

# Wild Bee Community Assemblages Across Agricultural Landscapes

Author(s): Erika M. Tucker and Sandra M. Rehan Source: Journal of Agricultural and Urban Entomology, 33(1):77-104. Published By: South Carolina Entomological Society <u>https://doi.org/10.3954/1523-5475-33.1.77</u> URL: <u>http://www.bioone.org/doi/full/10.3954/1523-5475-33.1.77</u>

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## Wild Bee Community Assemblages Across Agricultural Landscapes<sup>1</sup>

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J. Agric. Urban Entomol. 33: 77-104 (2017)

**ABSTRACT** Wild bees are essential to the functioning of both agricultural and natural ecosystems, yet these pollinator communities are declining worldwide. Agricultural intensification by means of habitat and floral resource loss is thought to be one of the leading causes of wild bee population deterioration. This study examined multiple agricultural land use systems in New Hampshire to determine how wild bee biodiversity and community interactions are affected by different land use practices. A total of 2292 wild bees were collected during these surveys, representing 112 species. A high species overlap was found at all land use systems, although all sites had some species exclusivity. Land use significantly affected species abundance and richness. The moderately managed sites supported both the greatest pollinator abundance and species richness, while the low management sites had the smallest abundance and the same level of richness as the high management sites. The findings of this study support the importance of floral landscape diversity in bee conservation efforts and suggest that not all agricultural practices negatively affect the pollinator community.

**KEY WORDS** Apoidea, ecological associations, New England, New Hampshire, plant-pollinator interactions, agricultural land use

One of the primary factors contributing to the decline of wild bee population levels is the loss of habitat for nesting sites and foraging grounds in response to agricultural intensification (Matson et al. 1997, Tilman et al. 2001, Tscharntke et al. 2005, Hernandez et al. 2009, Potts et al. 2010, Bartomeus et al. 2013, Vanbergen 2014, Senapathi et al. 2015). Agricultural intensification is an increase pesticide use, in agricultural land cover per unit space, or both. Intensification of the same kind of land cover often produces monocultures, which reduces both diversity and resource availability leading to lower pollinator richness and abundance (Matson et al. 1997, Potts et al. 2010, Bartomeus et al. 2013, Senapathi et al. 2015). The use of chemicals to control pest insects and undesirable plants in intensively managed systems is also high, negatively affecting pollinators by reducing potential forage as well as adversely altering prospective nesting sites (Hernandez et al. 2009, Potts et al. 2010).

The negative impact of agricultural intensification, its associated practices and the resulting landscape fragmentation, on biodiversity is supported by many

<sup>&</sup>lt;sup>1</sup>Accepted for publication 25 August 2017.

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studies (Robinson & Sutherland 2002, Tscharntke et al. 2005, Hernandez et al. 2009, Weiner et al. 2014). For example, studies in North American watermelon fields and tropical rainforests indicate negative impacts on bee abundance and species richness with the introduction of agricultural practices using pesticides (Kremen et al. 2002, Cairns et al. 2005, Kennedy et al. 2013). Studies on farms across Europe showed decreases in wild bee biodiversity compared to nearby natural and semi-natural areas as agricultural practices in non-mass flowering crops and animal production increased (Goulson et al. 2008, Le Féon et al. 2010, 2013, Potts et al. 2010). While much research supports this outcome, other studies have found contradictory results and there is a growing body of literature with findings suggesting that lands used for agricultural purposes support enhanced pollinator biodiversity compared to non-managed areas (Pimentel et al. 1992, Jackson & Jackson 2002, Rosenzweig 2003, Tscharntke et al. 2005, Winfree 2011).

Examples of agriculture increasing biodiversity in an ecosystem include, agroforestry areas and open cacao field systems (Hoehn et al. 2010). Organic farming techniques are often touted as supporting higher biodiversity than conventional practices (Holzschuh et al. 2007, Kovács-Hostyánszki et al. 2011). However, several studies have found no significant benefits of less managed agricultural farms, or organic farms, compared to conventional farming or naturalized lands (Weibull et al. 2000, Kleijn et al. 2001, Kehinde & Samways 2012). Research on pollinators and their services in vineyard settings also found organic management to have no positive effect on insect communities (Brittain et al. 2010, Bruggisser et al. 2010, Kehinde & Samways 2012).

There are, however, other factors to consider when evaluating the impact of habitat disturbance and agricultural land use practice. Belfrage et al. (2005) found farm size to be more influential than organic versus conventional practices in predicting species diversity and abundance. Many of these responses appear to be dependent on the system or region studied as well as the reference system to which practices are compared (Hernandez et al. 2009, Hoehn et al. 2010, Weiner et al. 2014). Floral diversity and abundance are also keys in determining bee community composition (Gathmann et al. 1994, Tscharntke et al. 1998, Hostetler & McIntyre 2001, Steffan-Dewenter & Tscharntke 2001, Carvell 2002, Potts et al. 2003, Gill et al. 2013, Rutgers-Kelly & Richards 2013, Ellis & Barbercheck 2015), which may be a more important factor in determining the bee community than specific agricultural practices.

The wild bee community is a complex system with the varied responses to agricultural influences requiring in-depth regionally relevant research before adequate bee conservation strategies can be successfully implemented (Potts et al. 2003, Hole et al. 2005, Kehinde & Samways 2012, Gill et al. 2016). Reconstructions of plant-pollinator networks can help in understanding complex communities (Grass et al. 2013, Weiner et al. 2014, Tucker & Rehan 2016). The interactions between plants co-occurring with pollinators form networks that determine the structure on the community, which when evaluated, provide information on pollinator floral preferences and habitat as well as identifying keystone species (Bartomeus et al. 2013, Burkle et al. 2013, Grass et al. 2013, Russo et al. 2013, Senapathi et al. 2015, Wright et al. 2015). This information can be used to ascertain system vulnerabilities and requirements needed for community, species, or interaction preservation (Montoya et al. 2006, Grass et al. 2013, Weiner et al. 2014, Tucker & Rehan 2016).

The northern New England area has a vast diversity of natural habitats intermixed with many farmlands of varying agricultural practices and management intensity. Previous research in northern New England has found that the pollinator community is likely to have high regional specificity requiring research into agricultural effects on bees in this area (Tucker & Rehan 2016). Modeling of historic wild bee population records and land use practices across the United States has also identified New England as a region with limited data, in need of further research on land management in relation to pollinator communities (Koh et al. 2016). With the wide diversity of bee community responses to agricultural practices in different locations, it is essential to research as many farming ecosystems and practices in different regions as possible to best understand how to conserve and promote wild bee populations. Additional regional specific research is also needed to evaluate how different agricultural land use affects bee biodiversity and community structure.

There are 113 bee species known to southern New Hampshire (Tucker & Rehan 2016). Our study aims to evaluate how agricultural practices affect wild bee communities by, 1) determining the variation in bee abundance and diversity across three land use types, 2) assessing bee community stability of plant-pollinator interactions among multiple landscapes to determine which are the most robust, and 3) identifying agricultural land practices most sustainable for wild bees in New Hampshire. This research will ultimately provide information essential to wild bee conservation efforts.

### **Materials and Methods**

**Experimental design.** Three agricultural land use types were chosen in Strafford County, New Hampshire, and categorized as conventional, organic and meadow systems. Each site averaged 200 acres and distance between sites averaged 4.5 km apart. Three replicate sites for each land use type were established for sampling. Within each replicate site bees were actively sampled along three 100-m long transects (for a total of nine sampling transects per land use type).

Meadow sites were located on former farmland that were mowed once each fall and composed only of naturally-occurring plant species. We considered naturally occurring plant species to be plants not purposely planted by humans. These consisted largely of native and weedy like flowers such as *Rudbeckia*, *Solidago*, and *Trifolium* species. The organic farm sites were located on non-pesticide use farmland adjacent to forestland. Sites were actively mowed every 4–6 wk. These sites were adjacent crops of strawberries, raspberries and apples. The conventional farm sites were located on pesticide use, agricultural farmland surrounded by woodlands. Transects were adjacent to apple orchard, and squash and melon crops. All sites were surrounded by extensive forestland.

Biweekly sampling over a total of 11 weeks in 2014 began the last week of April and continued through the end of September. Both pan trapping and sweep netting methods were used. Twenty-seven sampling transects (3 land use types  $\times$  3 replicates per land use type  $\times$  3 transects per replicate site) were used for pan trapping. Transects comprised 10 pan traps (7 cm diameter) of 3 alternating colors

(yellow, blue and white), each set 10 m from the next. Pan traps were positioned before 0800 hours, filled with soapy water and retrieved after 1600 hours. As trap contents were obtained, they were emptied through a small sieve to be deposited in a vial of 70% ethanol labeled with collection information.

Standardized sweep net sampling was also conducted, with a collapsible aerial net (Tucker & Rehan 2016), to collect bees from blooms of flowering plants. Dense patches of flowers present at each site (i.e., we did not plant flowers to sample) and spanning at least 1 m were identified and targeted for sweep samples. On the same days as pan trapping, flower species from each site were sampled for 5 min in 30-s intervals with 1-min pauses between to allow for bees to return from disturbance. Flowering plant species were sweep sampled between 1000 and 1400 hours. Flowers were imaged and identified in the field using field guides (Niering et al. 2001). The specimens from sweep sampling were placed in vials of 70% ethanol labeled with collection information.

**Specimen curation and preservation.** Voucher specimens of all species and associated data used for this study were deposited in the University of New Hampshire Insect Collection (Durham, NH). Bee specimens were pinned, given a unique barcode and identification number, and labeled with location, date, collection method and floral host where relevant. All specimens were subsequently identified to species using the interactive identification guides (Ascher et al. 2017) and recent taxonomic literature (Mitchell 1960, 1962, Gibbs 2011, Rehan & Sheffield 2011, Michener et al. 1994, Williams et al. 2014).

**Bee abundance and species richness analyses.** Datasets were compiled for both bee abundance and species richness to examine variation among management types, seasons, and replicate sites. Collection seasons were defined as early = April–May, mid = June–July, and late = August–September. Flower and bee species unique to each management system, unique to each site within a management system, common to all management systems and common to all sites in all management systems were determined. The flower dataset only contained sweep net sample data, and the bee datasets specific to sites within a land use type only contained pan trap sample data. Sweep net and pan trap samples were analyzed as separate datasets, as well as one combined dataset.

All statistical analyses were preformed using the software program SPSS Statistics (IBM Corp. 2016). Ordinal logistic generalized linear models (GLM) tests were conducted on each dataset. Land use type and season were used as predictor variables and used to build main effects in the model. Post-hoc Tukey HSD analyses were subsequently performed to determine the source of significant differences. To estimate the 'true' species richness of the bee communities sampled and determine how well each landscape type was sampled a rarefaction test conducted with a Chao-1 estimate (Chao 1984, 1987, Colwell & Coddington 1994), an ACE and ACE-1 estimate (Chao & Lee 1992) and Jackknife estimate (Burnham & Overton 1978, 1979) using the R 'SPECIES' package (Wang 2011) for each landscape type.

**Plant-pollinator analyses.** There was no flower data associated with samples from the pan traps; therefore, plant-pollinator networks were based solely on data from the sweep net samples. Separate datasets were constructed for each of the three management types and for each management type by season (early, mid and late season). The R package 'bipartite' was used to construct interaction networks (Memmott 1999, Dormann et al. 2008, 2009). The function *plotweb* was

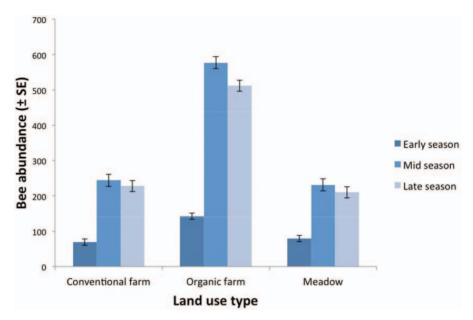
used to evaluate community interactions and produce a visual representation of the network (Tylianakis et al. 2007). To determine whether species were relatively independent of each other or dependent on keystone species, and to evaluate the stability and robustness of the plant-pollinator community, interaction network statistics were calculated using the function *networklevel* (Dormann et al. 2009). To identify the most influential participants in each community and evaluate individual bee and flower species contributions, statistics were calculated using the function *specieslevel* (Dormann et al. 2009).

Weighted nestedness and connectance were examined at the community level. Community patterns of species co-occurrence and biome structure were measured by considering interaction frequencies using weighted nestedness (Galeano et al. 2009), where chaotic interactions = 0 (no overlap between generalist and specialist species) and completely nested = 1 (generalist and specialist interactions completely overlap). Complexity and durability of a community to species loss was measured by connectance (Dunne et al. 2002) to evaluate the proportion of possible interactions actually achieved, where all possible interaction between species used = 1 (all bee species visit all flowers and system is relatively robust to species loss) and no interactions between species = 0 (only one bee species visits each flower and each flower is only pollinated by that one species so the system is greatly affected by individual species loss). We also examined the Pollination Service Index (PSI) normalized degree, and degree at the species level. Degree measures the unique interactions per individual species or species diet breadth (number of pollinator species per flower or number of floral hosts per bee). For unbiased comparisons between species a relative measure was used, normalized degree, which scales the species degree to the number of possible pairings between species. The relative importance of each pollinator (or pollen source) was measured with PSI (Dormann et al. 2008), where pollinator services essential to the functioning of the ecosystem = 1 and pollinator services unimportant for a functioning ecosystem = 0.

#### Results

Bee abundance. A total of 2292 bee specimens were recorded, with 541 from conventional farm (40 Andrenidae, 105 Apidae, 3 Colletidae, 383 Halictidae and 10 Megachilidae), 520 from meadow (28 Andrenidae, 198 Apidae, 5 Colletidae, 272 Halictidae and 17 Megachilidae), and 1231 from organic farm (67 Andrenidae, 332 Apidae, 6 Colletidae, 813 Halictidae and 13 Megachilidae) landscapes. Across all sites, 290 bee specimens were recorded from early season, 1052 from mid-season, and 950 from late season (Figure 1). Bee abundance was significantly different among land use types in the pan trap samples ( $\chi^2 = 9.385$ , df = 2, P = 0.009) and sweep net samples ( $\chi^2 = 12.029$ , df = 2, P = 0.002). Post-hoc comparisons indicate that the mean abundance in the organic farm sites was significantly greater than those in conventional farm (P = 0.006) and meadow (P = 0.029) in the sweep samples.

Bee abundance was significantly different among land use types ( $\chi^2 = 17.32$ , df = 2, *P* = 0.0002) and seasons ( $\chi^2 = 11.59$ , df = 2, *P* = 0.003) in the combined samples. Post-hoc comparisons of land use types indicate the mean abundance in



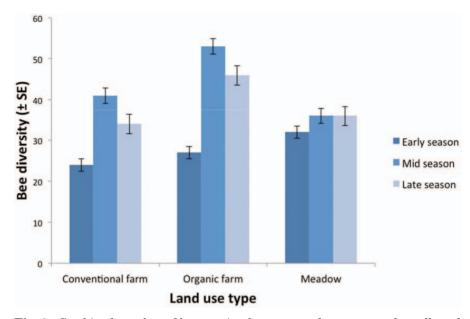
**Fig. 1.** Combined number of bee specimens from pan and sweep samples collected from each land use type by season. The organic farm land had significantly more bee abundance across all seasons. Across all land use types, there were significantly more bees collected mid-season.

the organic farm sites was significantly greater than those in meadow (P = 0.001) and conventional farm sites (P = 0.001). Post-hoc comparisons of seasons indicate the mean abundance in the mid-season was significantly greater than that in the early season (P = 0.032).

**Species richness.** A total of 112 bee species were recorded across all land use types, with 66 from the conventional farm sites (15 Andrenidae, 16 Apidae, 2 Colletidae, 26 Halictidae and 7 Megachilidae), 67 from the meadow sites (17 Andrenidae, 12 Apidae, 2 Colletidae, 29 Halictidae and 7 Megachilidae), and 78 from the organic farm sites (22 Andrenidae, 13 Apidae, 3 Colletidae, 32 Halictidae and 7 Megachilidae).

The rarefaction estimate of sampling completeness, using the ACE test lower bound, estimates true species richness to be 88 species for conventional farm (76% sampling effectiveness), 83 species for meadow (80%), and 87 species for organic farm (87%) sites. Other species richness tests provided similar species diversity estimates for the three landscape types (Chao = 86, 87, 85 species; ACE-1 = 96, 88, 89 species; Jackknife = 120, 92, 89 species). The overall estimate of sampling completeness for all farms was 83% of species sampled (ACE = 136 species; Chao = 140; ACE-1 = 144; Jackknife = 156).

Among land use types, 54 bee species were collected from early season, 75 from mid-season, and 60 from late season (Figure 2). Bee species richness was not significantly different in either the pan trap (land use:  $\chi^2 = 2.732$ , df = 2, P = 0.255; season:  $\chi^2 = 0.592$ , df = 2, P = 0.744) or sweep samples (land use:  $\chi^2 = 2.732$ , df =



**Fig. 2.** Combined number of bee species from pan and sweep samples collected from each land use type by season. Bee species richness was significantly greater on the organic farm land, while season had no significant impact on bee species richness.

2, P = 0.255; season:  $\chi^2 = 0.592$ , df = 2, P = 0.744). It was, however, significantly different in the combined dataset among land use types ( $\chi^2 = 8.774$ , df = 2, P = 0.012), but not significantly different among seasons ( $\chi^2 = 4.118$ , df = 2, P = 0.128). Post-hoc comparisons of land use types indicate the mean species richness in the organic farm sites was significantly greater than those in other land use types (conventional farm sites: P = 0.023; meadow sites: P = 0.047).

**Common and rare species.** Species reoccurrence and unique associations were determined for each of the different land use types as well as for each of the sites within a land use type. There were 34 bee species found in all land use types, 13 species in all conventional farm sites, 8 species in all meadow sites, and 16 species in all organic farm sites (Table 1). The most common bee species were Agapostemon virescens (F.) (Hymenoptera: Halictidae), Augochlorella aurata (Smith) (Hymenoptera: Halictidae), Bombus impatiens Cresson (Hymenoptera: Apidae), Lasioglossum coriaceum (Smith) (Hymenoptera: Halictidae), and Lasioglossum versatum (Robertson) (Hymenoptera: Halictidae), which were found at all sites on all land use types. Conversely, 15 bee species were exclusively found at conventional farm sites, 16 only at meadow sites, and 21 unique to organic farm sites (Table 2). In the pan trap samples from all land use types, 40 species were found to be unique to one land use type, with 32 of those species only represented by single occurrence specimens.

Flower species were more land use specific. Only three flower species were found at all land use types: *Taraxacum* sp. (dandelion), *Trifolium repens* (white

On all land use types	All conventional farm sites	All meadow sites	All organic farm sites
Agapostemon texanus	Agapostemon	Agapostemon	Agapostemon texanus
Agapostemon virescens	virescens Andrena asteris	virescens Augochlorella	Agapostemon
Andrena carlini	Augochlorella aurata	aurata Bombus impatiens	virescens Augochlorella aurata
Andrena cressonii	Bombus impatiens	Lasioglossum admirandum	Bombus impatiens
Andrena dunningi	Halictus confusus	Lasioglossum coriaceum	Calliopsis andreniformis
Andrena nivalis	Halictus ligatus	Lasioglossum cressonii	Halictus confusus
Andrena wilkella	Lasioglossum admirandum	Lasioglossum laevissimum	Halictus ligatus
Anthidium oblongatum	Lasioglossum coriaceum	Lasioglossum versatum	Lasioglossum coriaceum
Augochlorella aurata	Lasioglossum fuscipenne		Lasioglossum cressonii
Augochloropsis metallica	Lasioglossum leucozonium		Lasioglossum fuscipenne
Bombus bimaculatus	Lasioglossum nymphaearum		Lasioglossum laevissimum
Bombus impatiens	Lasioglossum pectorale		Lasioglossum leucozonium
Bombus vagans	Lasioglossum versatum		Lasioglossum pilosum
Calliopsis andreniformis			Lasioglossum tegulare
Ceratina calcarata			Lasioglossum versatum
Ceratina dupla			Peponapis pruinosa
Ceratina mikmaqi			
Halictus confusus			
Halictus ligatus			
Hylaeus affinis Lasioglossum admirandum Lasioglossum albipenne Lasioglossum coriaceum			
Lasioglossum cressonii			
Lasioglossum fuscipenne			
Lasioglossum laevissimum			
Lasioglossum leucozonium			
Lasioglossum lineatulum			
Lasioglossum nymphaearum	ļ.		
Lasioglossum pilosum			
Lasioglossum tegulare			
Lasioglossum versatum			
Osmia inermis			
0 1 1 1			

Table 1. List of the most commonly found species and site specificity.

Osmia inspergens

Conventional farm only	Organic farm only	Meadow only	Only in 1 site (pan trap samples)	Single occurrence species (pan trap samples)
Andrena carolina Andrena confederata Andrena fragilis Andrena hilaris Andrena regularis Anthidium manicatum Hylaeus annulatus Lasioglossum coeruleus Megachile relativa Melissodes desponsus Melissodes trinodis Nomada bella Nomada bella Nomada tiftonensis Sphecodes minor	Andrena alleghaniensis Andrena bisalicis Andrena bisalicis Andrena frigida Andrena geranii Andrena aesonii Andrena nasonii Andrena nasonii Anthophora terminalis Hylaeus mesillae Hylaeus modestus Lasioglossum bruneri Lasioglossum heterognathum Lasioglossum heterognathum Lasioglossum truncatum Lasioglossum truncatum Lasioglossum truncatum Lasioglossum truncatum Lasioglossum truncatum Peponapis pruinosa	Andrena erythronii Andrena krigiana Andrena krigiana Andrena simplex Bombus fervidus Bombus perplexus Calliopsis nebraskensis Colletes inæqualis Lasioglossum atvoodi Lasioglossum imitatum Nomada florilega Osmia cornifrons Osmia georgica Osmia taurus Sphecodes levis	Andrena alleghaniensis Andrena bisalicis Andrena braccata Andrena carolina Andrena carolina Andrena arythronii Andrena ressonii Andrena frigida Andrena geranii Andrena nasonii Andrena nasonii Andrena vilkella Andrena vilkella Andrena vilkella Andrena uvilkella Andrena uvilkella Andrena seranii Anthidium manicatum Bombus fervidus Bombus griseocollis Colletes inaequalis Heriades carinata Hylaeus annulatus Lasioglossum atwoodi	Andrena alleghaniensis Andrena bisalicis Andrena erythronii Andrena fragilis Andrena fragilis Andrena geranii Andrena nasonii Andrena nosertsonii Andrena robertsonii Anthidium manicatum Bombus fervidus Colletes inaequalis Hylaeus annulatus Colletes inaequalis Hylaeus annulatus Lasioglossum heterograthum Lasioglossum heterograthum Lasioglossum truncatum Lasioglossum truncatum Lasioglossum truncatum

Table 2. List of the most uncommon bee species and site specificity.

Conventional farm only	Organic farm only	Meadow only	Only in 1 site (pan trap samples)	Single occurrence species (pan trap samples)
	$Sphecodes\ clematidis$		Lasioglossum cinctipes	Melissodes desponsus
			Lasioglossum coeruleus	Melissodes trinodis
			Lasiogiossum neterognatnum Lasioglossum oblongum	Nomada betta Nomada florilega
			Lasioglossum truncatum	Nomada tiftonensis
			Lasioglossum zonulum	Osmia cornifrons
			Megachile centuncularis	Osmia georgica
			Megachile relativa	Osmia taurus
			$Melissodes\ desponsus$	Sphecodes autumnalis
			$Melissodes\ trinodis$	Sphecodes levis
			Nomada bella	Sphecodes minor
			Nomada florilega	
			Nomada tiftonensis	
			Osmia cornifrons	
			Osmia georgica	
			Osmia taurus	
			Sphecodes autumnalis	
			Sphecodes levis	
			$Sphecodes\ minor$	
			Xylocopa virginica	

Table 2. Continued.

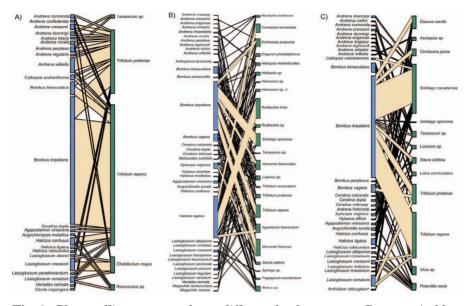
At conventional farm sites only	At meadow	At organic	At all sites on
	sites only	farm sites only	all land use types
Chelidonium majus Ranunculus sp.	Lonicera sp. Daucus carota Asclepias sp. Centaurea jacea Solidago canadensis Silene latifolia Vicia sp. Lotus corniculatus Potentilla recta	Rudbeckia sp. Asclepias tuberosa Rudbeckia hirta Coreopsis lanceolata Echinacea purpurea Hieracium sp. Heliopsis sp. Lupinus sp. Rubus sp. Trifolium incarnatum Vernonia fasciculata Agastache foeniculum Monarda fistulosa Erigeron philadelphicus Heliopsis helianthoides Salvia patens Hieracium sp. 2 Fagopyrum esculentum Syringa sp.	Taraxacum sp. Trifolium repens Trifolium pratense

 Table 3. List of the most uncommon and common flower species and site specificity.

clover) and *Trifolium pratense* (red clover). Most of the flowers (73%) sampled were distinct among land use types (Table 3), with 2 species unique to conventional farm sites, 9 species found only at meadow sites, and 19 species exclusive to organic farm sites.

**Plant-pollinator interactions.** Plant-pollinator networks were constructed for each land use type (meadow, organic and conventional farms; Figure 3) as well as for the three seasons (early, mid, late) within each land use type. Although weighted nestedness was similar in all three land use types, the rest of the community composition changed among land use types varying in size (number of species), interactions and connectance (Table 4). The community composition was largest at organic farm sites with 38 bee species and 23 plant species. Weighted nestedness (species co-occurrence) was greatest in both conventional and organic farm sites (0.42), while connectance (resilience to species loss) was greatest in conventional farm sites (0.32). This indicates the plant-pollinator community is at its most complex at the conventional and organic farm sites and when community size is at its lowest in conventional farm sites it is also most robust and resilient to species loss.

Within each land use type, community composition varied by season, but seasonal variations in community composition within each land use type were similar to the seasonal variations observed in each of the other land use types (with the exception of conventional farm sites, where the community size was too small early and late season to accurately calculate all community statistics as indicated by N/A; Table 5). All land use types had the largest community size mid-season,



**Fig. 3.** Plant pollinator networks at different land use types. Bees are in blue on the left and flowers are in green on the right with number of interactions indicated by the breadth of the tan connections: A) conventional farm sites with 129 bees collected and total community size of 24 bee and 5 plant species, B) organic farm sites with 524 bees collected and a total community size of 39 bee and 23 plant species, C) meadow sites with 206 bees collected and a total community size of 33 bee and 13 plant species.

but organic farm and meadow had highest weighted nestedness in late season (0.90 and 0.59, respectively) and highest connectance early season (0.57 and 0.50, respectively).

**Keystone pollinators and host plants.** We used three species level network measures to assess the importance of individual bees (Table 6) at each land use type: degree (number of species associated with), normalized degree, and PSI. For conventional farm sites we found three bee species to be the most important pollinators, possibly keystone species in this habitat. Lasioglossum cressonii (Robertson) (Hymenoptera: Halictidae) and L. versatum had the broadest floral host breadth with the highest number of unique flower species interactions (3), and *B. impatiens* had the highest PSI value (0.68), which is likely due to its high abundance (70). At meadows, only one *B. impatiens* may be considered a keystone species. In this habitat, it is the most influential pollinator with highest abundance (123), floral host breadth (10) and PSI value (0.72). At organic farm sites, two bees were instrumental to the structure of the community. Bombus impatiens was most fundamental to the community with the most abundance (195), while Halictus ligatus Say (Hymenoptera: Halictidae) had the broadest floral breadth (16) and highest PSI (0.77). The organic farm sites had the highest number (59%)of generalist pollinators, categorized herein as a species associated with more than one flower species, contributing to the community. Generalist pollinators at Table 4. Community level statistics. High values from this study in bold. Statistics from previous studies evaluating overall community networks are included for comparison. N/A indicate unavailable data or statistics.

Land use type	Weighted nestedness	Connectance	Number of bee species	Number of plant species	Unique species interactions	Total community size
Conventional farm	0.42	0.32	24	Ð	38	29
Organic farm	0.42	0.13	38	23	111	61
Meadow	0.39	0.14	33	13	62	46
Previous studies						
Seacoast NH (Tucker & Rehan 2016)	0.51	0.09	63	34	197	66
Agricultural farm PA (Russo et al. 2013)	N/A	0.16	64	25	261	89
Forest/grassland CO (Clements & Long 1923)	0.59	0.07	83	93	536	176
Deciduous forest NC (Motten 1982)	0.48	0.25	35	13	143	48
Woodland IL (Schemske et al. 1978)	0.61	0.29	23	9	40	29
Shrublands Spain (Bartomeus et al. 2008)	0.59	0.26	16	23	67	39

Land use type	Season	Weighted nestedness	Connectance	Number of bee species	Number of plant species	Total community size
Conventional farm	Early Mid	N/A 0.26	0.33 <b>0.48</b>	6 22	იი	9 25
Orcanic farm	Late Early	N/A N/A	N/A 0.50	7 5	1 6	ი u
	Mid	0.38	0.14	36	$\frac{2}{16}$	52
Meadow	Late Early	<b>0.59</b> 0.53	0.29 <b>0.57</b>	14 7	8 61	22 9
	Mid Late	0.05 <b>0.90</b>	0.32 0.31	19 13	9	<b>28</b> 17
Agricultural farm PA (Russo et al. 2013)	Early Mid	2.80* <b>13.05</b> *	0.23	$\frac{23}{46}$	8 20	31 66
	Late	7.89*	0.16	34	19	53

	Bee Species	Abundance	Degree/ floral hosts	Normalized degree	ISd
Andrena commoda	mmoda	2	2	0.40	0.02
Andrena c	Andrena confederata	1	1	0.20	0.11
Andrena cressonii	ressonii	ç	2	0.40	0.04
Andrena dunningi	dunningi	2	2	0.40	0.26
Andrena hilaris	hilaris	1	1	0.20	0.03
Andrena nivalis	iivalis	2	2	0.40	0.07
Andrena perplexa	verplexa	c,	2	0.40	0.20
Andrena regularis	egularis	1	1	0.20	0.03
Andrena wilkella*	$vilkella^*$	8	2	0.40	0.18
Calliopsis	Calliopsis andreniformis	c,	2	0.40	0.03
Bombus bi	Bombus bimaculatus	7	2	0.40	0.06
Bombus impatiens	patiens	70	2	0.40	0.68
Ceratina dupla	upla	1	1	0.20	0.01
Agapostem	Agapostemon virescens	1	1	0.20	0.01
Augochlore	Augochloropsis metallica	1	1	0.20	0.33
Halictus confusus	nfusus	4	2	0.40	0.11
Halictus ligatus	gatus	1	1	0.20	0.01
Halictus r	Halictus rubicundus	1	1	0.20	0.03
Lasiogloss	Lasioglossum abanci	1	1	0.20	0.11
Lasiogloss	Lasioglossum cressonii	7	റ	0.60	0.40
Lasioglos	Lasioglossum paradmirandum	1	1	0.20	0.01
Lasioglos	Lasioglossum versatum	c,	ന	0.60	0.15
Heriades carinata	carinata	1	1	0.20	0.03
Osmia inspergens	spergens	1	1	0.20	0.03

Land use type	Family	Bee Species	Abundance	Degree/ floral hosts	Normalized degree	ISd
Organic farm	Andrenidae	Andrena crataegi	5	1	0.04	0.10
		Andrena cressonii	2	2	0.09	0.05
		Andrena erigeniae	1	1	0.04	0.20
		Andrena imitatrix	1	1	0.04	0.05
		Andrena miserabilis	c,	2	0.09	0.25
		Andrena nivalis	2	1	0.04	0.04
		Andrena perplexa	1	2	0.09	0.09
		Andrena sigmundi	1	1	0.04	0.05
		Andrena vicina	2	2	0.09	0.13
		$Andrena\ wilkella^*$	1	2	0.09	0.09
	Apidae	Anthophora terminalis	c,	3	0.13	0.03
		Bombus bimaculatus	26	5	0.22	0.29
		Bombus griseocollis	c,	2	0.09	0.05
		Bombus impatiens	195	13	0.57	0.71
		Bombus vagans	28	6	0.39	0.19
		Ceratina calcarata	4	c,	0.13	0.41
		Ceratina dupla	2	2	0.09	0.03
		Ceratina mikmaqi	2	2	0.09	0.22
		Melissodes subillata	4	c,	0.13	0.11
		Xylocopa virginica	21	7	0.30	0.16
	Colletidae	Hylaeus mesillae	1	1	0.04	0.05
		Hylaeus modestus	c,	1	0.04	0.15
	Halictidae	Agapostemon virescens	10	7	0.30	0.14
		Augochlorella aurata	2	2	0.09	0.02
		Halictus confusus	2	2	0.09	0.06
		Halictus ligatus	166	16	0.70	0.77

Table 6. Continued.

Land use type	Family	Bee Species	Abundance	Degree/ floral hosts	Normalized degree	ISd
		Lasioglossum albipenne	1	1	0.04	0.05
		Lasioglossum cinctipes	2	2	0.09	0.06
		Lasioglossum cressonii	8	2	0.09	0.48
		Lasioglossum fuscipenne	1	1	0.04	0.03
		$Lasioglossum\ leucozonium^*$	4	1	0.04	0.40
		Lasioglossum pectorale	1	1	0.04	0.03
		$Lasioglossum\ pilosum$	4	5	0.22	0.18
		Lasioglossum tegulare	1	1	0.04	0.07
		Lasioglossum versatum	1	1	0.04	0.10
	Megachilidae	Heriades carinata	1	1	0.04	0.03
		Megachile centuncularis	1	1	0.04	0.10
		Megachile inermis	2	2	0.09	0.09
Meadow	Andrenidae	Andrena braccata	2	1	0.08	0.03
		Andrena carlini	1	1	0.08	0.14
		Andrena commoda	1	1	0.08	0.14
		Andrena cressonii	2	2	0.15	0.06
		Andrena dunningi	1	1	0.08	0.20
		Andrena erigeniae	1	1	0.08	0.20
		Andrena hirticincta	1	1	0.08	0.02
		Andrena krigiana	1	1	0.08	0.14
		Andrena sigmundi	1	1	0.08	0.14

Table 6. Continued.

Family	Bee Species	Abundance	Degree/ floral hosts	Normalized degree	ISd
ν	Andrena simplex	1	1	0.08	0.02
Α	Andrena wilkella*	1	1	0.08	0.25
Ŭ	Calliopsis nebraskensis	2	1	0.08	0.03
B	Bombus bimaculatus	11	4	0.31	0.48
B	Bombus impatiens	123	10	0.77	0.72
B	Bombus perplexus	1	1	0.08	0.13
ğ	Bombus vagans	6	9	0.46	0.20
Ŭ	Ceratina calcarata	1	1	0.08	0.02
Ŭ	Ceratina dupla	2	1	0.08	0.03
Ŭ	Ceratina mikmaqi	2	1	0.08	0.03
X	Xylocopa virginica	က	2	0.15	0.07
H,	Hylaeus affinis	1	1	0.08	0.02
Ą	Agapostemon virescens	2	2	0.15	0.16
$A_l$	Augochlorella aurata	ന	2	0.15	0.38
Η	Halictus confusus	2	2	0.15	0.10
Η	Halictus ligatus	7	4	0.31	0.10
Η	Halictus rubicundus	1	1	0.08	0.25
Γ	Lasioglossum albipenne	2	1	0.08	0.25
Ľ	Lasioglossum coriaceum	1	1	0.08	0.13
Ľ	Lasioglossum cressonii	4	2	0.15	0.14
Γ	Lasioglossum imitatum	1	1	0.08	0.07
Γ	Lasioglossum lineatulum	1	1	0.08	0.07
Γ	Lasioglossum versatum	13	4	0.31	0.21
ί	$Anthidium\ oblongatum^*$	1	1	0.08	0.20

Table 6. Continued.

conventional farm sites comprised half (50%) of the bee species and organic farm sites contained many more specialist than general pollinators (30%).

Degree, normalized degree, and PSI were also used to assess the importance of flower species (Table 7) at each land use type. For conventional farm sites, red clover had the greatest pollinator breadth (15), however white clover had the highest PSI value (0.79). At organic farm sites, *Rubus* sp. (berry brambles) in this community appears to be paramount to current function with the most pollinator species (11) and highest PSI (0.75). At meadow sites, *Solidago canadensis* (Canadian goldenrod) had the greatest breadth of pollinators, while *Lotus corniculatus* (Bird's-foot trefoil) was most essential to ecosystem functioning (PSI = 0.72). Only three flower species were specialists, *Coreopsis lanceolata, Erigeron philadelphicus* and a species of *Syringa*, all found on organic farm sites (Table 7).

#### Discussion

Bee abundance and species richness. Seasonal differences appear to have less influence on overall bee abundance and richness than land use type. Abundance was significantly greater mid-season than early season, but not significantly different than late season. Despite the number of species present only being significantly different between mid and early season, the specific species composition was highly varied among all seasons.

Land use type did strongly influence the bee community. While it may have been expected that meadow sites would have higher bee abundance and species richness, both metrics were significantly highest in organic farm sites. One reason that bee abundance and species richness were greater in organic farm sites may be the higher diversity of floral resources as has often been correlated with larger bee communities (Andersson et al. 2013, Rutgers-Kelly & Richards 2013, Ellis & Barbercheck 2015). Our results correspond with previous studies showing that the impact of agriculture on bees is often dependent on the habitat or region studied (Hernandez et al. 2009, Hoehn et al. 2010, Cariveau & Winfree 2015, Gill et al. 2016). These data also support the theory that managed habitat areas are not necessarily detrimental to bees and some agricultural practices may help promote bee abundance (Jackson & Jackson 2002, Rosenzweig 2003, Westphal et al. 2003, Carre et al. 2009, Winfree et al. 2009).

**Common and rare species.** We found that *B. impatiens* was the most abundant and common bee species found at all sampling sites. *Bombus impatiens* is recurrently the most abundant species in studies of agricultural ecosystems of Pennsylvania (Russo et al. 2013) and urban gardens of New York (Matteson et al. 2008). Four additional halictid bee species, *A. virescens, A. aurata, L. coriaceum,* and *L. versatum,* were also found at all sites in abundance, though they were not necessarily the most abundant of the species sampled. The abundance of halictid species is consistent with findings from other studies in the northeast (Richards et al. 2011, Rutgers-Kelly & Richards 2011, Hinners et al. 2012, Russo et al. 2013, Lerman & Milam 2016).

The prevalence of *Taraxacum* sp. (dandelion) and white clover in all sites is not surprising as both are considered weedy in the northeast and even invasive in some states (USDA 2017). Red clover, while also found at all sites, is not on the USDA's weed list and is often associated with bee surveys (Fussell & Corbet 1992,

land use type. Highest values are in bold. Asterisks indicate non-native	
ecies statistics for each lan	
Table 7. Flower spe	species

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Land use type	Family	Flower species	Degree/bee visitors	Normalized degree	ISd
Conventional farm	Asteraceae	Taraxacum sp.	5	0.08	0.42
	Fabaceae	Trifolium pratense* Trifolium repens*	<b>15</b> 13	<b>0.63</b> 0.54	0.53 <b>0.79</b>
	Papaveraceae	$Chelidonium\ majus^*$	Ð	0.21	0.71
	Ranunculaceae	Ranunculus sp.	co	0.13	0.53
Organic farm	Apocynaceae	Asclepias tuberosa	7	0.18	0.30
	Asteraceae	Coreopsis lanceolata	1	0.03	0.20
		Echinacea purpurea	8	0.21	0.19
		Erigeron philadelphicus	1	0.03	0.07
		Heliopsis helianthoides	4	0.10	0.32
		Heliopsis sp.	5	0.13	0.19
		Hieracium sp.	2	0.05	0.08
		Hieracium sp. 2	4	0.10	0.54
		Rudbeckia hirta	5	0.13	0.44
		Rudbeckia sp.	8	0.21	0.29
		Solidago speciosa	5	0.13	0.23
		Taraxacum sp.	2	0.05	0.50
		Vernonia fasciculata	6	0.23	0.11

Land use type	Family	Flower species	Degree/bee visitors	Normalized degree	ISd
	Fabaceae	Lupinus sp.	4	0.10	0.24
		$Trifolium\ incarnatum^*$	c,	0.08	0.31
		$Trifolium\ pratense^*$	7	0.18	0.21
		$Trifolium\ repens^*$	9	0.15	0.24
	Lamiaceae	Agastache foeniculum	8	0.21	0.23
		Monarda fistulosa	5	0.13	0.32
		Salvia patens*	3	0.08	0.09
	Oleaceae	Syringa sp.*	1	0.03	0.25
	Polygonaceae	$Fagopyrum\ esculentum^{*}$	3	0.08	0.02
	Rosaceae	Rubus sp.	11	0.28	0.75
Meadow	Apiaceae	$Daucus\ carota^*$	7	0.21	0.26
	Apocynaceae	Asclepias sp.	3	0.09	0.61
	Asteraceae	Centaurea jacea*	4	0.12	0.23
		Solidago canadensis	12	0.36	0.49
		Solidago speciosa	1	0.03	0.01
		Taraxacum sp.	9	0.18	0.62
	Caprifoliaceae	Lonicera sp.	0	0.06	0.34
	Caryophyllaceae	Silene latifolia*	4	0.12	0.09
	Fabaceae	Lotus corniculatus*	5	0.15	0.72
		$Trifolium\ pratense^*$	4	0.12	0.27
		$Trifolium\ repens^*$	4	0.12	0.39
		Vicia sp.	4	0.12	0.51
	Rosaceae	$Potentilla\ recta^*$	9	0.18	0.59

Table 7. Continued.

Richards et al. 2011, Rundlöf et al. 2014). Even though *Taraxacum* and clovers comprise mostly non-native species, they are central flora in many ecosystems (Tommasi et al. 2004, Richards et al. 2011, Larson et al. 2014, Lerman & Milam 2016, Tucker & Rehan 2016). The importance of these two flowers is evinced in their ability to grow in a wide range of habitats in the northeast, over multiple seasons, while providing floral resources to a diversity of bee species (Larson et al. 2014, Lerman & Milam 2016, Tucker & Rehan 2016, Tucker & Rehan 2016).

All three land use types had a relatively high percentage of unique bee species (conventional farm 30%, organic farm 33%, meadow 25%), and even higher percentages of unique flower species (conventional farm 40%, organic farm 83%, meadow 69%). Interestingly, all but three flower species (C. lanceolata, E. philadelphicus and Syringa sp.) received visitations from multiple bee species. Two flowers were visited by H. ligatus and the third by L. cressonii. The lack of additional species collected on these flowers was likely due to the short flower bloom duration. We found an overall higher percent of generalist pollinators in conventional and organic farms. While most of the specialist bee species collected were categorized as such due to few specimen collections (<3), three confirmed specialist bee species, Andrena braccata Viereck, Andrena hirticinta Provancher, and Andrena simplex Smith (all Hymenoptera: Andrenidae), were collected from S. canadensis, which is a known host plant along with other species of Solidago (LaBerge 1967, Mitchell 1960). Our findings of a greater species richness of generalist bees is consistent with other studies that suggest generalist species were more resilient and better adapted to agricultural landscapes in comparison to specialist pollinators (Weiner et al. 2014, Winfree et al. 2011). Taken together, our data confirm former studies indicating that a broad range of habitat and land use types are necessary to achieve maximum levels of biodiversity (Carvell 2002, Tscharntke et al. 2005, Mandelik et al. 2012). A diversity of foraging landscapes and the subsequent pollinator species richness may help to ensure the ability of an ecosystem to recover after a major disturbance or local extinction (Tscharntke et al. 2005, Kehinde & Samways 2012, Senapathi et al. 2015).

**Plant-pollinator interactions.** Previous research, on a broad spectrum of pollinator orders, has examined how plant-pollinator networks change with land use in Africa (Grass et al. 2013), South America (Marrero et al. 2014), and Germany (Weiner et al. 2014). However, bee centric studies are needed to examine plant-pollinator networks at the species level across different land use types and agricultural settings. Here we present the first such study in New England, with continuous sampling of the same locations throughout the collecting season. We found an apparent inverse relationship between connectance and community size (Table 4). This inverse relationship where larger communities have more unique interactions, but less connectance, appears in many plant-pollinator networks (Table 4; Clements & Long 1923, Schemske et al. 1978, Motten 1982, Bartomeus et al. 2008, Russo et al. 2013). The inverse relationship is biologically intuitive since a larger community provides a greater number of potential interactions. However, not all pollinators are compatible with all flowers and vice versa because at the species level bee biology differs as does floral nutritional resources. We also found that plant-pollinator networks in mixed grassland and agricultural ecosystems appear to have greater species richness and unique interactions than forested woodland or scrubland ecosystems (Table 4; Clements and Long 1923, Schemske et al. 1978, Motten 1982, Bartomeus et al. 2008, Russo et al. 2013,

Tucker & Rehan 2016). Our seasonal network characteristics differed slightly from a similar study in Pennsylvania where the plant-pollinator community was both largest and most complex mid-season (Russo et al. 2013), whereas most of our networks were largest mid-season, but most complex late season (Table 5).

Many of the essential bee species reported in our plant-pollinator community across different land use types parallel those reported in other pollinator studies across eastern North America (Table 6; Richards et al. 2011, Kammerer et al. 2015, Lerman & Milam 2016, Mallinger et al. 2016). While none of the floral species we sampled were specific to a single bee species, many floral species were found to be essential to the community (Table 7). The flowers identified in this study correspond with plants identified as central to habitat function in previous studies across the northeast (Table 7; Morse 1980, Ginsberg 1983, Fussel & Corbet 1992, Tommasi et al. 2004, Carvell et al. 2007, Denisow & Wrzesien 2007, Richards et al. 2011, Larson et al. 2014). Here we provide essential regionally specific information on bee habitat across different agricultural settings. The widespread importance of clovers, berry brambles, goldenrods and other weedy species to the bee community suggests the need to promote and maintain areas supporting such habitat.

Determining the impact of agricultural landscapes on the bee community and comparisons across regions is critical to the conservation of wild bees and the indispensable pollination services they provide. New England is an area for which research pertaining to effects of agricultural practices on the pollinator community is sparse. We found bee abundance and species richness to be highest in organic farm sites. We found both a great overlap of bee species among land use types, whereas floral species were largely land use type specific. This suggests a heterogeneous landscape may not only increase floral diversity, but pollinator species richness and community stability as well. This study provides important baseline data to establish the plant-pollinator community dynamics in New England across agricultural landscapes. Additional long-term research is needed to determine the habitat requirements needed for maintaining the most diverse and stable community possible over time. However, based on the findings of this study we recommend conserving both areas of natural weedy flora and semi-natural areas with supplemental flowering plants, especially those that bloom early season. A combination of flowers that bloom across seasons and mixed among or bordering crop areas, along with reduced pesticide use, appears to increase both bee abundance and species richness.

#### Acknowledgments

We thank Dusty Durant, Elizabeth Haas, Robert Hafford and Wyatt Shell (University of New Hampshire) for their help with fieldwork and specimen processing. We also thank Sam Droege (US Geological Survey) and Joan Milam (University of Massachusetts) for providing reference material for bee identifications. Funding from the University of New Hampshire and the Tuttle Foundation provided support for this research. Partial funding was provided by the New Hampshire Agricultural Experiment Station. This work was supported by the USDA National Institute of Food and Agriculture Hatch Project 1004515.

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