

Farming for bees: annual variation in pollinator populations across agricultural landscapes

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- Abstract**
- 1 Wild bees comprise a diverse group of pollinators essential to healthy ecosystems and crop pollination. Despite their importance, the way in which many driving factors affect specific bees or pollinators in specific regions remains unknown. Northern New England is one such place lacking detailed study. Accordingly, we collected bees from three different landscape types for three consecutive years in northern New England.
 - 2 Annual, seasonal and landscape factor affects were examined. We found that season and landscape type significantly influenced the bee community. Bee abundance and species richness were highest during the warmer seasons. At the landscape scale, overall bee abundance and species richness were greatest in the organic farm landscapes and lowest in the meadow landscapes.
 - 3 We also examined the bee community across multiple taxonomic levels: guild, family and species. Wild bee abundance varied significantly depending on the taxonomic level analyzed. Within genera, certain species had significantly higher abundances in meadow type landscapes, whereas other species had higher abundances in the organic or the conventional farm type landscapes.
 - 4 These results support the need for more regionally and taxonomically specific studies on wild bees, their habitat requirements and the influence of environmental factors across agricultural and unmanaged landscapes.

Keywords agricultural land use, Apoidea, ecological associations, New England, New Hampshire, plant–pollinator interactions, wild bees.

Introduction

Land use is one of the leading drivers of wild bee diversity and community structure worldwide, yet the specific effect this factor has on wild bees can be variable and is often regionally and taxonomically specific. Increased land management for agriculture that capitalizes on monocultures and pesticide use generally results in the loss of wild bee nesting habitat and floral resources, ultimately negatively impacting bee diversity (Matson *et al.*, 1997; Tilman *et al.*, 2001; Tschamtkke *et al.*, 2005; Hernandez *et al.*, 2009; Potts *et al.*, 2010; Bartomeus *et al.*, 2013; Vanbergen, 2014; Senapathi *et al.*, 2015). However, some land converted for agricultural use has the opposite effect on pollinators, with increases in both pollinator abundance and richness as a result of increasing overall floral resources and habitat provisions (Pimentel *et al.*, 1992; Jackson & Jackson, 2002; Rosenzweig, 2003; Tschamtkke *et al.*, 2005; Winfree

et al., 2011). Other studies have reported different results, with no significant variation being found among organic farms, conventional farms and naturalized lands (Weibull *et al.*, 2000; Kleijn *et al.*, 2001; Kehinde & Samways, 2012).

Comparisons among conventional farming, organic farming and naturalized land or meadows in both New Hampshire and California found that organic farm landscapes support the greatest abundance and richness of bees (Forrest *et al.*, 2015; Tucker & Rehan, 2017). By contrast, similar studies across Europe have found that farmland supports significantly less bee diversity than nearby natural and semi-natural areas (Goulson *et al.*, 2008; Le Féon *et al.*, 2010, 2013; Potts *et al.*, 2010). The level at which bee diversity is examined also has a great impact on how particular landscapes are evaluated. Not surprisingly, different functional groups, or guilds, have different requirements and can react differently with respect to the same environmental factors (Potts *et al.*, 2005; Moretti *et al.*, 2009; Neame *et al.*, 2013; Sheffield *et al.*, 2013). Bumble bees are often found to be more sensitive to soil disturbance and land use intensification than solitary ground nesting bees (Le Féon

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et al., 2010; but see also Steffan-Dewenter & Tscharnkte, 2001). Stem and ground nesting bees are dependent on available plant materials, habitat composition and land management, whereas parasitic guilds are more greatly affected by host availability and landscape connectivity (Tscharnkte *et al.*, 1998; Steckel *et al.*, 2014; Ullmann *et al.*, 2016). The propensity for guilds to display different trends in abundance and richness in a given landscape extends beyond nesting habit. In a comparison of exotic versus native guilds, the increase in exotic bee species diversity over the last 140 years was in sharp contrast to the decrease in diversity exhibited by native species (Bartomeus *et al.*, 2013). Although many studies examine guild level changes in the bee community to provide a broad overview, research at finer taxonomic levels has revealed the need to examine bees not just at guild or family level, but also at the species level. Species within the same genus can have variable responses to the same anthropogenic drivers (Cariveau & Winfree, 2015). In Sweden, Svensson *et al.* (2000) found that open type habitat was preferred by three *Bombus* species and forest boundaries by two other bumble bee species.

Even when examining bee diversity at the species level within the same sites, there are often annual variations in species composition and seasonal variations within a species driven by biological constraints (Minckley *et al.*, 1999; Price *et al.*, 2005; Grixti & Packer, 2006; Russo *et al.*, 2013; Tucker & Rehan, 2016). Many studies have found annual variations in species composition to be significant, with one 6-year study of a single perennial shrub species by Herrera (1988) reporting that only one-third of pollinators occurred every year and those annual species had highly variable abundances (Petanidou & Ellis, 1993; Steinbach & Gottsberger, 1994; Herrera, 1995; Fishbein & Venable, 1996; Guitián *et al.*, 1996). High seasonal variation in species composition and abundance is also common (Oertli *et al.*, 2005; Tylanakis *et al.*, 2005; Price *et al.*, 2005; Russo *et al.*, 2013; Tucker & Rehan, 2016). With high landscape specificity, ecological fluctuations and species turnover between years and seasons, it is important to conduct regionally specific long-term studies (Oertli *et al.*, 2005; Rollin *et al.*, 2015).

Northern New England contains a great diversity of habitat and landscape types, with farmlands typically surrounded by forested areas, yet it is a region of limited bee research (Koh *et al.*, 2016; Tucker & Rehan, 2016). To help fill this gap in knowledge, we conducted a comprehensive survey of the wild bees in southern New Hampshire comprising three different landscape types repeatedly sampled over a 3-year period. The present study aimed to: (i) characterize bees in multiple landscapes and determine best land management practices, with the hypothesis that moderately managed landscapes positively influence bee species richness and abundance, and (ii) establish how specific groups of bees in this region are affected by landscape, with the hypothesis that heavily managed landscapes would negatively impact ground nesting bees.

Materials and methods

Experimental design

The present study took place in Strafford County, New Hampshire, where we sampled wild bees in the same sites for three consecutive years: from 2014 to 2016. It follows closely the

previous 1-year study by Tucker & Rehan (2017) but adds a significant amount of new data from an additional 2 years of sampling. Nine field sites averaged 80 ha each, were an average distance of 4.5 km apart, and were categorized into three different landscape types: meadow, organic farm or conventional farm. Organic farm sites were composed of regularly mowed (every 4–6 weeks), nonpesticide use land adjacent to forest, as well as strawberry, raspberry and apple crops. Conventional farm sites were also regularly mowed and composed of pesticide use agricultural farmland with apple, squash and melon crops surrounded by forest. Meadow sites were located on former and fallow non-pesticide use farmland composed of naturally occurring plant species (largely native and weedy plants, naturally occurring and not managed by humans) and only mowed once each autumn. Three sites were established for each landscape type, with each site containing three 100-m long sampling transects (totalling nine sampling transects for each landscape type).

Bees were sampled biweekly every year from the end of April through to the end of September using both pan traps and sweep net methods in accordance with previously reported procedures (Tucker & Rehan, 2016). Ten pan traps (diameter 7 cm; 100 mL) of three alternating colours (white, yellow and blue) were set out along each sampling transect and spaced 10 m from the next. Traps were filled with soapy water, set out before 08.00 h and retrieved after 16.00 h. Upon retrieval, traps were emptied through a sieve and placed in a vial of 70% ethanol labelled with collection information. A relatively large area of blooming flowers (spanning ≥ 1 m) was identified at each site and targeted for sweep sampling. Sweep samples were taken from the blooms of flowering plants with collapsible aerial nets (Bioquip 7112CP; Bioquip Products, Rancho Dominguez, California; 30.5 cm in diameter, 12.7 cm in length aluminum handles) on the same days as the pan trapping at between 10.00 h and 14.00 h. Sweep netting was conducted for 5 min at 30-s intervals with pauses of 1 min to transfer specimens to labelled vials containing 70% ethanol and to allow bees to return from disturbance. Flowers sampled were imaged and identified on site in conjunction with Audubon Society's field guide to North American wildflowers (Niering *et al.*, 2001).

Specimen curation and preservation

Bees were processed in accordance with basic procedures described in Droege (2015), pinned, assigned a unique QR code (two-dimensional barcode) identification number and labelled with collection data. Bees were identified to species level using the interactive guides available at Discover Life (www.DiscoverLife.org) and relevant taxonomic literature (Mitchell, 1960, 1962; Michener *et al.*, 1994; Gibbs, 2011, 2012; Rehan & Sheffield, 2011; Williams *et al.*, 2014). Voucher specimens from the present study and associated data are deposited in the University of New Hampshire Insect Collection.

Statistical analysis

Datasets were compiled to examine variation in bee species abundance and richness for annual, seasonal and landscape factors. Seasons were standardized by collection week and defined as 'early-season' (late April–early June), 'mid-season'

(late June–early August) and ‘late-season’ (early August–late September). Landscape factors were categorized as specified in the experimental design: ‘organic farm’, ‘contemporary farm’ and ‘meadow’. Datasets were compiled for all bees combined, as well as at the family, guild and species (those with 100+ specimens collected) levels. Nesting habit was used to define guilds: stem nesters, ground nesters and kleptoparasites. Network datasets were based solely on sweep net data (as floral interactions are required) and analyzed for each annual, seasonal and landscape factor.

All statistical analyses were performed using R software (R Core Team, 2015) and associated packages. Annual, seasonal and landscape effects were analyzed with Poisson distribution generalized linear models using the R packages ‘ggfortify’ (Horikoshi & Tang, 2015) and ‘multcomp’ (Hothorn *et al.*, 2008). Analyses with significant results were analyzed with a post-hoc Tukey’s test to determine sources of significant differences. Network analyses were analyzed at both the community (function *networklevel*; Dormann *et al.*, 2009) and species (function *specieslevel*; Dormann, 2011) level using the R package ‘bipartite’ (Dormann *et al.*, 2008). At the community level, weighted nestedness (WN), weighted connectance (WC) and community size (bee + plant species) were calculated and examined to evaluate ecosystem structure and durability (Dunne *et al.*, 2002; Galeano *et al.*, 2009). Nestedness measures the overlap in generalist and specialist interactions, with values closer to ‘1’ indicating that the community is highly nested and values close to ‘0’ indicating communities with little interaction overlap. Connectance measures the number of potential interactions in a community compared with those actually used, where 1 = all possible interactions used and 0 = all species interactions unique. At the species level degree, weighted degree (WD; diet breadth) and Pollination Service Index (PSI) were calculated and examined to evaluate the importance of each species in a system (Dormann *et al.*, 2008). PSI measures the relative importance of each species in the community, where essential species = 1 and species functionally replaceable by another species = 0. Species coexistence and exclusivity in relation to annual, seasonal and landscape factors were visualized using the interactive tool VENNY (Oliveros, 2007).

Results

In total, 9105 bees representing 209 species in five families were collected over the 3-year period. Bee abundance was significantly highest mid-season when temperatures are at their warmest ($\chi^2 = 1487.7$; d.f. = 2; $P < 0.001$) (Fig. 1). Community structure analyses also indicated the preference for warmer temperatures overall with weighted nestedness peaking mid-season, weighted connectance dipping and the overall community size greatly increasing mid-season (Table 1).

Landscape effects

Bee abundance was significantly affected by landscape type ($\chi^2 = 1060.9$; d.f. = 2; $P < 0.001$) (Fig. 2). Post-hoc analyses examining landscape treatment effect revealed that organic farm landscapes had significantly more bees than either conventional

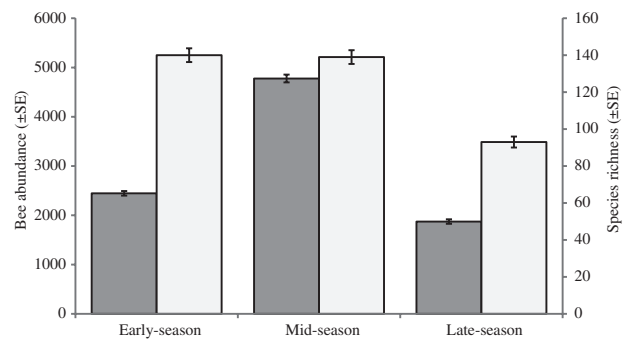


Figure 1 Graph showing bee abundance and richness relative to season ($n = 9$ samples per season). Season significantly affected bee abundance based on generalized linear model (GLM) results (dark grey bars) with a post-hoc analysis showing that abundance was significantly greatest mid-season. Species richness was also significantly affected by season based on GLM results (light grey bars) with a post-hoc analysis showing that early and mid-season was significantly higher than late-season.

farm or meadow landscapes ($\chi^2 = 1060.9$; d.f. = 2; $P < 0.001$). Somewhat surprisingly, meadow landscapes had the lowest bee abundance, although this was not significantly lower than conventional farm landscapes. Bee richness was also significantly affected by landscape type and followed a trend similar to that of bee abundance ($\chi^2 = 55.7$; d.f. = 2; $P < 0.001$) (Fig. 2). Of the 209 species documented, 38% (81 species) were found in all landscapes. Post-hoc analyses showed that organic farm landscapes had significantly more bee species than the other two landscape types, whereas meadow landscapes had significantly less species compared with the other two landscapes. In addition to having the greatest abundance and richness of bees, community level statistics revealed that organic landscapes had the highest weighted nestedness, as well as the greatest floral richness (Table 1). Meadow landscapes had the lowest weighted nestedness and, despite having slightly more floral species than conventional farm landscapes, meadow landscapes had the overall smallest total community size (Table 1).

Effects on specific bees

Landscape type significantly affected bee abundance ($\chi^2 = 1060.9$; d.f. = 2; $P < 0.001$), although the resulting effect was different depending on the specific guild examined (Fig. 3A). Post-hoc analyses examining landscape effects on specific guilds revealed that ground nesting bees had significantly higher abundance in organic landscapes and, in contrast to expectations, a significantly lower abundance in meadow landscapes ($\chi^2 = 1348.0$; d.f. = 2; $P < 0.001$). Kleptoparasitic bees followed this pattern, with an abundance significantly lower in meadows than in the other two landscapes ($\chi^2 = 16.5$; d.f. = 2; $P < 0.001$). Stem nesting bees followed a different pattern, with post-hoc analyses showing a significantly reduced abundance in conventional farm landscapes ($\chi^2 = 107.9$; d.f. = 2; $P < 0.001$). The proportion of bees representing specific guilds corroborates the total abundance estimates in each landscape. Ground nesters comprised 50% of all bees in organic farm landscapes compared with 28% and 22% of bees in conventional farm and

Table 1 Results of community network analyses based on sweep net samples

Effect	Weighted nestedness	Weighted connectance	Number of bee species	Number of plant species	Total community size
Early-season	0.56	0.08	72	21	93
Mid-season	0.59	0.06	96	36	132
Late-season	0.52	0.08	49	18	67
Conventional farm	0.48	0.06	71	18	89
Meadow	0.43	0.07	53	20	73
Organic farm	0.61	0.05	105	38	143

Highest values (relative to communities sampled) for each factor and variable evaluated are shown in bold.

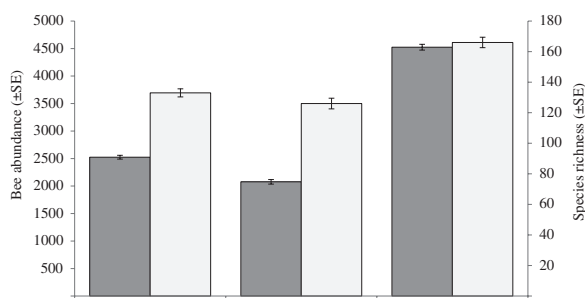


Figure 2 Graph showing bee abundance and richness relative to landscape ($n = 12$ samples per landscape). Landscape significantly affected bee abundance based on generalized linear model (GLM) results (dark grey bars) with a post-hoc analysis showing that abundance was significantly greatest in the organic farm landscape. Species richness was also significantly affected by landscape based on GLM results (light grey bars) and followed the same trend as abundance with a post-hoc analysis showing that richness was significantly greatest in the organic farm landscape.

meadow landscapes. Kleptoparasitic bees represented 16% of bees in meadow landscapes compared with 42% and 43% in conventional and organic farm landscapes. Conventional farm landscapes had a much lower representation of stem nesting bees (19%) than the meadow and organic farm landscapes (37% and 44%, respectively).

Landscape type had significant and variable effects not only on overall bee abundance, but also among bee families ($\chi^2 = 863.0$; d.f. = 8; $P < 0.001$) (Fig. 3B). Halictidae dominated all landscapes, representing 71–81% of all bees collected. Apidae was the next most abundant, representing 11–20% of bees collected followed by Andrenidae (3–5%) and Megachilidae (2–5%), and then Colletidae, which was consistently least abundant with 1% of all bees. Organic landscapes had significantly greater numbers of Andrenidae ($\chi^2 = 68.195$; d.f. = 2; $P < 0.001$), Apidae ($\chi^2 = 323.270$; d.f. = 2; $P < 0.001$) and Halictidae ($\chi^2 = 808.020$; d.f. = 2; $P = 0.001$) than meadow or conventional farm landscapes. Megachilidae had a significantly greater abundance in meadow landscapes than in conventional farm landscapes ($\chi^2 = 9.860$; d.f. = 2; $P = 0.007$). Conversely, significantly lower abundances of Apidae were found in conventional farm landscapes and significantly lower abundances of Andrenidae in meadow landscapes than in other landscapes (Fig. 3B).

Bee species, even within the same genera, varied significantly in landscape abundance. We evaluated bees that had at least 100 specimens collected because these bees are likely to have high

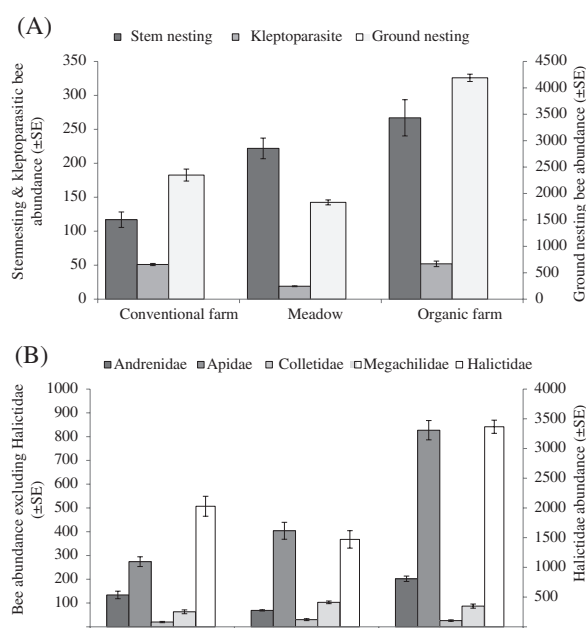


Figure 3 (A) Landscape significantly affected abundance of stem nesters based on generalized linear model (GLM) results (dark grey bars), kleptoparasites (medium grey bars) and ground nesters (light grey bars) ($n = 4$ samples per guild per landscape). (B) Landscape significantly affected the abundance of Andrenidae, Apidae, Halictidae and Megachilidae, although Colletidae was relatively rare with no detectable difference among landscapes ($n = 3$ samples per family per landscape).

impact on the community in addition to ensuring an adequate sample size. Most bee species examined had significantly higher abundances in organic farm landscapes, including four species of *Lasioglossum* [*Lasioglossum leucomomum* (Lovell, 19008) $\chi^2 = 543.53$; d.f. = 2; $P < 0.001$; *Lasioglossum leucozonium* (Schrank, 1781) $\chi^2 = 86.058$; d.f. = 2; $P < 0.001$; *Lasioglossum pilosum* (Smith, 1853) $\chi^2 = 880.55$; d.f. = 2; $P < 0.001$; *Lasioglossum tegulare* (Robertson, 1890) $\chi^2 = 173.52$; d.f. = 2; $P < 0.001$] (Table 2). By contrast to the trend exhibited by most bees, three species of *Lasioglossum* had significantly higher abundance in meadow landscapes [*Lasioglossum coriaceum* (Smith, 1853) $\chi^2 = 43.373$; d.f. = 2; $P < 0.001$; *Lasioglossum cressonii* (Robertson, 1890) $\chi^2 = 30.727$; d.f. = 2; $P < 0.001$] (Table 2) and one species in conventional farm landscapes [*Lasioglossum admirandum* (Sandhouse, 1924) $\chi^2 = 141.43$; d.f. = 2; $P < 0.001$] (Table 2). Bee species abundance varied not only among landscape types, but also annually and seasonally and significantly so. Although overall bee abundance was

Table 2 Bee abundance significantly varied by landscape, year and season

Species	Landscape			Year			Season		
	Meadow	Organic	Conventional	2014	2015	2016	Early	Mid	Late
<i>Agapostemon virescens</i>	282* (14%)	600 (13%)	672 (27%)	410* (18%)	544 (17%)	601 (17%)	441 (18%)	665* (14%)	449 (24%)
<i>Augochlorella aurata</i>	189 ^a (9%)	357 ^b (8%)	254 ^c (10%)	161* (7%)	297 (9%)	342 (9%)	341 (14%)	355 (7%)	104* (6%)
<i>Bombus bimaculatus</i>	27 (1%)	98* (2%)	20 (1%)	48 (1%)	38 (2%)	59 (1%)	26 (1%)	92* (2%)	27 (1%)
<i>Bombus impatiens</i>	198 ^a (10%)	382 ^b (8%)	146 ^c (6%)	423* (18%)	156 (5%)	147 (4%)	27 ^a (1%)	358 ^b (7%)	341 ^c (18%)
<i>Ceratina calcarata</i>	50 (2%)	69 (2%)	23* (1%)	33 ^a (1%)	49 ^{ab} (2%)	60 ^b (2%)	57 (2%)	47 (1%)	38 (2%)
<i>Halictus confusus</i>	52* (3%)	88 (2%)	90 (4%)	24* (1%)	104 (3%)	102 (3%)	31 (1%)	173* (4%)	26 (1%)
<i>Halictus ligatus</i>	39 ^a (2%)	509 ^b (11%)	101 ^c (4%)	310* (14%)	188 (6%)	151 (4%)	99 ^a (4%)	413 ^b (9%)	137 ^c (7%)
<i>Lasioglossum admirandum</i>	24 ^a (1%)	2 ^b (<1%)	104 ^c (4%)	21 (1%)	35 (1%)	74* (2%)	45 (2%)	67 (1%)	18* (1%)
<i>Lasioglossum coriaceum</i>	169* (8%)	77 (2%)	87 (3%)	65 (3%)	187* (6%)	81 (2%)	179 ^a (7%)	102 ^b (2%)	52 ^c (3%)
<i>Lasioglossum cressonii</i>	127 ^a (6%)	83 ^b (2%)	54 ^c (2%)	67 ^a (3%)	114 ^b (4%)	83 ^{ab} (2%)	84 ^a (3%)	142 ^b (3%)	38 ^c (2%)
<i>Lasioglossum leucocomum</i>	2 ^a (<1%)	317 ^b (7%)	28 ^c (1%)	2 ^a (<1%)	205 ^b (6%)	140 ^c (4%)	93 ^a (4%)	240 ^b (5%)	14 ^c (1%)
<i>Lasioglossum leucozonium</i>	63 (3%)	180* (4%)	60 (2%)	44 ^a (2%)	72 ^b (2%)	187 ^c (5%)	45 ^a (2%)	173 ^b (4%)	85 ^c (5%)
<i>Lasioglossum pilosum</i>	3 ^a (<1%)	541 ^b (12%)	68 ^c (3%)	92 ^a (4%)	173 ^b (5%)	347 ^c (10%)	184 ^a (8%)	357 ^b (7%)	71 ^c (4%)
<i>Lasioglossum tegulare</i>	62 ^a (3%)	289 ^b (6%)	119 ^c (5%)	69 ^a (3%)	160 ^b (5%)	271 ^c (7%)	82 ^a (3%)	316 ^b (7%)	102 ^c (5%)
<i>Lasioglossum versatum</i>	311 ^a (15%)	20 ^b (<1%)	150 ^c (6%)	85 ^a (4%)	262 ^b (8%)	134 ^c (4%)	63 ^a (3%)	400 ^b (8%)	18 ^c (1%)

Different factors influenced closely-related bees within the same genus differently. Only species with ≥ 100 specimens collected over the 3-year study are shown. Values in columns represent the absolute bee abundance for a particular factor. Asterisks and superscript letters indicate significant differences between treatments based on a post-hoc analysis. Values in parentheses are the proportion of all bees for a given factor that each species represents (i.e. in the 'Mid-Season' column for *A. virescens*, there were 665 specimens collected, representing 14% of all bees collected mid-season, and this abundance was significantly higher than early- and late-seasons).

significantly greatest in 2016 ($\chi^2 = 1060.9$; d.f. = 2; $P < 0.001$), *Bombus impatiens* Cresson, 1863 and *Halictus ligatus* Say, 1837 had significantly higher abundances in 2014 and represented a much greater proportion of the bees sampled (*B. impatiens* $\chi^2 = 188.88$; d.f. = 2; $P < 0.001$; *H. ligatus* $\chi^2 = 61.683$; d.f. = 2; $P < 0.001$) (Table 2). The greatest annual bee abundance and overall proportion of individuals also varied significantly within the genus *Lasioglossum* by species (Table 2). Variation in seasonal abundance of pooled years was more conservative, with mid-season almost always containing the highest absolute and relative bee abundance (Table 2). *Ceratina calcarata* Robertson, 1900 and *L. coriaceum* were the exception, with a higher absolute and proportional abundance early-season, which corresponded to an unusually high overall bee abundance during the 2015 early-season (35% of all bees compared with 21% in 2014 and 23% in 2016) (Table 2). Although some species abundance was found to have relatively consistent phenological patterns across years, most species exhibited considerable variation in seasonal abundance among years (Table 3). These differences in annual and seasonal phenology do not appear to be directly related to local weather, despite 2016 being significantly drier than the New Hampshire 30-year average.

Discussion

The present study aimed to evaluate the bee community, characterize bees in multiple landscapes, and establish how specific bees were affected by landscape and season in the New England region. We found that moderately managed landscapes positively influenced the bee community. We did not find any significant support for heavily managed landscapes (conventional farms) negatively affecting ground nesting bees in this region. However, we did find that specific bees varied greatly depending on the group or taxonomic level examined.

Table 3 Annual seasonal variation in top five most abundant species (≥ 600 specimens) collected

	2014	2015	2016
<i>Agapostemon virescens</i>			
Early-season	60	212	169
Mid-season	171	237	257
Late-season	179	95	175
<i>Augochlorella aurata</i>			
Early-season	81	146	114
Mid-season	50	117	188
Late-season	30	34	40
<i>Bombus impatiens</i>			
Early-season	8	15	4
Mid-season	218	72	68
Late-season	197	69	75
<i>Halictus ligatus</i>			
Early-season	32	52	15
Mid-season	217	110	86
Late-season	61	26	50
<i>Lasioglossum pilosum</i>			
Early-season	39	70	75
Mid-season	45	100	212
Late-season	8	3	60

Abundance for each species is coloured by year, with darker colours indicating greater abundances and lighter colours indicating lower abundances.

Landscape effects

In the present study, moderately managed organic farm landscapes supported overall larger and more diverse bee communities than either the more naturalized or heavily managed landscapes. The combined effect of no pesticide use at the

organic farm sites and semi-regular mowing produced the most florally diverse landscapes of all those that we surveyed. Our finding of greater species abundance and richness in organic farm landscapes compared with conventional farm and meadow landscapes is similar to a comparable study conducted in California (Forrest *et al.*, 2015). The present study provides additional support for increased landscape heterogeneity positively influencing overall wild bee diversity and often being more influential than specific landscape or farm type (Tscharntke *et al.*, 2012; Kennedy *et al.*, 2013; Le Féon *et al.*, 2013; Steckel *et al.*, 2014; Moreira *et al.*, 2015; Kammerer *et al.*, 2016; Mallinger *et al.*, 2016). In addition to the greater variety of floral resources and habitat available, more heterogeneous landscapes can stabilize the pollinator community by lessening the impact of temperature fluctuations as found in a study conducted by Papanikolaou *et al.* (2017) on temperature and precipitation effects with respect to wild bee abundance in Germany.

Effects on specific bees

We found that landscape significantly affected bee diversity, although there were highly variable effects depending on the guild, family or species examined. We had expected ground nesting bees to prefer the meadow landscape because it had the least disruption of soil and potential habitat. By contrast to our hypothesis, we found ground nesting bee abundance to be lowest in undisturbed meadow landscapes and highest in managed organic farm landscapes, which is similar to the results of a study by Forrest *et al.* (2015). This may be because undisturbed and overgrown vegetation limits the amount of exposed bare ground, which was reported to strongly influence ground nesting bees (Petanidou & Ellis, 1996; Potts *et al.*, 2005). Kleptoparasitic bees were also uncommon in meadow landscapes, both in terms of absolute and relative abundance, which lends support to studies showing that kleptoparasite diversity is often more greatly influenced by host availability than landscape type (Sheffield *et al.*, 2013; Steckel *et al.*, 2014). Although some studies have not found consistent patterns in bee guilds and landscapes, we provide additional evidence showing that landscape type significantly influences the abundance of nesting guilds found across habitats (Steffan-Dewenter *et al.*, 2002; Cane *et al.*, 2006; Burkle *et al.*, 2013).

Not only did landscape type influence the abundance of bee guilds differently, but also it affected species in the same genus differently, in agreement with the findings of a Swedish study on bumble bees (Svensson *et al.*, 2000). In our examination of the most abundant species across sampled landscapes, the most common species, which included four species of *Lasioglossum*, preferred the more heterogeneous organic farm landscapes. However, three other species of *Lasioglossum* strongly preferred meadow landscapes and one species significantly preferred conventional farm landscapes. These species also displayed significant annual variations in absolute and relative abundance, unlike the overall trends observed across all bee species (Table 2) (Herrera, 1988, 1995; Petanidou & Ellis, 1993; Steinbach & Gottsberger, 1994; Fishbein & Venable, 1996; Guitián *et al.*, 1996). Although variations in abundance between years and seasons as a result of the unique biology of each species might

be expected, the inconsistencies in phenological patterns across years in highly abundant species is somewhat unexpected and currently lacks explanation (as has been found in some other studies: Minckley *et al.*, 1999; Steffan-Dewenter *et al.*, 2002; Price *et al.*, 2005; Grixti & Packer, 2006; Cariveau *et al.*, 2013; Russo *et al.*, 2013; Cariveau & Winfree, 2015; Tucker & Rehan, 2016).

Conclusions

Understanding how wild bees respond to ever changing environments is critical for future sustainable agriculture and conservation efforts. Certain functional groups or specific species may react differently compared with the general New England bee community. We found that habitat heterogeneity and increased floral diversity to generally promote wild bee diversity, although this varied among species. Although most studies have found that increased landscape heterogeneity and floral diversity positively impacts bee diversity, not all regions or bee taxa respond the same, making the present study an important contribution to future species monitoring efforts (Steffan-Dewenter, 2003). Our data broadly suggest the need to maintain as much floral and habitat diversity in the landscape as possible to benefit the greater bee community in New England and beyond. However, if the conservation of a species or specific group that is at a higher risk of decline is the goal, the complexity of interacting factors and requirements unique to that species or group must be considered separately from the overall bee population.

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