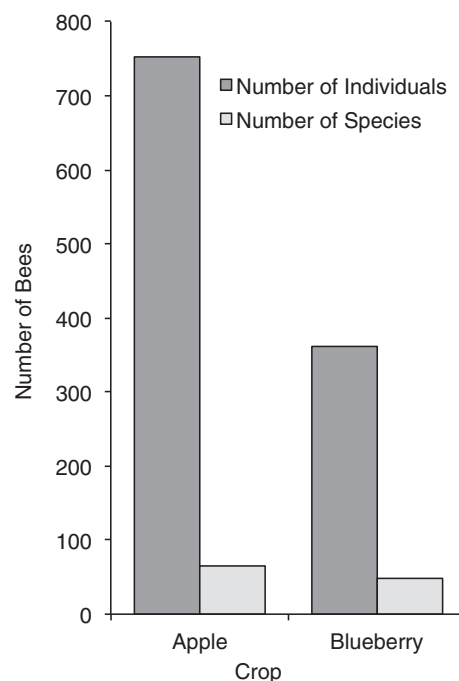


Figure 1 Number of bees (individuals and species) collected from two crop types.

driven by significantly greater abundances of *A. virescens*, *A. carlini*, *E. pruinosa*, *Lasioglossum pectorale* and *L. tegulare*, in apple (see Supporting information, Table S1). Phylogenetic community structure compared as MPD was not significantly different between crop types, whereas it was distinct at the tips of the phylogenetic tree: MNTD of the bee community in apple at orchard 2 was significantly more clustered than expected (MNTD SES = -1.031, $P = 0.048$) (Table 3). All other communities were not significantly different from expected/randomized ones (= null models). The relative distribution of functional traits was significantly different between crops for both nesting habit (Wald $\chi^2 = 4.157$, $P = 0.008$, d.f. = 107.1) (Fig. 3A) and social behaviour (Wald $\chi^2 = 4.528$, $P = 0.02$, d.f. = 107.1) (Fig. 3B). In apple, the proportion of ground nesting bees was significantly higher (Wald $\chi^2 = 4.147$, $P = 0.003$, d.f. = 107.1; ratio ground : stem nester 4 : 1) than in blueberry (ratio 2 : 1) (Fig. 3A). The most dominant social behaviour at both crops was solitary ($n = 686$; 61%), followed by social ($n = 253$; 23%), then subsocial ($n = 137$; 12%), and finally cleptoparasitic ($n = 39$; 4%) (Fig. 3B). The proportion of solitary bees was significantly higher in apple (one-third of the community) than blueberry (one-half of the community; Wald $\chi^2 = 3.299$, $P = 0.02$, d.f. = 107.1).

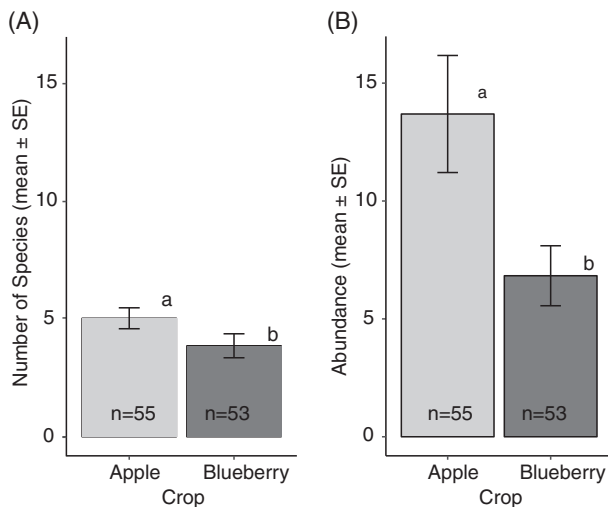
Crop-pollinator network

The crop-pollinator network consists of 76 bee species between two crops: apple and blueberry. There were differences between crops: there were 30% more bee species associated with apple than with blueberry, resulting in a higher value for connectance (Fig. 4A and Table 4). This indicates that the apple-pollinator

Table 1 Abundance of the 10 most abundant bee genera and species at two crop types

	Apple	Blueberry	Overall
Genera			
<i>Andrena</i>	305 (40.5%)	114 (31.5%)	419 (37.6%)
<i>Lasioglossum</i>	149 (19.8%)	58 (16.0%)	207 (18.6%)
<i>Ceratina</i>	68 (9.0%)	69 (19.1%)	137 (12.3%)
<i>Osmia</i>	66 (8.8%)	51 (14.1%)	117 (10.5%)
<i>Halictus</i>	26 (3.5%)	25 (6.9%)	51 (4.6%)
<i>Eucera</i>	37 (4.9%)	3 (0.8%)	40 (3.6%)
<i>Agapostemon</i>	23 (3.1%)	12 (3.3%)	35 (3.1%)
<i>Nomada</i>	21 (2.8%)	13 (3.6%)	34 (3.0%)
<i>Calliopsis</i>	14 (1.9%)	2 (0.6%)	16 (1.4%)
<i>Apis</i>	9 (1.2%)	6 (1.7%)	15 (1.3%)
Species			
<i>Andrena crataegi</i>	133 (17.7%)	46 (12.7%)	179 (16.1%)
<i>Lasioglossum tegulare</i>	83 (11.0%)	37 (10.2%)	120 (10.8%)
<i>Ceratina calcarata</i>	60 (8.0%)	49 (13.5%)	109 (9.8%)
<i>Andrena carlini</i>	64 (8.5%)	19 (5.2%)	83 (7.4%)
<i>Andrena barbilabris</i>	56 (7.4%)	10 (2.8%)	66 (5.9%)
<i>Osmia atriventris</i>	46 (6.1%)	16 (4.4%)	62 (5.6%)
<i>Eucera pruinosa</i>	37 (4.9%)	3 (0.8%)	40 (3.6%)
<i>Agapostemon virescens</i>	23 (3.1%)	10 (2.8%)	33 (3.0%)
<i>Andrena vicina</i>	24 (3.2%)	7 (0.8%)	31 (2.8%)
<i>Halictus ligatus</i>	15 (2.0%)	14 (3.9%)	29 (2.6%)

Percentage of site total is shown in brackets (%).

**Figure 2** Bee species richness and abundance at two crops. Mean \pm SE of (A) numbers of species and (B) abundance per transect and sampling event. Small letters indicate statistical significance; *n*, sample size.

associations are more complex and robust to species loss. Weighted nestedness was close to zero for both crops, demonstrating a chaotic association with little overlap of generalist and specialist bee interactions (Table 4). Overall, 50% ($n = 38$) of the bee species were collected from only one crop type, of which were 35% from apple and 15% from blueberry (Fig. 4A and Table 4). These were generally low in abundance ($n < 4$), and some of these were singletons, occurring only once ($n = 23$;

Table 2 Summary of mixed effect negative binomial generalized linear models (glmer.Nb) for species richness and abundance of wild bees at two crops

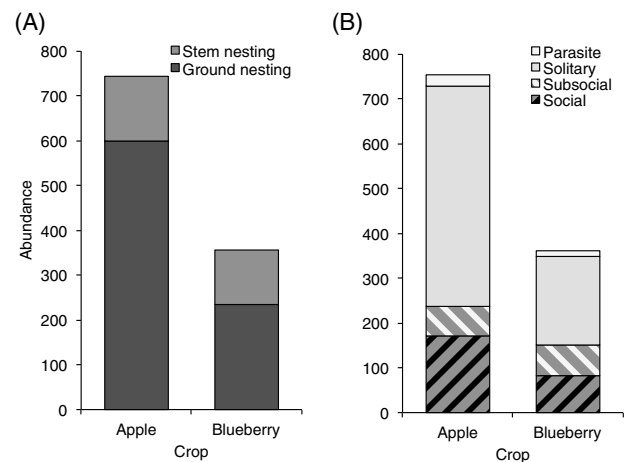
Contrast	Estimate	SE	Z value	$Pr(> Z)$	Pseudo- r^2
Species richness					
Intercept	1.525	0.228	6.679	<0.0001	0.15
Apple-blueberry	-0.300	0.138	-2.179	0.0293	
Abundance					
Intercept	2.491	0.412	5.915	<0.0001	0.32
Apple-blueberry	-0.7807	0.191	-4.095	<0.0001	

Shown are the model coefficient (estimate), standard error (SE), Z value, P value ($Pr(>|Z|)$) of the chi-squared statistic and pseudo- r^2 (r^2).

Table 3 Summary of community phylogenetic diversity measured as mean pairwise distance (MPD) and mean nearest taxon (MNT) at two crop types and two orchards

Contrast	MPD.Obs.	P (mpd. Obs)	MNTD.Obs.	P (mntd. obs)
Apple orchard 1	-1.3915	0.297	1.1404	0.783
Apple orchard 2	1.0393	0.760	-1.0310	0.048
Blueberry orchard 1	-1.2334	0.207	1.1062	0.776
Blueberry orchard 2	-0.8219	0.371	-0.9402	0.294

Shown are standardized effect sizes based on comparison of observed versus randomized community for MPD (MPD.Obs) and MNTD (MNTD.Obs) and the P value $P(\text{mpd.obs})$ and $P(\text{mntd.obs})$.

**Figure 3** Bee functional trait distribution in terms of (A) nesting type and (B) social behaviour at two crop types.

30%). There were more singletons in apple ($n = 17$; 22%) than in blueberry ($n = 6$; 8%). Of particular note was *Lasioglossum pilosum*, which occurred with $n = 12$ individuals in apple (Fig. 4A; see also Supporting information, Table S1). PSI values for bee species were generally low, ranging from 0.0013 for singletons to 0.1635 for the most abundant species *A. crataegi* (see Supporting information, Table S1), indicating that there are no indicator/key stone species in the system and that pollination services performed by individual bee species were comparably important.

Table 4 Summary of crop-pollinator network level analyses for apple and blueberry

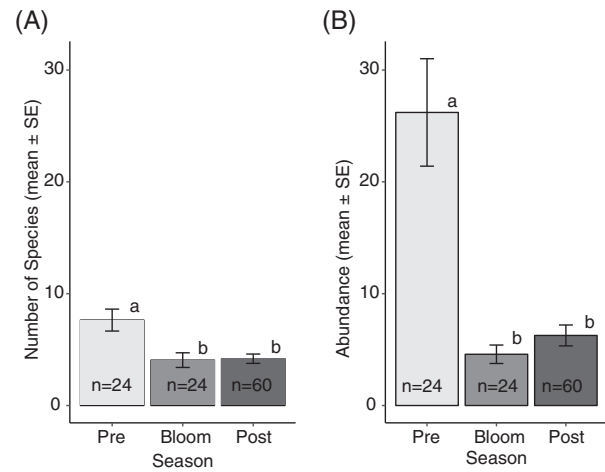
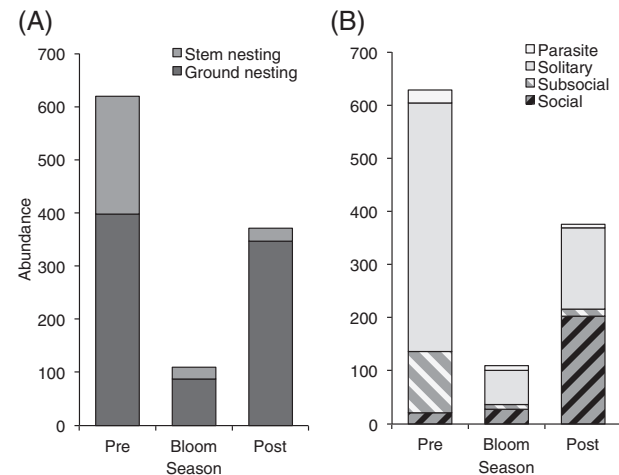
Crop	Bee species at one crop	Number of bee species	Relative number of bee species	Weighted nestedness	Connectance
Apple	27	66	0.857	-0.2688	0.879
Blueberry	11	50	0.649	0.1499	0.720

Table 5 Summary of mixed effect negative binomial generalized linear models (glmer.Nb) for species richness and abundance of wild bees through the season; before blooming period (pre), during bloom (bloom) and after blooming period (post)

Contrast	Estimate	SE	Z value	$Pr(> Z)$	Pseudo- r^2
Species richness					
Intercept	1.199	0.243	4.944	<0.0001	0.26
Pre-bloom	0.619	0.187	3.306	0.001	
Post-bloom	0.033	0.169	0.198	0.843	
Pre – post	0.586	0.151	-3.889	0.0001	
Abundance					
Intercept	1.456	0.372	3.913	<0.0001	0.64
Pre-bloom	1.624	0.240	6.760	<0.0001	
Post-bloom	0.276	0.212	1.303	0.193	
Pre – post	1.347	0.192	7.036	<0.0001	

Shown are the model coefficient (estimate), standard error (SE), Z value, P value ($Pr(>|Z|)$) of the chi-squared statistic and pseudo- r^2 (r^2).

pruinosa ($n = 40$; 4%) and *A. virescens* ($n = 26$; 2%). On average, significantly more bee species per transect and sampling event were collected before the blooming period (6.54 ± 4.14) than during bloom (3.46 ± 2.77) and afterward (3.57 ± 2.78 ; Wald $\chi^2 = 17.382$, $P = 0.0002$, d.f. = 106.2) (Fig. 5A and Table 5). Similarly, significantly more bee individuals were collected before the blooming period (26.21 ± 25.54) than during bloom (4.58 ± 4.04) and afterward (6.27 ± 7.24 ; Wald $\chi^2_2 = 62.072$, $P < 0.0001$, df 106.2) (Fig. 5B and Table 5). There were marked differences in the bee community throughout the season. Species composition changed significantly during the three periods (Wald $\chi^2 = 14.8$, $P < 0.001$, d.f. = 107.1). In pre-bloom, the community was composed of significantly more *A. crataegi*, *A. carlini*, *Andrena barbilaris*, *Andrena vicina*, *C. calcarata* and *O. atriventris*. During post-bloom, significantly more *E. pruinosa*, *A. virescens*, *L. tegulare*, *H. ligatus* and *Lasioglossum pectorale* were present (Fig. 4B). The functional trait community structure was significantly different between seasons in terms of nesting habit (Wald $\chi^2 = 9.101$, $P = 0.001$, d.f. = 105.1) and social behaviour (Wald $\chi^2 = 12.3$, $P = 0.001$, d.f. = 105.1). Nesting habit differed significantly during the pre-bloom period because there were significantly more ground and stem nesting bees (Fig. 6A and Table 6). Similarly, social behaviour was significantly different in pre-bloom as compared with the rest of the season. These differences were mainly driven by significantly more solitary, subsocial and cleptoparasitic bees during pre-bloom and significantly more social bees during post-bloom (Fig. 6B and Table 6).

**Figure 5** (A) Species richness (mean \pm SE) and (B) abundance of wild bees collected with pan traps during three seasons (pre-bloom, bloom and post-bloom). Small letters indicate statistical significance; n , sample size.**Figure 6** Bee functional trait distribution in terms of (A) nesting type and (B) social behaviour at throughout the season. Period before apple and blueberry bloom (pre), during bloom (bloom), after bloom (post).

Discussion

We evaluated the wild bee fauna at species and community level in apple and blueberry orchards in New England throughout the period of bee activity (May to August). Species richness was similar between both crops. Apple harboured numerically more bees, whereas bees in blueberry were more diverse. There were marked differences between the crop-specific bee communities. The apple associated bee community was phylogenetically more clustered at the genus level and as hypothesized dominated by solitary ground nesting bees within the genus *Andrena*. It also had a higher abundance of social bees and more unique species than blueberry. By contrast to our prediction, the community in blueberry was dominated by solitary stem nesting *Ceratina*, whereas *Bombus* was almost absent. There was a marked turnover in the bee fauna throughout the season. Bees fluctuated in species richness and abundance

Table 6 Summary of multivariate generalized linear models (manyglm) for bee functional trait structure in terms of nesting habit and social behaviour through the season

	Pre-bloom	Post-bloom	Pre – post
Nesting overall	6.784 ($P < 0.001$)	2.420 ($P = 0.081$)	8.467 ($P < 0.001$)
Ground nesting	4.868 ($P < 0.001$)	1.731 ($P = 0.135$)	4.168 ($P < 0.001$)
Stem nesting	4.725 ($P < 0.001$)	1.691 ($P = 0.085$)	7.370 ($P < 0.001$)
Social overall	7.736 ($P < 0.001$)	4.425 ($P = 0.002$)	11.586 ($P = 0.022$)
Solitary	6.261 ($P < 0.001$)	0.214 ($P = 0.853$)	7.919 ($P = 0.001$)
Subsocial	3.997 ($P < 0.001$)	0.880 ($P = 0.413$)	5.788 ($P = 0.001$)
Social	0.523 ($P = 0.633$)	3.656 ($P = 0.003$)	4.146 ($P < 0.001$)
Cleptoparasitic	2.097 ($P < 0.043$)	2.332 ($P = 0.008$)	4.564 ($P < 0.001$)

Shown are the Wald χ^2 test statistic and P -value [Wald χ^2 (P)], for comparisons among the three periods, pre-bloom, bloom and post bloom; degrees of freedom (2,105).

throughout the season, suggesting differences in community composition and functional trait structure. Our results demonstrate that a distinct and diverse bee fauna is associated with apple and blueberry throughout the season, which may perform vital crop pollination services and enhance fruit production in orchards.

Wild bee species richness and diversity

The present study collected three quarters of the crop-associated wild bee species pool using pan traps. This compares well with previous species pool proportions collected from multiple apple orchards in New York State (Russo *et al.*, 2015), although it is somewhat lower than the $\geq 88\%$ from high-bush blueberry in Michigan and Maine (Tuell *et al.*, 2009; Bushmann & Drummond, 2015). Here, a larger proportion of the local species pool could have been obtained with additional collection methods (e.g. bee visitation transects, blue vein traps) (Cane *et al.*, 2000; O'Connor *et al.*, 2019) and/or a higher sampling effort; but see Russo *et al.* (2015). In the present study, bee species richness was similar for both crops – apple and blueberry ($n = 53$ and 51) – and numbers are comparable to other studies investigating wild bees in apple orchards (Russo *et al.*, 2015; Blitzer *et al.*, 2016) and low-bush blueberry fields (*Vaccinium angustifolium*) in Maine (Bushmann & Drummond, 2015), although it was higher than in cranberry fields (*Vaccinium macrocarpon*) in Massachusetts (MacKenzie & Eickwort, 1996). Here, species diversity in apple, calculated as Simpson's invert ($1/D$), was similar to apple orchards in Nova Scotia, Canada (Sheffield *et al.*, 2013). We found that the blueberry associated bee fauna was more diverse than the apple associated. This is driven by large abundances of three *Andrena* species, *A. crataegi*, *A. carlini* and *Andrena barbilabris* in apple. This could also partly be associated with differences in flower volume: apple trees were generally larger and had more flowers than blueberry shrubs. Furthermore, differences in flower morphology could also have had an effect because the flat open cup-shaped apple flowers may attract more bees than the bell-shaped blueberry flowers. Similarly, species of the genus *Andrena* were also abundant at multiple apple orchards across the north-eastern US (Gardner & Ascher, 2006; Russo *et al.*, 2015; Grab *et al.*, 2019).

Bee communities in apple and blueberry crops

Three numerically dominant genera, *Andrena*, *Lasioglossum* and *Ceratina*, accounted for the largest proportion of bees in the community in both crops. Our results are in line with previous wild bee surveys in apple and blueberry orchards across the northeast U.S.A. (Gardner & Ascher, 2006; Tuell *et al.*, 2009; Bushmann & Drummond, 2015; Russo *et al.*, 2015), although they differ from previously conducted wild bee surveys in mixed produce farms in New Hampshire (Tucker & Rehan, 2017; Tucker & Rehan, 2018). Here, the apple associated bee fauna was dominated by solitary ground nesting bees of the genus *Andrena*, which comprised 40% of the community. One species, *A. crataegi*, was predominant, accounting for 18% of bees in the community. Our results support a previous study, investigating the bee fauna across multiple apple orchards in the Finger Lakes Region of western New York State, where the genus *Andrena* in general (Gardner & Ascher, 2006) and the species *A. crataegi* in particular was predominant (Russo *et al.*, 2015). By contrast, a range of other species was dominant across northeast American apple orchards. For example, among halictid bees, *Lasioglossum leucozonium* was dominant in Nova Scotia, Canada (Sheffield *et al.*, 2013), whereas *Augochlora pura* was dominant in Pennsylvania (Kammerer *et al.*, 2016). We found that the bee community in blueberry was dominated by solitary ground nesting bees of the genus *Andrena* (32%). The subsocial stem nesting bee *C. calcarata* (13%) was the most dominant species. Unexpectedly, *Bombus* accounted for less than 1%. This stands in stark contrast to the blueberry bee community in Maine, where *Bombus* accounted for 30% (Bushmann & Drummond, 2015). Similar to our study, *C. calcarata* was most abundant in high bush blueberry in Michigan (Tuell *et al.*, 2009). By contrast to our findings, among andrenid bees, *Andrena bradleyi* was dominant in North Carolina (Rogers *et al.*, 2014), *A. carlini* was dominant in Michigan (Isaacs & Kirk, 2010) and the halictid bee *Lasioglossum cressonii* was dominant in Maine (Bushmann & Drummond, 2015). This phenomenon of one particular species being dominant in the community might reflect the patchy distribution of insects (Gaston *et al.*, 1997; Tscharntke & Brandl, 2004; Ewers & Didham, 2006). Turnover and differences of dominant species in fragmented, i.e. agricultural, landscapes might arise from local specifics in environmental factors, inducing climate, surrounding land use and habitat types, as well as biotic factors such as competition

and parasitism (Tschamtké & Brandl, 2004; Diekötter *et al.*, 2008). This suggests that local surveys using a combination of active and passive approaches, including transect walks, sweep netting and traps (Rhoades *et al.*, 2017; O'Connor *et al.*, 2019) of crop-associated wild bees, are invaluable because broad patterns and generalizations cannot be drawn across regions or agricultural systems.

Community composition. The bee community composition differed markedly between apple and blueberry crops. Differences were driven by more abundant *A. virescens*, *A. carlini*, *E. pruinosa*, *L. pectorale* and *L. tegulare* in apple. Some of these species have previously been found to be abundant in the apple associated bee community, including *A. virescens* (Sheffield *et al.*, 2013) and *A. carlini* (Russo *et al.*, 2015). The apple associated bee community was distinct in terms of phylogenetic diversity: At orchard 2, there was more clustering at the tips of the phylogenetic tree, indicating a paucity of species representation in certain clades of the tree. This is most likely driven by fewer species within the genera *Andrena*, *Lasioglossum* and *Nomada*. *Andrena* and *Lasioglossum* species have previously been shown to be sensitive and responded negatively to more intensified agricultural land use types (Hendrix *et al.*, 2018; Grab *et al.*, 2019).

Community functional traits. The majority of the community comprised solitary ground nesting bees, some subsocial stem nesting and social ground nesting, and very few cleptoparasitic bees. Apple harboured more solitary and social ground nesting bees than blueberry, which was largely driven by more *Andrena* and *Lasioglossum* species. Our findings support previous ones in apple and blueberry orchards. Large numbers of solitary *Andrena* were associated with apple in New York (Russo *et al.*, 2015; Blitzer *et al.*, 2016), whereas large numbers of solitary and social ground nesters (*Andrena* and *Lasioglossum*) were associated with apple in Canada (Sheffield *et al.*, 2013). Here, the majority of bees in blueberry were also solitary and ground nesting, driven by large numbers of *Andrena* and *Agapostemon*. This is in line with the wild bee fauna in low-bush blueberry in Maine (Bushmann & Drummond, 2015). We found very few (4%) cleptoparasitic bees, which belonged to only two genera, *Nomada* and *Sphcodes*. This aligns well with previous findings, where similarly few cleptoparasitic bees were collected using pan traps in apple orchards in Nova Scotia (Sheffield *et al.*, 2013), sweep netting in apple orchards in New York State (Blitzer *et al.*, 2016) or a combination of pan traps and hand collecting in blueberry orchards in Maine (Bushmann & Drummond, 2015). These results indicate that orchards can provide flower resources to harbour a diverse bee community in terms of species, although functional guild diversity might be diminished in homogenized agricultural landscapes (Woodcock *et al.*, 2019).

Bee phenology

There was a marked turnover in the bee community throughout the season for both crops. Surprisingly, only a tenth of the bee

fauna was collected during the 2-week bloom period, whereas more than half of the fauna was collected during the 2 weeks before bloom in early May. This suggests that the resident bee fauna depends on early spring flower resources in the vicinity, which could have been provided by herbaceous lanes between the fruit crops and along nearby roadsides. Alternatively, when the crop is in bloom the bees might be collecting nectar and pollen from the flowers and not visiting the pan traps. During both pre-bloom and bloom, solitary ground nesting *Andrena* species were predominant in the bee community, comprising more than one third of the individuals. The pre-bloom community was dominated by the solitary ground nesting species *A. crataegi* and the subsocial stem nesting bee *C. calcarata*. During bloom period solitary ground nesting *A. crataegi* and social ground nesting *L. tegulare* were predominant. The latter of which was also most abundant in the post-bloom period. Unlike our study, a survey in highbush blueberry in Michigan (Tuell *et al.*, 2009) collected almost one half of the individuals and more than a third of the bee species during bloom period. Differences could arise from collection methods used, as Tuell *et al.* (2009) mounted pan traps on poles, whereas here the traps were placed on the ground. It is conceivable that pole mounted pan traps would have yielded a higher proportion of sampled bees during bloom period. However, similar trends emerged for both studies, as to which genera were dominant during the three periods. Similar to our findings, *Andrena* was dominant during pre- and bloom period, whereas *Ceratina* was abundant before, and *Lasioglossum* during bloom (Tuell *et al.*, 2009).

We conclude that fruit orchards in New Hampshire harbour a species and trait diverse wild bee fauna, fluctuating through time. Bee communities in apple and blueberry are crop-specific and dominated by very few species, which vary depending on season and crop. Our results provide baseline survey data, the first of its kind, in blueberry and apple orchards in New Hampshire, which informs us about the resident bee community in and around these crop environments. These can be used to inform farmers about wild bee pollination services in their orchards and to implement improved management and conservation strategies. Important considerations include available nesting habitat and alternate flower resources for wild bees in agricultural landscapes. Future studies should incorporate crop-flower visitations and fruit quality/quantity to address pollination services by wild bees in more detail.

Acknowledgements

We thank Gianna DeMarco, Stephanie Gardner, Josh Hall, István Mikó and Madeline Young for specimen collection, processing, identification and data basing. This work was supported by the USDA National Institute of Food and Agriculture Hatch project 1004515, the New Hampshire Agricultural Experiment Station, and the Foundation for Food and Agriculture Research, Pollinator Health Fund grant number 549038.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Abundance of bee species collected from two crop types (apple and blueberry) at two orchards in New Hampshire (May to August 2018).

Fig. S2. (A) Coleman's rarefaction and (B) species accumulation curves for bees. Species richness for two crop types based on the number of (A) individuals (mean \pm SD) and (B) samples (mean \pm SD).

Table S1. Bee species collected from apple and blueberry crops at two orchards in New Hampshire (U.S.A.) in May to August 2018. Overall abundance (pan) and abundance at each crop type and orchard, including social behaviour and nesting habit, number of associated crops (No. of links) and pollination service index (PSI). *Species also collected with sweep netting.

References

- Arrington, M. & DeVetter, L.W. (2018) Floral morphology differs among new northern highbush blueberry cultivars. *Journal of Horticulture*, **5**, 1–4.
- Ascher, J.S., Kornbluth, S. & Golet, R.G. (2014) Bees (hymenoptera: Apoidea: Anthophila) of Gardiners Island, Suffolk County, New York. *Northeastern Naturalist*, **21**, 47–71.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48.
- Benjamin, F.E. & Winfree, R. (2014) Lack of pollinators limits fruit production in commercial blueberry (*Vaccinium corymbosum*). *Environmental Entomology*, **43**, 1574–1583.
- Blitzer, E.J., Gibbs, J., Park, M.G. & Danforth, B.N. (2016) Pollination services for apple are dependent on diverse wild bee communities. *Agriculture Ecosystems & Environment*, **221**, 1–7.
- Brown, M.J., Dicks, L.V., Paxton, R.J. *et al.* (2016) A horizon scan of future threats and opportunities for pollinators and pollination. *PeerJ*, **4**, e2249.
- Bushmann, S.L. & Drummond, F.A. (2015) Abundance and diversity of wild bees (hymenoptera: Apoidea) found in Lowbush blueberry growing regions of Downeast Maine. *Environmental Entomology*, **44**, 975–989.
- Campbell, A.J., Wilby, A., Sutton, P. & Wackers, F.L. (2017) Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agriculture Ecosystems & Environment*, **239**, 20–29.
- Cane, J.H., Minckley, R.L. & Kervin, L.J. (2000) Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. *Journal of the Kansas Entomological Society*, **73**, 225–231.
- Cane, J.H., Griswold, T. & Parker, F.D. (2007) Substrates and materials used for nesting by north American Osmia bees (hymenoptera: Apiformes: Megachilidae). *Annals of the Entomological Society of America*, **100**, 350–358.
- Chao, A. (1984) Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, **1**, 265–270.
- Colwell, R. K. (2013) Estimates: Statistical estimation of species richness and shared species from samples. Version 9.1. URL <http://purl.oclc.org/estimates> [Accessed 01 June 2014].
- Diekötter, T., Billeter, R. & Crist, T.O. (2008) Effects of landscape connectivity on the spatial distribution of insect diversity in agricultural mosaic landscapes. *Basic and Applied Ecology*, **9**, 298–307.
- Dormann, C.F. (2011) How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, **1**, 1–20.
- Dormann, C.F., Gruber, B. & Freund, J. (2008) Introducing the bipartite package: Analysing ecological networks. *R news*, **8**, 8–11.
- Dormann, C.F., Freund, J., Bluethgen, N. & Gruber, B. (2009) Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, **2**, 7–24.
- Droege, S. (2015) *The Very Handy Manual: How to Catch and Identify Bees and Manage a Collection*. Native Bee Inventory and Monitoring Lab, USGS Patuxent Wildlife Research Center, Beltsville, Maryland.
- Dunne, J.A., Williams, R.J. & Martinez, N.D. (2002) Food-web structure and network theory: the role of connectance and size. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 12917–12922.
- van Engelsdorp, D., Hayes, J. Jr., Underwood, R.M. & Pettis, J. (2008) A survey of honey bee colony losses in the U.S., fall 2007 to spring 2008. *PLoS ONE*, **3**, e4071.
- Ewers, R.M. & Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews of the Cambridge Philosophical Society*, **81**, 117–142.
- Free, J.B. (1964) Comparison of the importance of insect and wind pollination of apple trees. *Nature*, **201**, 726–727.
- Galeano, J., Pastor, J.M. & Iriando, J.M. (2009) Weighted-interaction nestedness estimator (WINE): a new estimator to calculate over frequency matrices. *Environmental Modelling & Software*, **24**, 1342–1346.
- Gardner, K.E. & Ascher, J.S. (2006) Notes on the native bee pollinators in New York apple orchards. *Journal of the New York Entomological Society*, **114**, 86–91.
- Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R. *et al.* (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science*, **339**, 1608.
- Garratt, M.P., Breeze, T.D., Jenner, N., Polce, C., Biesmeijer, J.C. & Potts, S.G. (2014) Avoiding a bad apple: insect pollination enhances fruit quality and economic value. *Agriculture Ecosystems & Environment*, **184**, 34–40.
- Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997) Interspecific abundance range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579–601.
- Gibbs, J. (2011) Revision of the metallic Lasioglossum (Dialictus) of eastern North America (hymenoptera: Halictidae: Halictini). *Zootaxa*, **3073**, 1–216.
- Gibbs, J., Packer, L., Dumesh, S. & Danforth, B.N. (2013) Revision and reclassification of Lasioglossum (Evylaeus), L. (Hemihalictus) and L. (Sphecodogastra) in eastern North America (hymenoptera: Apoidea: Halictidae). *Zootaxa*, **3672**, 1–117.
- Gibbs, J., Joshi, N.K., Wilson, J.K. *et al.* (2017) Does passive sampling accurately reflect the bee (Apoidea: Anthophila) communities pollinating apple and sour cherry orchards? *Environmental Entomology*, **46**, 579–588.
- Giles, V. & Ascher, J.S. (2006) A survey of the bees of the black rock Forest preserve, New York (hymenoptera: Apoidea). *Journal of Hymenoptera Research*, **15**, 208–231.
- Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.
- Goulson, D., Nicholls, E., Botias, C. & Rotheray, E.L. (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, **347**, 1255957–1–9.
- Grab, H., Branstetter, M.G., Amon, N. *et al.* (2019) Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. *Science*, **363**, 282–284.
- Hedtke, S.M., Patiny, S. & Danforth, B.N. (2013) The bee tree of life: a supermatrix approach to apoid phylogeny and biogeography. *BMC Evolutionary Biology*, **13**, 1–13.

- Hendrix, S.D., Forbes, A.A. & MacDougall, C.E.D. (2018) Variation in the phylogenetic diversity of wild bees at produce farms and prairies. *Agriculture Ecosystems & Environment*, **259**, 168–173.
- Isaacs, R. & Kirk, A.K. (2010) Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *Journal of Applied Ecology*, **47**, 841–849.
- Javorek, S.K., Mackenzie, K.E. & Vander Kloet, S.P. (2002) Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: *Vaccinium angustifolium*). *Annals of the Entomological Society of America*, **95**, 345–351.
- Kammerer, M.A., Biddinger, D.J., Rajotte, E.G. & Mortensen, D.A. (2016) Local plant diversity across multiple habitats supports a diverse wild bee community in Pennsylvania apple orchards. *Environmental Entomology*, **45**, 32–38.
- Kembel, S.W., Cowan, P.D., Helmus, M.R. *et al.* (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
- Kleijn, D., Winfree, R., Bartomeus, I. *et al.* (2015) Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, **6**, 7414.
- Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. & Tscharntke, T. (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 303–313.
- Klein, A.-M., Brittain, C., Hendrix, S.D., Thorp, R., Williams, N. & Kremen, C. (2012) Wild pollination services to California almond rely on semi-natural habitat. *Journal of Applied Ecology*, **49**, 723–332.
- Kremen, C., Williams, N.M., Aizen, M.A. *et al.* (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, **10**, 299–314.
- MacKenzie, K.E. & Eickwort, G.C. (1996) Diversity and abundance of bees (hymenoptera: Apoidea) foraging on highbush blueberry (*Vaccinium corymbosum* L) in Central New York. *Journal of the Kansas Entomological Society*, **69**, 185–194.
- Magurran, A.E. (2004) *Measuring Biological Diversity*. Blackwell, U.K.
- Matteson, K.C., Ascher, J.S. & Langellotto, G.A. (2008) Bee richness and abundance in New York city urban gardens. *Annals of the Entomological Society of America*, **101**, 140–150.
- Michener, C.D. (2007) *The Bees of the World*. The Johns Hopkins University Press, Baltimore, Maryland.
- Michener, C.D., McGinley, R.J. & Danforth, B.N. (1994) *The Bee Genera of North and Central America*. Smithsonian Institution Press, Washington, District of Columbia.
- Mitchell, T.B. (1960) *Bees of the Eastern United States*, Vol. 1. Technical Bulletin No. 141. North Carolina Agricultural Experiment Station, Raleigh, North Carolina.
- Mitchell, T.B. (1962) *Bees of the Eastern United States*, Vol. 2. Technical Bulletin No. 152. North Carolina Agricultural Experiment Station, Raleigh, North Carolina.
- O'Connor, R.S., Kunin, W.E., Garratt, M.P.D. *et al.* (2019) Monitoring insect pollinators and flower visitation: the effectiveness and feasibility of different survey methods. *Methods in Ecology and Evolution*, **00**, 1–12.
- Ollerton, J., Winfree, R. & Tarrant, S. (2011) How many flowering plants are pollinated by animals? *Oikos*, **120**, 321–326.
- Paradis, E. & Schliep, K. (2018) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, **35**, 526–528.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010) Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, **25**, 345–353.
- Pratt, C. (1988) Apple flower and fruit: morphology and anatomy. *Horticultural Reviews* (ed. by J. Janick), pp. 273–308. Timber Press, Portland.
- R Development Core Team (2017) *R: A language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Austria Version 3.2.4. <http://www.R-project.org/R> [accessed 13 April 2017].
- Ratti, C.M., Higo, H.A., Griswold, T.L. & Winston, M.L. (2008) Bumble bees influence berry size in commercial *Vaccinium* spp. cultivation in British Columbia. *Canadian Entomologist*, **140**, 348–363.
- Rehan, S.M. & Sheffield, C.S. (2011) Morphological and molecular delineation of a new species in the *Ceratina dupla* species-group (hymenoptera: Apidae: Xylocopinae) of eastern North America. *Zootaxa*, **2873**, 35–50.
- Revell, L.J. (2012) Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.
- Rhoades, P., Griswold, T., Waits, L., Bosque-Pérez, N.A., Kennedy, C.M. & Eigenbrode, S.D. (2017) Sampling technique affects detection of habitat factors influencing wild bee communities. *Journal of Insect Conservation*, **21**, 703–714.
- Rogers, S.R., Tarry, D.R. & Burrack, H.J. (2014) Bee species diversity enhances productivity and stability in a perennial crop. *PLoS ONE*, **9**, e97307.
- Russo, L., Park, M., Gibbs, J. & Danforth, B. (2015) The challenge of accurately documenting bee species richness in agroecosystems: bee diversity in eastern apple orchards. *Ecology and Evolution*, **5**, 3531–3540.
- Selfridge, J.A., Frye, C.T., Gibbs, J. & Jean, R.P. (2017) The bee fauna of inland sand dune and ridge woodland communities in Worcester County, Maryland. *Northeastern Naturalist*, **24**, 421–445.
- Sheffield, C.S., Kevan, P.G., Pindar, A. & Packer, L. (2013) Bee (hymenoptera: Apoidea) diversity within apple orchards and old fields in the Annapolis Valley, Nova Scotia, Canada. *Canadian Entomologist*, **145**, 94–114.
- Sheffield, C.S., Frier, S.D. & Dumes, S. (2014) *Biodiversity and Systematics Part 2, Arthropods of Canadian Grasslands*, Vol. 4 (ed. by D. J. Giberson and H. A. Cárcamo), pp. 427–467. Biological Survey of Canada, Ottawa, Canada.
- Simpson, E.H. (1949) Measurement of diversity. *Nature*, **163**, 688.
- Tscharntke, T. & Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology*, **49**, 405–430.
- Tucker, E.M. & Rehan, S.M. (2016) Wild bee pollination networks in northern New England. *Journal of Insect Conservation*, **20**, 325–337.
- Tucker, E.M. & Rehan, S.M. (2017) Wild bee community assemblages across agricultural landscapes. *Journal of Agricultural and Urban Entomology*, **33**, 77–104.
- Tucker, E.M. & Rehan, S.M. (2018) Farming for bees: annual variation in pollinator populations across agricultural landscapes. *Agricultural and Forest Entomology*, **20**, 541–548.
- Tuell, J.K., Ascher, J.S. & Isaacs, R. (2009) Wild bees (hymenoptera: Apoidea: Anthophila) of the Michigan highbush blueberry agroecosystem. *Annals of the Entomological Society of America*, **102**, 275–287.
- United States Department of Agriculture (USDA). (2011) *National Agricultural Statistics Service, Crop Production Annual Summary and Crop Values Annual Summary*. <http://www.nass.usda.gov/Publications/index.asp> [accessed on 15 January 2019].
- Wang, Y., Naumann, U., Wright, S., Eddebuettel, D. & Warton, D. (2012) mvabund-an R package for model-based analysis of multivariate abundance data. *Methods in Ecology and Evolution*, **3**, 471–474.
- Warton, D.I., Wright, S.T. & Wang, Y. (2012) Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution*, **3**, 89–101.
- Webb, C.O. (2000) Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *American Naturalist*, **156**, 145–155.

- Webb, C.O., Ackerly, D.D., McPeck, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.
- Williams, P.H., Thorp, R.W., Richardson, L.L. & Colla, S.R. (2014) *Bumble Bees of North America: An Identification Guide*. Princeton University Press, Princeton, New Jersey.
- Winfree, R., Williams, N.M., Gaines, H., Ascher, J.S. & Kremen, C. (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology*, **45**, 793–802.
- Winfree, R., Fox, J.W., Williams, N.M., Reilly, J.R. & Cariveau, D.P. (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, **18**, 626–635.
- Wolf, A.T. & Ascher, J.S. (2008) Bees of Wisconsin (Hymenoptera: apoidea: Anthophila). *The Great Lakes Entomologist*, **41**, 129–168.
- Wood, T.J., Holland, J.M. & Goulson, D. (2015) A comparison of techniques for assessing farmland bumblebee populations. *Oecologia*, **177**, 1093–1102.
- Woodcock, B.A., Garratt, M.P.D., Powney, G.D. *et al.* (2019) Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield. *Nature Communications*, **10**, 1481.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A. & Smith, G.M. (2009) *Mixed Effect Models and Extensions in R*. Springer, New York, New York.

Accepted 4 February 2020