Effects of Farmland and Seasonal Phenology on Wild Bees in Blueberry Orchards

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Abstract - A diverse wild bee fauna can greatly enhance crop yields, but on-going declines in populations of global pollinators may jeopardize food security in the future. Diversity of wild bees in agricultural settings is shaped by a multitude of factors including farming practice, farm size and surrounding land-use type. However, these factors may vary greatly across regions and agricultural systems, making broad generalizations difficult. Therefore, there is a critical need to describe communities of wild bees in relation to farm size and adjacent land-use type. We collected wild bees using pan trapping and sweep netting throughout the summer season. We compared wild bees among 3 blueberry orchards of varying sizes and percentage of adjacent forest margins. We used complementary metrics to characterize the bee fauna at the species and community level including phylogenetic diversity, functional traits, and indicator species. We found that bee diversity and abundance was highest at the smaller orchard, which had more adjacent forest. A particularly depauperate bee fauna was found at the 2 larger orchards with less adjacent forest. Here, the blueberry-associated bee communities differed markedly among the 3 surveyed orchards. The large and medium orchards harbored clustered communities and had almost no parasitic bees. Our results support the notion that environmental filtering by larger agricultural landscapes act on species and functional traits and can lead to community homogenization. Our study provides the first-of-its-kind data for wild bees in New Hampshire's blueberry orchards. These results can inform farmers about the diversity and pollination services of wild bees and guide implementation of improved management and conservation strategies for the preservation of wild bees in their orchards.

Introduction

Wild pollinators provide critical pollination services in native and agricultural ecosystems, thereby enhancing agricultural crop production with an estimated value for $235–577 billion annually (FAO 2020, Kleijn et al. 2015, Klein et al. 2007, Kremen et al. 2007, Ollerton et al. 2011). Rapid agricultural intensification during the last half century has led to a heightened reliance on pollination services by managed bees, foremost the domesticated *Apis mellifera* L. (Honey Bee), but also *Bombus* (bumblebees), *Megachile* (leafcutter bees), or *Osmia* (mason bees), due to their easy deployment during crop-flowering times (Klein et al. 2007, Potts et al. 2010). However, in recent decades, domesticated bee colonies have shown drastic reductions in numbers and performance, due to stress, diseases, and parasites (Brown et al. 2016, Goulson et al. 2015, Potts et al. 2010, van Engelsdorp

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et al. 2008). This decline led to increased research interest in assessing wild bees as alternative pollinators for crops in farms and orchards.

Biodiversity is multidimensional; it encompasses taxonomic, phylogenetic, and functional diversity (Naeem et al. 2016). Agricultural landscapes in northeastern North America harbor a diverse and locally distinct wild bee fauna (Bushmann and Drummond 2015, Dibble et al. 2017, Gardner and Ascher 2006, Gibbs et al. 2017, Russo et al. 2015, Sheffield et al. 2013, Tuell et al. 2009, Winfree et al. 2008). Improved crop productivity and fruit set have been linked to wild bee species richness (Campbell et al. 2017, Klein et al. 2012), abundance (Isaacs and Kirk 2010), phylogenetic diversity (Grab et al. 2019), and functional trait diversity (Blitzer et al. 2016). Nonetheless, only a very few dominant species in the community provide the majority of the crop-pollination services, and these vary across space and time (Kleijn et al. 2015; Winfree 2019; Winfree et al. 2011, 2015). This situation makes it difficult to generalize across a broad range of agricultural systems and necessitates the characterization of wild bees at a local scale.

Agricultural farming practices can affect the wild bee fauna in a variety of ways. An organic farming approach that generally cultivates mixed crops in small stands interspaced with semi-natural areas and wild flower plantings can foster a diverse bee community (Kennedy et al. 2013, Kleijn et al. 2015, Tscharntke and Brandl 2004, Winfree et al. 2011). Conventional farming practices that typically convert heterogeneous landscapes to cultivate crops in large stands using agrochemicals can lead to a species-poor wild bee fauna (Bartomeus et al. 2013, Goulson et al. 2015, Klein et al. 2007, Potts et al. 2010, Tscharntke and Brandl 2004) with diminished phylogenetic diversity (Grab et al. 2019, Hendrix et al. 2018) and reduced bee abundance (Odanaka and Rehan 2019; Tucker and Rehan 2017, 2018). However, some taxa are more prone to suffer declines or be extripated from an area than others, which is most likely due to their life-history traits (Bartomeus et al. 2013, Grab et al. 2019, Harrison et al. 2018). Thus, using functional traits and indicator species can reveal important information on relationships between species and their habitat (De Caceres and Legendre 2009). Indicator species, which are sensitive to certain environmental conditions, can be used to assess communities in response to changing environments (Carignan and Villard 2002). Here, we combine phylogenetic with functional trait and indicator species analyses, to characterize the wild bee fauna at 3 blueberry orchards with different farming practices.

Vaccinium corymbosum L. (High-bush Blueberry) is a native crop to North America and grown globally, where acreage in cultivation has increased by 164% during the last decade (DeVetter et al. 2015). The United States is the world largest supplier, growing >249 thousand tons worth $797 million annually and accounting for more than 67% of the global production (Brazelton and Strik 2007, DeVetter et al. 2015, USDA 2019b). In New England, High-bush Blueberry is a locally important fruit crop worth $11.4 million each year (USDA 2019a). Blueberry plants are primarily bee pollinated. Pollinators include wild bee species in the genera *Bombus*, *Andrena*, *Osmia*, and *Lasioglossum* (Javorek et al. 2002, Ratti et al. 2008). Wild bee surveys in blueberry orchards in Maine, Michigan, Nova Scotia, and Vermont revealed that dominant genera in the community varied geographically and included

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Andrena, *Augochlorella, Bombus, Ceratina*, and *Lasioglossum* (Bushmann and Drummond 2015, Isaacs and Kirk 2010, Nicholson et al. 2017, Rogers et al. 2014, Tuell et al. 2009).

This study aimed to characterize the wild bee community at 3 High-bush Blueberry orchards in New Hampshire. We investigated bees throughout the summer season using multiple metrics at 3 orchards that varied in size and adjacent forest cover. We compared bees at the species level using richness and diversity, and at the community level using composition, phylogenetic diversity, functional traits, and indicator species. Based on previous studies, we expected a higher bee diversity (in terms of species, phylogeny, and functional traits) on smaller farms with more adjacent forest.

Methods

Study area

We selected 3 orchards growing predominantly High-bush Blueberry located at least 17 km apart in Strafford County, NH (43.2383° N, 71.0236° W). Orchards differed in size and the percentage of surrounding forest. We calculated the percentage of adjacent forest in the total area encompassed by a 500-m strip around the perimeter of the farm margins by using field observations in conjunction with Google earth maps. The first orchard was relatively small in size (2.8 ha) and surrounded by 90% forest. The medium-sized orchard covered an area of 6.4 ha and had 70% adjacent forest. The largest of our study orchards covered an area of 13.0 ha and was surrounded by 50% forest. The sizes of the selected orchards are at the smaller end of most farms in New Hampshire, which average 12–16 ha (New Hampshire State Council on the Arts 2020).

Bee sampling

We collected bees from 2 May to 29 August 2018 using pans and sweeps in accordance with previously described procedures (Tucker and Rehan 2016). In each orchard, we selected 3 replicate 100-m transects close to the middle of the blueberry fields to collect bees. Per transect, we placed 9 pan traps (7 cm diameter) with alternating colors (blue, yellow, and white) and filled with soapy water on the ground for 8 h during time of highest bee activity (8:00–16:00 h) on warm and low-wind days. We obtained our bee samples by straining the liquid in the traps through a sieve and transferring the retained content into a jar filled with 70% ethanol. We made our bee collections on a weekly base during bloom period (17 to 31 May) and bi-weekly thereafter. Each sampling event per farm consisted of 27 traps. We conducted 12 sampling events: 2 before bloom (2–16 May), 3 during bloom (17–31 May), and 7 after bloom (1 June–29 August), totalling 972 trap samples across the 3 orchards. Some traps were lost due to disturbance, resulting in a total of 765 sampling events (small orchard: $n = 288$, medium: $n = 252$, and large: $n = 225$). In addition, we supplemented pan trapping with sweep netting during bloom in the same transects. We conducted sweeps during midday using collapsible aerial nets (7112CP; Bioquip Products, Compton, CA). To directly collect bees from their

flowers, we performed sweeps by walking the transects along the blueberry bushes for 10 min at 30-sec intervals with pauses of 1 min to transfer netted bees into vials with 70% ethanol and allow disturbed foraging bees to return to flowers.

Bee processing, identification, and functional traits

We processed bees following the procedures described in Droege (2015), where specimens were washed, fluff-dried, and pin mounted. We identified bee species using taxonomic literature (Gibbs 2011; Gibbs et al. 2013; Michener 2007; Mitchell 1960, 1962; Rehan and Sheffield 2011; Williams et al. 2014); specimens are stored in the Rehan Lab at York University. We classified bee species into functional traits that showed ecological relevance in previous studies and are related to nesting habit and social behavior (Ascher et al. 2014, Cane et al. 2007, Giles and Ascher 2006, Matteson et al. 2008, Michener, 2007, Rehan and Sheffield 2011, Selfridge et al. 2017, Sheffield et al. 2014, Wolf and Ascher 2008). We categorized ground- or stem-nesting bees depending on their nest substrate: wood or pithy stems vs. soil. We also classified bees into 4 behavior types in relation to their degree of sociality: solitary (bees living solitary or loosely communal), subsocial (bees showing prolonged parental care [e.g., small carpenter bees]), social (primitively and advanced eusocial bees [*Apis*, *Bombus*, and some Halictidae]), and parasitic (those with a cleptoparasitic lifestyle).

Data analyses

We calculated species richness, diversity, and sampling coverage of the farm-associated bee community using the standardized method of Hill numbers via abundance-based rarefaction and extrapolation (Chao and Jost 2012, Chao et al. 2014) in the package 'iNEXT' (version 2.0.20; Hsieh et al. 2016). We further compared common and unique species and species occurring with 1 or 2 individuals (singletons and doubletons, respectively). This and the following analyses were carried out in R v3.6.1 (R Development Core Team 2019).

We carried out the following statistical analyses with pan-trap samples. We compared bee species richness and abundance among orchards using generalized linear mixed-effect models. Here, we employed the negative binomial distributions for over dispersed data using glmer.nb in 'lme4' (version 1.1-21) with orchards as fixed effects and transects as random effects (Bates et al. 2015, Zuur et al. 2009). We compared bee communities among orchards including: (i) species composition, (ii) functional trait structure, and (iii) phylogenetic diversity. We employed the manyglm function to analyze community composition and functional trait structure using the multivariate extension of generalized linear models based on negative binomial distribution (Warton et al. 2012) in 'mvabund' (version4.0.1; Wang et al. 2012). We used the block function to analyze orchard as fixed effect and transect as random effect. We produced residual vs. fitted value plots to check mean–variance assumptions in the models (Warton et al. 2012). We used the multivariate Wald χ^2 test statistic to evaluate differences among orchards.

We compared phylogenetic community structure among orchards by modifying a published phylogenetic tree that covers >13,000 wasp and bee species

globally (Hedtke et al. 2013). Bee species collected here and not yet contained in the tree ($n = 67$) were added using add.species.to.genus in 'phytools' (version 0.7-70; Revell, 2012). This function binds species at random height to the terminal edge of each corresponding genus on a genus-level backbone tree. We removed any species not found in this study using the function drop.tip in 'ape' (Version 5.0; Paradis and Schliep 2018). The modified tree contained a total of 81 species from 17 genera and 5 families. We then converted it into a distance matrix using the function cophenetic.phylo in 'ape' (Paradis and Schliep 2018), which computes pairwise distances between pairs of tips from a phylogenetic tree using its branch lengths. We analyzed phylogenetic diversity of each community in 'picante' (version8.0; Kembel et al. 2010). We calculated mean pairwise distance (MPD), a measure of branch length for each species in the community, using ses.mpd in R (Webb 2000, Webb et al. 2002). This function detects phylogenetic over-dispersion or clustering in a community, as standardized effect sizes (SES). We calculated SES values by comparing the observed communities at each orchard to randomized ones (= null model) through 999 permutations. Positive SES values indicate evenness, i.e., species are spread randomly across the phylogeny, while negative SES values indicate phylogenetic clustering, i.e., species are closer related than expected. We calculated SES values with and without abundance-weighted criterion, allowing for interpretation of mean phylogenetic distances for abundance and species. We also conducted indicator species analyses for the 3 farms using the function multipatt in 'indicspecies' (Version 1.6; De Caceres and Jansen 2016). Using abundance data, this measure generates lists of species that are particular to focal groups.

We assessed seasonal variation in the bee fauna by classifying sampling time into 3 periods based on blueberry bloom: pre-bloom, bloom, and post-bloom as defined above. We designated the start of bloom as the date when >5% of flowers in the field had first come into bloom, and end of bloom as the date when <5% of the flowers remained in bloom. We analyzed seasonal differences in numbers of bee species and abundance using mixed effect models based on negative binomial distributions using glmer.nb in 'lme4', with seasons as fixed factors and transects in orchards as random variables (Bates et al. 2015, Zuur et al. 2009). We analyzed seasonal differences in community composition and trait structure turnover using manyglm (Warton et al. 2012) in 'mvabund' (Wang et al. 2012). We used the block function to analyze season as a fixed effect and transects in orchards as random effects. Statistical differences were evaluated using the multivariate Wald χ^2 test.

Results

From the 3 sites combined, we collected a total of 812 individual bees from 81 species, 17 genera, and 5 families (See Supplemental Fig. S1 and Supplemental Table S1, both available in Supplemental File 1 online at https://www.eaglehill.us/NENAonline/suppl-files//n27-4-N1805-Rehan-s1, and for BioOne subscribers, at https://dx.doi.org/10.1656/N1805.s1); the most abundant family was Apidae ($n = 281$; 35% of total) while the most species rich was Halictidae ($n = 29$; 36% of all

species). The genera *Ceratina*, *Andrena*, and *Lasioglossum* were numerically dominant. The most common species was *Ceratina calcarata* Robertson, comprising 11% of all collected bees. The most frequently collected bees, i.e., occurring in all transects, were *Agapostemon virescens* Fabricius, *Andrena nasonii* Robertson, and *Halictus confusus* Smith. Almost half of the collected species were singletons (n = 21; 26%) or doubletons (n = 16; 20%). Of the 2 sampling methods used, pan traps yielded much higher bee abundance (92%) and species richness (96%). However, sweeps captured 3 additional species not caught in the traps: *Halictus rubicundus* Christ, *Lasioglossum acuminatum* McGinley, and *Xylocopa virginica* L.

Species richness, diversity, and abundance

The blueberry-associated bee fauna was more diverse at the smallest orchard in comparison to the 2 larger orchards, and estimated species richness was lowest at the largest orchard (Table 1, Fig. 1a). Bee abundance was highest at the smallest orchard, and sampling coverage was > 90% for all 3 orchards (Table 1, Fig. 1b). The wild bee fauna at each orchard were comprised of common and unique species: the smallest orchard had the highest proportion of unique species and more singletons and doubletons (Table 1). When unique species occurred, these were generally low in abundance (n < 4), but 2 unique species were collected in May with >10 individuals: *Andrena violae* Robertson, a floral specialist on violets, at the small orchard, and *Andrena barbilabris* Kirby, a solitary generalist, at the medium-sized orchard (Supplemental Table S1). The smallest orchard had twice as many species and over 4x more bees (abundance) than the largest orchard (Fig. 2). These differences were significant among orchards (species: Wald χ^2 = 33.70, P < 0.0001; abundance: Wald χ^2 = 43.34, P < 0.0001; Table 2).

Community structure

Community structure in terms of phylogenetic diversity was significantly more reduced than expected at the 2 larger orchards. MPD calculated among species was

Table 1. Bee species richness, diversity, and abundance at 3 orchards (small, medium and large). Shown are observed species richness; 3 Hill numbers (via abundance-based rarefaction and extrapolation): Chao's estimators for species richness ± standard error (± SE), Simpson's diversity, and Shannon diversity; number of singletons and doubletons; number and percent of common and unique species; bee abundance and percentage of total; and percent sampling coverage.

	Small	Medium	Large
Observed species richness	62	45	31
Estimated species richness ± SE	71.5 ± 7.1	49.5 ± 5.9	35.3 ± 6.8
Simpson's Diversity	18.9	13.9	9.6
Shannon Diversity	28.9	21.2	16.0
Singletons	18	11	10
Doubletons	14	8	6
Common species	31 (50%)	24 (53%)	11 (35%)
Unique species	29 (47%)	13 (29%)	5 (16%)
Abundance	415 (51%)	310 (38%)	87 (11%)
Sampling coverage	96%	97%	90%

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significantly reduced (i.e., reduced phylogenetic distances) at the medium-size and largest orchards (Fig. 3); however, there was no significant difference when abundance-weighted data were used.

The wild bee communities were orchard specific. Composition differed significantly among orchards (Wald χ^2 = 10.80, P < 0.001), as did functional trait structure (Wald χ^2 = 9.62, P < 0.001; Table 3, Fig. 4). Strikingly, the community at the smallest orchard was comprised of significantly more cleptoparasitic bees (12%) than the 2 larger orchards (1% each). The largest orchard had significantly fewer ground-nesting social and solitary as well as stem-nesting subsocial bees (Table 3, Fig. 4). These differences were mainly driven by significantly more cleptoparasitic *Nomada* sp. nr. *maculata*, stem-nesting subsocial *Ceratina dupla* Say*,* and ground-nesting social *Augochlorella aurata* Smith at the smallest orchard. Conversely there were significantly more *Andrena crataegi* Robertson and

Figure 1. Abundance based rarefaction-extrapolation curves at 3 orchards (small, medium, and large). Showing (a) species diversity estimate (Simpson) and (b) sample coverage estimation. Solid lines show interpolated values, shapes show sampling endpoints (observed), and dotted lines show extrapolated values to abundance x2.
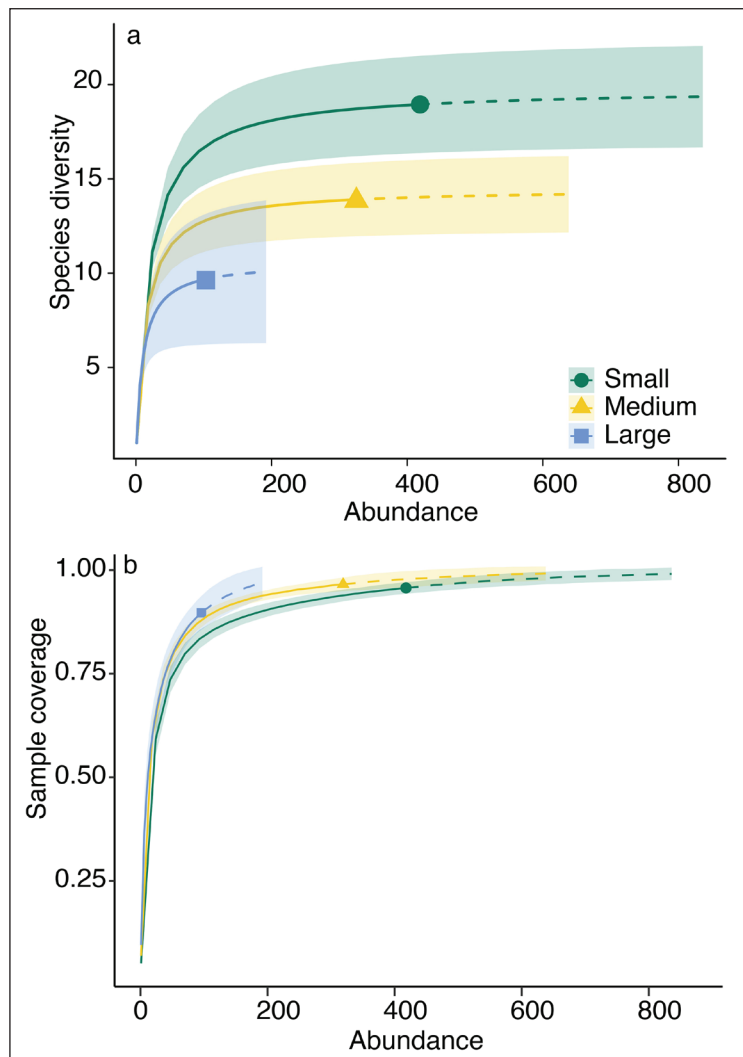
Lasioglossum tegulare Robertson at the medium-sized orchard, and significantly fewer stem-nesting subsocial *C. calcarata*, ground-nesting solitary *A. nasonii,* and ground-nesting social *L. tegulare* at the largest orchard (Supplemental Table S1).

A total of 9 species were found to be indicators of 2 different orchards (Table 4): the smallest orchard (*n* = 3; *A. violae*, *A. aurata*, and *N. maculata*) and
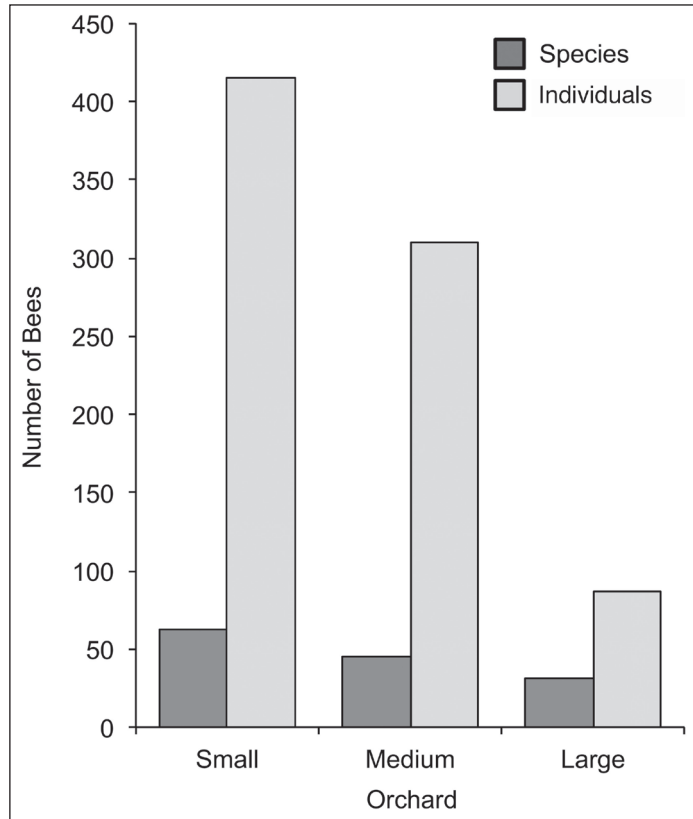

Figure 2. Number of bees (species and individuals) collected from 3 orchards.

Table 2. Summary of mixed-effect negative binomial generalized linear models (glmer.nb) for wild bee species richness and abundance at 3 orchards. Shown are the model coefficient (Estimate), standard error (SE), z value, P value (Pr(>|z|)) of the χ^2 statistic, and Pseudo-R^2 ; number of observations = 85, number of transects = 9.

Contrast	Estimate	SE	z value	Pr(>|z|)	Pseudo-R^2
Species					
Intercept	1.932	0.104	18.557	<0.0001	0.30
Small–medium	0.352	0.159	2.208	0.0699	
Small–large	1.108	0.191	5.803	<0.0001	
Medium–large	0.756	0.201	3.772	0.0005	
Abundance					
Intercept	2.490	0.136	18.325	<0.0001	0.33
Small–medium	0.149	0.200	0.745	0.7369	
Small–large	1.446	0.230	6.290	<0.0001	
Medium–large	1.297	0.237	5.483	<0.0001	

the medium-sized orchard (*n* = 2; *A. barbilabris* and *A. crataegi*). Additionally, 4 species were found to be shared between the small and medium-sized orchards (*C. calcarata*, *C. dupla*, *L. tegulare*, and *N. armatella* Cockerell). The largest orchard had no indicators.

Phenological comparison

More bees were collected during pre-bloom, than during post-bloom and bloom periods (Fig. 5). Abundance of collected bees was significantly lower during bloom (16%) as compared to before (50%) (Wald χ^2 = 50.258, *P* < 0.0001; Table 5). There were significantly fewer species during pre-bloom than during post-bloom (Wald χ^2

Figure 3. Phylogenetic community structure across orchards, measured as mean pairwise distance (MPD) for abundance using abundance-weighted data (closed symbols) and for species (open symbols). * indicates significantly different from random (*P* < 0.05).
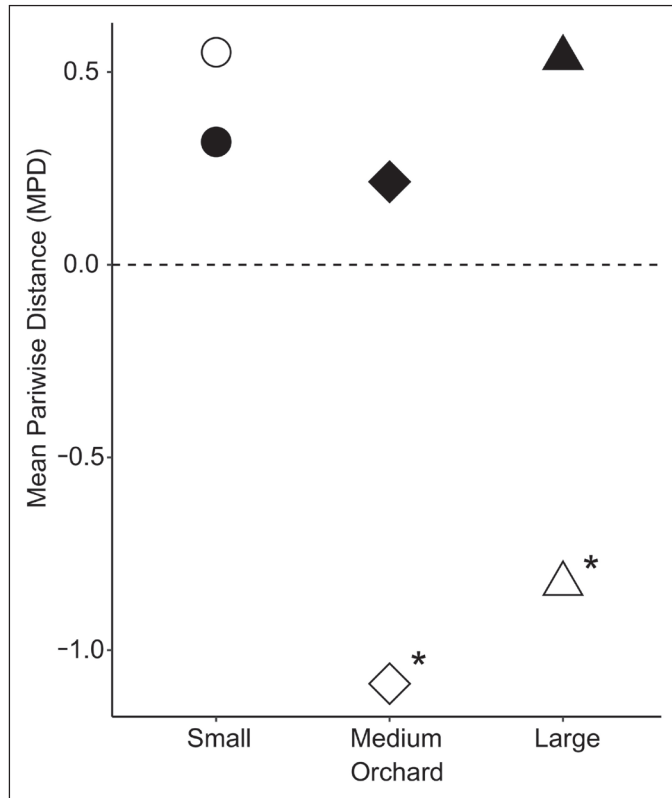

Table 3. Summary of multivariate generalized linear models (manyglm) for bee functional trait structure at 3 orchards (small, medium, large). Shown are the Wald χ^2 test statistic and *P*-value for comparisons between the 3 orchards; number of observations = 85, number of transects = 9. stem nesting social bees have been excluded from pairwise comparisons as these only occurred at the small orchard.

	Small–medium	Small–large	Medium–large
Overall	4.924 (*P* = 0.005)	8.264 (*P* = 0.001)	6.928 (*P* = 0.001)
Cleptoparasitic	4.211 (*P* = 0.002)	4.536 (*P* = 0.001)	1.151 (*P* = 0.154)
Ground-nesting social	1.195 (*P* = 0.229)	4.711 (*P* = 0.001)	3.710 (*P* = 0.001)
Ground-nesting solitary	1.999 (*P* = 0.108)	3.056 (*P* = 0.009)	4.676 (*P* = 0.001)
Stem-nesting solitary	0.635 (*P* = 0.542)	0.035 (*P* = 0.976)	0.562 (*P* = 0.590)
Stem-nesting subsocial	0.826 (*P* = 0.512)	4.023 (*P* = 0.001)	3.274 (*P* = 0.004)

= 19.242, $P < 0.0001$; Table 5). There was a marked seasonal turnover in wild bee community composition (Wald $\chi^2 = 12.2$, $P < 0.001$) and functional trait structure (Wald $\chi^2 = 10.2$, $P < 0.001$; Table 6). Compared to pre-bloom, the post-bloom period had significantly fewer cleptoparasitic *Nomada* sp. nr. *maculata*. During pre-bloom,

Figure 4. Distribution of bee functional traits for nesting habit and social behavior at 3 orchards (small, medium, and large).
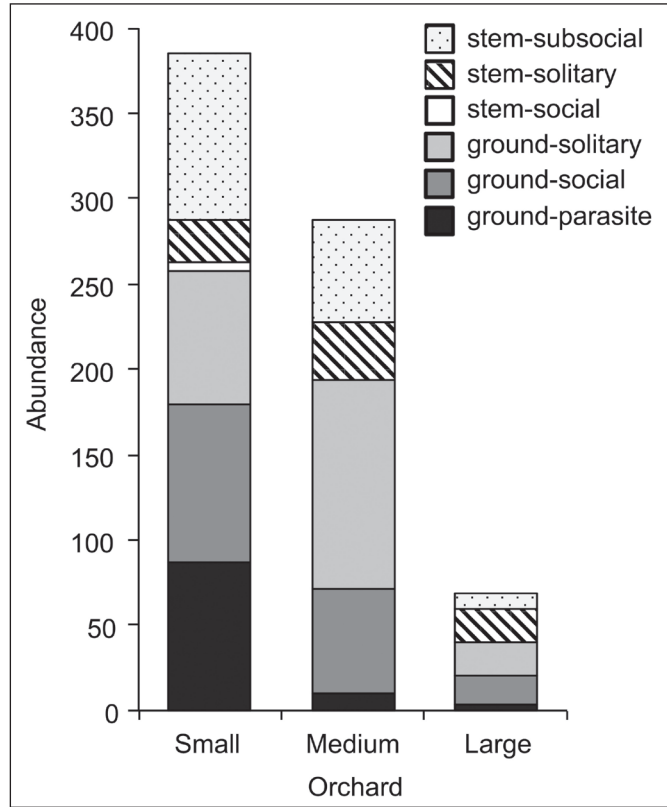
Table 4. Table showing indicator species found at the small, medium, and combination of small and medium-sized orchards. Including information regarding each species' nesting biology, phenology, behavior, and feeding strategy. There were no indicator species for large orchards.

Orchard	Species	Nesting	Phenology	Behavior	Feeding strategy
Small					
	Andrena violae	Ground	March–April	Solitary	Specialist
	Augochlorella aurata	Ground	May–November	Social	Generalist
	Nomada maculata	Ground	March–June	Cleptoparasite	Cleptoparasite
Medium					
	Andrena barbilabris	Ground	April–July	Solitary	Generalist
	Andrena crataegi	Ground	May–July	Solitary	Generalist
Small and medium					
	Ceratina calcarata	Stem	May–August	Social	Generalist
	Ceratina dupla	Stem	May–August	Social	Generalist
	Lasioglossum tegulare	Ground	May–August	Social	Generalist
	Nomada armatella	Ground	May–August	Cleptoparasite	Cleptoparasite

there were significantly more solitary ground-nesting andrenids (*A. crataegi*, *A. nasonii*, and *A. carlini* Cockerell) and solitary stem-nesting megachilids within the genus *Osmia* (Table 6, Fig. 6). During post-bloom, captures had significantly fewer stem-nesting subsocial apids (*C. calcarata* and *C. dupla*). Post-bloom period had significantly more halictids, especially the ground-nesting social bees *Lasioglossum tegulare* and *Augochlorella aurata* (Table 6, Fig. 6).

Discussion

This study describes the wild bee fauna at 3 blueberry orchards of different sizes and surrounding land-use types throughout a single season. As expected, species richness, diversity, and abundance were higher at the smallest orchard, which also had the most adjacent forest. The bee fauna was particularly depauperate at the largest orchard, surrounded by the least amount of adjacent forest. At the community level, there were marked differences among orchards. The smallest orchard harbored a phylogenetically even bee community, while at the medium-sized and largest orchards, communities were phylogenetically more clustered and had almost no parasitic bees. Our results indicate that orchard size and adjacent land-use type affect wild bee communities in New England's blueberry orchards.
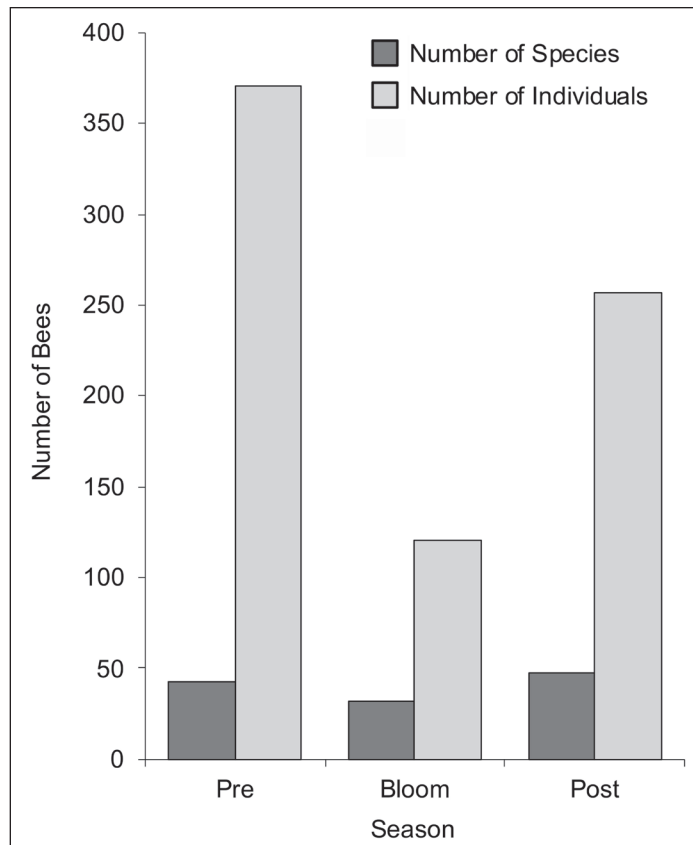

Figure 5. Number of bees (species and individuals) collected in 3 seasons (pre-bloom, bloom, and post-bloom).

Sampling approach and adequacy

Both bee-collection methods combined, pan trapping and sweep netting, delivered a high proportion of the local species pool (>90%) at each of the 3 orchards (Fig. 1). This result compares well to the 88% previously collected from High-bush Blueberry in Michigan (Tuell et al. 2009). Here, the majority of bees were collected using pan traps, (>90% of the species and abundance), while sweeps yielded 3 additional species. These results indicate that sweeps should be used to complement but not replace pan trapping when conducting biodiversity studies (Wilson et al. 2008). Similar to our study, a higher proportion of wild bees were collected with pan traps than hand collecting in *Vaccinium angustifolium* Aiton (Low-bush Blueberry) in Maine (Bushmann and Drummond 2015).

Species richness, diversity and abundance

Wild bees were more diverse and abundant at the smallest orchard with high proportions of adjacent native habitat. This small orchard harbored twice as many species and over 4 times as many bees as the largest study orchard (Fig. 2).

Table 5. Summary of mixed-effect negative binomial generalized linear models (glmer.nb) for (A) species richness and (B) abundance of wild bees at three seasons; before blooming period (pre-bloom), during bloom (bloom) and after blooming period (post-bloom). Shown are the model coefficient (Estimate), standard error (SE), z value, P value (Pr(>|z|)) of the χ^2- Statistic and R^2 (Pseudo-R^2), number of observations = 85, number of transects = 9, number of orchards = 3.

Contrast	Estimate	SE	z value	Pr(>|z|)	Pseudo-R^2
Species richness					
Intercept	1.8561	0.1852	10.023	<0.0001	0.38
Pre-bloom–bloom	-0.3447	0.1843	-1.871	0.0614	
Bloom–post-bloom	-0.3083	0.1730	-1.783	0.0746	
Pre-bloom–post-bloom	-0.6530	0.1491	-4.379	<0.0001	
Abundance					
Intercept	2.6555	0.2362	11.243	<0.0001	0.65
Pre-bloom–bloom	-0.8234	0.2062	-3.993	<0.0001	
Bloom–post-bloom	-0.3417	0.1926	-1.774	0.0760	
Pre-bloom–post-bloom	-1.1651	0.1651	-7.056	<0.0001	

Table 6. Summary of multivariate generalized linear models (manyglm) for bee functional trait structure through the season. Shown are the Wald χ^2 test statistic and P-value for comparisons among the 3 periods: pre-bloom, bloom and post-bloom; number of observations = 85, number of transects = 9, number of orchards = 3.

	Pre-bloom–Bloom	Bloom–Post-bloom	Pre-bloom–Post-bloom
Overall	4.970 (P = 0.002)	4.439 (P = 0.004)	9.901 (P = 0.001)
Cleptoparasitic	2.052 (P = 0.065)	1.494 (P = 0.172)	4.085 (P = 0.001)
Ground-nesting social	0.532 (P = 0.595)	2.685 (P = 0.007)	3.383 (P = 0.003)
Ground-nesting solitary	3.322 (P = 0.003)	0.677 (P = 0.552)	4.911 (P = 0.001)
Stem-nesting solitary	2.505 (P = 0.016)	2.197 (P = 0.047)	5.125 (P = 0.001)
Stem-nesting subsocial	1.700 (P = 0.092)	2.232 (P = 0.033)	4.415 (P = 0.001)

Similar patterns were previously found in *Malus domestica* Borkh. [= *M. pumila* Mill.] (Apple) orchards in New York (Russo et al. 2015) and Pennsylvania (Kammerer et al. 2016), in *Prunus dulcis* (Mill.) D.A. Webb (Almond) fields in California (Klein et al. 2012) and at blueberry farms in Michigan (Isaacs and Kirk 2010). A more encompassing study over 4 years across 40 Low-bush Blueberry sites in Maine (Bushmann and Drummond 2015) found that organic farming practices and the presence of floral resources had positive effects on bees.

Bee communities

The wild bee communities at the 3 blueberry orchards were numerically dominated by 3 genera from different families: *Ceratina* (Apidae)*, Andrena* (Andrenidae), and *Lasioglossum* (Halictidae)*. This finding supports results from previous wild bee surveys conducted over multiple years in blueberry orchards
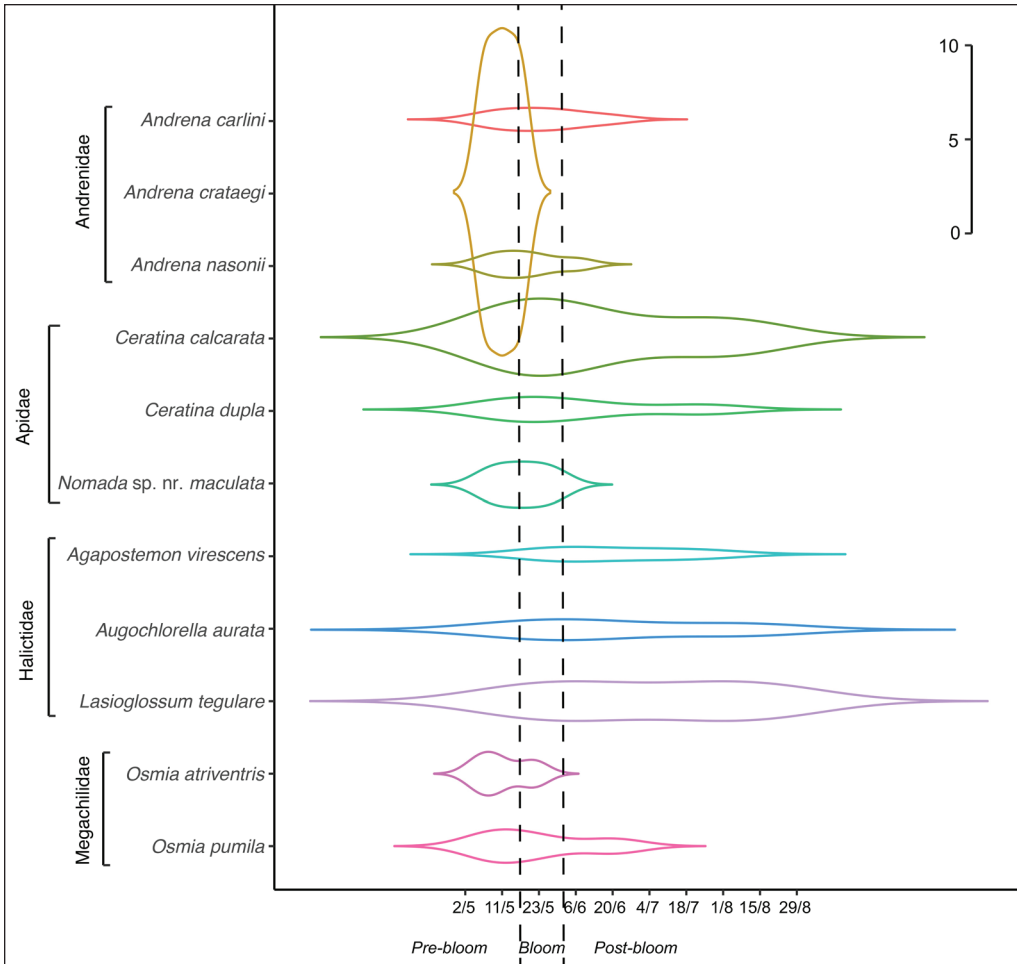

Figure 6. Phenology plot throughout the season (May–August). The 10 most abundant bee species are shown. Length of violin plots represents duration of activity throughout the season, width represents relative abundance (based on all species abundances) and fluctuation over time. Scale bar shows relative abundance.

across the northeastern United States, e.g., in Michigan, New York, and Maine (Bushmann and Drummond 2015, MacKenzie and Eickwort 1996, Tuell et al. 2009). However, our results differ from previously conducted surveys of wild bees in New Hampshire, where the halicitd bees *Agapostemon* and *Augochlorella* were numerically dominant (Tucker and Rehan 2017, 2018). Here, very few (<1%) *Bombus* were collected. This result contrasts sharply to the high abundance of *Bombus* in the blueberry bee community in Maine (Bushmann and Drummond, 2015) and Vermont (Nicholson et al. 2017). Differences could be due to sampling methods, though bees were collected using pan traps (in addition to hand collections) in Maine and with sweep netting in Vermont, methods that we employed. We collected the majority of bees (>90%) using pan-trapping, while sweep netting during bloom resulted in very few bees, of which *Andrena* were the most frequently collected (85%). We found the overall most dominant species was the stem-nesting subsocial bee *C. calcarata*, comprising one-tenth of all collected bees. Similarly, this bee was the most dominant in blueberry (Tuell et al. 2009) and in biofuel crops (Gardiner et al. 2010) in Michigan. *Ceratina calcarata* is a common and widespread bee across North America (Rehan and Sheffield 2011, Shell and Rehan 2016) providing vital pollination services for multiple vegetable and fruit crops (Kennedy et al. 2013).

Dominant species in the communities varied among the 3 orchards. The most abundant bee species was the ground-nesting solitary *Andrena crataegi* in the medium-sized orchard and the stem-nesting solitary megachilid *Osmia atriventris* Cresson in the largest orchard. The cleptoparasitic apid bee *Nomada* sp. nr. *maculata* was predominant in the smallest orchard; these bees parasitize the commonly occurring (17%) andrenid bees (Alexander 1991). The high abundance of cleptoparasitic bees (which represent the topmost trophic layer) in the smallest orchard with most adjacent forest may indicate a more intact ecosystem (Hudson et al. 2006). Previous surveys in blueberry orchards showed a variety of different dominant bees, e.g., the andrenid bees *Andrena bradleyi* Viereck in North Carolina (Rogers et al. 2014) and *A. carlini* in Michigan (Isaacs and Kirk 2010), the apid bee *B. bimaculatus* Cresson in Vermont (Nicholson et al. 2017) and the halictid bee *Lasioglossum cressonii* Robertson in Low-bush Blueberry in Maine (Bushmann and Drummond 2015). Such variations in dominant species in the community reflect the insects' patchy distribution through space and time (Ewers and Didham 2006, Gaston et al. 1997, Tscharntke and Brandl 2004), which is particularly pronounced in fragmented agricultural landscapes with stark local differences in abiotic (climate, surrounding land-use and habitat types) and biotic (competition and parasitism) factors (Diekötter et al. 2008, Tscharntke and Brandl 2004). These findings demonstrate the importance of local wild bee surveys in agricultural systems, as large-scale generalizations are difficult to draw.

The wild bee community composition and trait structure differed markedly among orchards. The smallest orchard harbored 10 times more cleptoparasitic bees than the medium-sized and largest orchards (Fig. 3). Similarly, a higher proportion of cleptoparasites were sampled at less-intensely managed sites at apple farms in Nova Scotia (Sheffield et al. 2013), whereas few were found at conventional fruit orchards in Michigan and New York (Blitzer et al. 2016, Tuell et al. 2009). We found

that all 3 orchards had high proportions of stem-nesting subsocial, ground-nesting solitary, and social bees, which is in line with previous findings in blueberry (Tuell et al. 2009) and Apple (Blitzer et al. 2016, Sheffield et al. 2013) orchards.

The wild bee communities at the medium-sized and largest orchards were distinctly different form the smallest orchard in terms of phylogenetic diversity (Fig. 4). The communities were phylogenetically more clustered, indicating that these were comprised of closer-related species than expected. This finding might be associated with fewer species within the genera *Lasioglossum* and *Nomada* at the medium-sized and largest orchards. Our results support previous findings where phylogenetic diversity of wild bee communities at farms was diminished in response to agricultural intensification (Grab et al. 2019, Hendrix et al. 2018, Odanaka and Rehan 2019).

We identified 9 indicator species. Of these, were 3 were solely associated with the smallest orchard and 4 with the smallest and medium-sized orchards. The species included cleptoparasitic *Nomada*, ground-nesting *Andrena* active during spring*,* and stem-nesting *Ceratina*. None were associated with the largest orchard, which also had the least amount of adjacent forest. It is possible that surrounding forest habitat, which was higher at the smallest and medium-sized orchards, may have affected the presence of these species.

Seasonal variations

Wild bee communities showed a distinct seasonal turnover at all orchards. Almost one half of the total number of individual bees was collected before blueberry bloom in early May, while only one fifth was collected during the 2 weeks of bloom in mid-May and one third in the 2 months after bloom (Fig. 5). The pre-bloom community was dominated by ground nesting solitary andrenid bees (*A. crataegi, A. nasonii*, and *A. carlini*) their cleptoparasites (*Nomada* spp.), and stem/cavity-nesting solitary megachillid *Osmia* spp. (Fig. 6). The stem-nesting subsocial apid bees *C. calcarata* and *C. dupla* were abundant in May, during pre-bloom and bloom*,* and the ground-nesting social halictid bees *Lasioglossum tegulare* and *A. aurata* were abundant after bloom. Seasonal patterns were also found at blueberry farms in Michigan, but surveys there collected the largest proportion of bees during bloom, by using pole-mounted pan traps (Tuell et al. 2009). Differences could be due to the fact that their most abundant bee species, including *Andrena carolina* and *Lasioglossum pilosum*, were collected with low numbers in this study. In our study, pan traps were placed on the ground and supplemented with sweep netting during bloom, which yielded only 7% of the total bees collected during this period. It is possible that pole-mounted pan traps would have resulted in a higher proportion of sampled bees during the bloom period in our study.

Conclusions

Blueberry orchards in southern New Hampshire harbor a diverse and species-rich wild bee fauna, that fluctuates seasonally. Bee communities were orchard-specific and might be associated with local factors, such as orchard size and percentage of adjacent forest. This study provides the first baseline survey data for wild bees

at blueberry agroecosystems in New Hampshire. These data can inform regional farmers about the pollination services provided by wild bees in their orchards and to consider farm size and forest margins for preservation of wild bees in agricultural landscapes.

Acknowledgements

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