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Wild bee pollination networks in northern New England

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Abstract Conserving and maintaining a diverse assemblage of wild bees is essential for a healthy and functioning ecosystem, as species are uniquely evolved to deliver specific plant–pollination requirements. Understanding the biology and ecology of bees in poorly studied regions is the first step towards conservation. Detailed surveys in New Hampshire reveal a broad diversity of 118 species of wild bees in different guilds and habitats including 17 bee species representing new state records. Network analyses reveal a complex community structure and relatively poorly connected plant–pollinator associations, thus species may be susceptible to disturbance. Phenological analyses document that at least one representative of five native bee families was present throughout the foraging season and both abundance and diversity were highest in June and July. This study provides important baseline information on bee abundance, diversity, phenology, and host plant associations necessary for future conservation efforts.

Keywords Plant–pollinator interactions · Apoidea · Bee phenology · Ecological associations · Hymenoptera · Biodiversity · Bipartite network

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Introduction

Understanding complex interactions between species and their environment has long been a goal of biodiversity research and is essential for conservation efforts (Weiner et al. 2014). One of the most import interaction networks to both agriculture and the natural environment is the relationship between plants and pollinators; bees in particular pollinate almost 90 % of the world's flowering plants (Ollerton et al. 2011), 87 of our agricultural crops (Klein et al. 2007), and account for 35 % of our current food production (Stine et al. 2015). The pollination services of wild bees alone are estimated at $3 billion in the US (Stine et al. 2015) and $200 billion worldwide annually (Gallai et al. 2009). Maintenance of wild bee populations is essential for both natural ecosystems and pollinator dependent crops (Stine et al. 2015; Julier and Roulston 2009; Vaughan et al. 2015), yet it is well documented that population levels are declining worldwide (Bartomeus et al. 2013; Burkle et al. 2013; Garibaldi et al. 2013). Bees are declining primarily from climate change and loss of habitat for nesting sites and floral resources (Potts et al. 2010; Bartomeus et al. 2013; Kerr et al. 2015). Despite loss of floral resources identified as one of the primary impairments to healthy wild bee populations, there is a dearth of basic information on wild bee biology and their floral associations, which is necessary for the successful development of conservation and management strategies (Gill et al. 2016).

Conserving or restoring wild bee habitat has the potential for both short and long-term agricultural and food security benefits (Bailes et al. 2015). Northern New England has many naturalized and conserved areas with the potential to support a broad diversity of wild bees in many unique ecological niches (Goldstein and Ascher 2016; Koh

et al. 2016; Chandler and Peck 1992). It encompasses an expansive assortment of ecosystem types including coastline, wetland, peatland, grassland, shrubland, hardwood, conifer and Appalachian forest, and agricultural land. Despite the potential for diversity across the northeastern US (Koh et al. 2016; Bartomeus et al. 2013), the bee fauna and associated floral hosts are generally poorly known (Wagner et al. 2014; Ascher et al. 2014; Goldstein and Ascher 2016). Recent surveys across northern New England have documented species lists, new state records, and recent population declines (Bushmann and Drummond 2015; Goldstein and Ascher 2016). Yet, the status of the wild bee community in New Hampshire remains undocumented as does much information concerning their floral associations and basic biology (Goldstein and Ascher 2016). Studies on plant–pollinator networks combined with phenological information can provide us with essential information on bee habitat, feeding and pollination requirements necessary for community preservation, pollinator floral preferences, and keystone species (Bartomeus et al. 2013; Burkle et al. 2013; Russo et al. 2013; Senapathi et al. 2015; Wright et al. 2015). Changes in the structure of these interaction networks can infer important information about the stability or robustness of the bee community as well as the greater ecosystem.

Since there is limited research on the wild bees in this region, community composition, bee population status and how they interact with the local flora remain unknown. Major surveys and descriptions of bee fauna are prerequisite to further studies of bee diversity and population biology. Our study aims to establish important baseline data for bee biodiversity research in northern New England by, (1) cataloguing wild bee diversity, (2) documenting plant–pollinator associations, and (3) identifying phenological patterns.

Methods

Experimental design

Collections were conducted at three one acre sites in Strafford County, New Hampshire (geographic coordinates: 43.11, −70.95; 43.15, −70.94; 43.17, −70.93), which were divided into nine transects. Sampling began the last week of April and continued biweekly through the end of September 2014 for a total of 11 collection weeks. Two sampling methods were used, pan trapping and sweep netting. For the pan trapping, we used 27 sampling transects (nine transects from each of the three one acre sites). Pan trap collection procedures essentially followed Richards et al. (2011). Transects were composed of ten pan traps (New Horizons Support Services, Inc.; 3.5 oz.) of three alternating colors, yellow, blue, and white, each set 10 m from the next. Pan traps were filled with soapy water, set out before 0800 hours and collected after 1600 hours. Upon collection, trap contents were poured through a small sieve and placed in vials of 70 % ethanol labeled with collection information.

Bees were also collected from blooms of flowering plants in the same sites as pan traps by sweep netting with a collapsible aerial net (Bioquip 7112CP; 30.5 cm diameter, 12.7 cm aluminum handles). Sampling at each site proceeded for 5 min per flower type in 30-s intervals on the same day as pan trapping. Sweep samples were conducted between 1000 and 1400 hours and sampled flowering plant species were identified using field guides. Sweep contents were placed in vials of 70 % ethanol labeled with collection information.

Curation and preservation

Specimens were pinned and labeled according to location, date, collection method and floral host where relevant and given a unique barcode and University of New Hampshire ID Number. With the exception of five specimens missing heads (identified as *Lasioglossum* sp.), all specimens were identified to species using the interactive identification guides on DiscoverLife.org and recent taxonomic literature (Mitchell 1960, 1962; Gibbs 2011; Rehan and Sheffield 2011; Michener et al. 1994; Williams et al. 2014). All species were compared to the compilation of distribution records on the Discover Life website (www.discoverlife.org) to determine what species have previously been documented in the state of New Hampshire and from Bartomeus et al. (2013). The very handy manual (Droege 2015) was used to identify exotic bee introductions. Voucher specimens are deposited in the University of New Hampshire Insect Collection, Durham, New Hampshire.

Abundance and diversity analyses

Tests of normality and subsequent statistical tests were performed using the program JMP Pro 12.1.0. Datasets were tested for distribution normality and unpaired two-tailed t tests were then conducted to assess if collection method had a significant impact on number of species or specimens collected. To determine total species abundance and diversity of bees all samples and methods were pooled. To estimate the 'true' species richness of the bee communities sampled and determine how well the community was sampled a rarefaction test conducted with a Chao-1 estimate (Chao 1984, 1987; Colwell and Coddington 1994), an ACE and ACE-1 estimate (Chao and Lee 1992) and Jackknife estimate (Burnham and Overton 1978, 1979) using the R 'SPECIES' package (Wang 2011).

Plant–pollinator analyses

Plant–pollinator networks were based exclusively on sweep net samples, as there was no flower information associated with the pan trap samples. Interaction networks were constructed with R using the 'bipartite' package (Memmott 1999; Dormann et al. 2008, 2009). To evaluate community interactions over the April to September collection season, all sweep samples were pooled and the function *plotweb* was used to build the network. The function *networklevel* was used to calculate interaction network statistics for evaluating the stability and robustness of the plant–pollinator community and to determine whether species are relatively independent of each other or dependent on keystone species. The function *specieslevel* was used to calculate statistics for evaluating individual bee and flower species contributions and to identify the most influential participants in the community. To evaluate how community interactions changed throughout the year, the pooled data was divided by season (early = April and May; mid = June and July; late = August and September). Each seasonal data division was evaluated with the same functions, *plotweb*, *networklevel* and *specieslevel*, as the overall network analysis (full = April to September).

At the community level we examined weighted nestedness and connectance. Weighted nestedness (Galeano et al. 2009) considers interaction frequencies to measure community patterns of species co-occurrence and biome structure, where 1 = completely nested (generalist and specialist interactions completely overlap) and 0 = chaotic interactions (no overlap between generalist and specialist species). Connectance (Dunne et al. 2002) uses the proportion of possible interactions actually achieved to measure the complexity and durability of a community to species loss, where 1 = all possible interaction between species used (all bee species visit all flowers and system is relatively robust to species loss) and 0 = no interactions between species (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). At the species level we examined degree, normalized degree and Pollination Service Index (PSI). Degree measures the species diet breadth or unique interactions per individual species (number of floral hosts per bee or number of pollinator species per flower). Normalized degree scales the species degree to the number of possible pairings between species to give a relative measure that can be used for unbiased comparisons between species. PSI (Dormann et al. 2008) measures the relative importance of each pollinator in the community where 1 = pollinator services essential to the functioning of the ecosystem and 0 = pollinator services unimportant for a functioning ecosystem. As such, this metric is only calculated for the bee species and not the flower species.

Phenology analyses

Three phenological analyses were conducted: total bee abundance and flight duration, sweep net sample only bee flight duration, and sweep net sample only flower duration. These three analyses facilitated the comparison of coinciding phenologies to aid in determining what floral resources are potentially available to each of the identified bee species throughout the season. Phenologies were plotted with the R ggplot2 package and *geom_violin* function (Wickham 2009). Duration of plant–pollinator interactions (node duration; Russo et al. 2013) was calculated to identify plant species that support pollinators and bee species associated with plants for longer periods. To aid in identifying the highest and most diverse bee flight periods additional plots where produced to evaluate bees by season.

Results

Abundance and diversity

A total of 2292 bee specimens were collected over the 2014 collection period, 856 specimens from sweep-net samples and 1436 specimens from pan trap samples. The difference in number of specimens collected by each method was not significant ($t = -1.47$, $df = 19$, $P = 0.16$). A total of 118 bee species were collected (Supplementary Table 1), 63 from sweep-net samples and 96 from pan trap samples. The difference in number of species collected by each method was significant ($t = -3.94$, $df = 18$, $P = 0.0009$). The rarefaction estimate of sampling completeness, using the Chao 1 test, estimates a lower bound true species richness of 147 species, which translates to 80 %. Other species richness tests provided similar species diversity estimates (ACE = 148; ACE-1 = 158; Jackknife = 165). Of the bee specimens collected, 24 genera and five families are represented (all families in North America except Melittidae; Supplementary Table 1). Representatives of all five native bee families (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae) were collected from both pan trap and sweep-net samples. Halictidae was the most abundant bee family collected (1468 specimens) and Colletidae was the least abundant (14 specimens; Fig. 1). *Bombus* was the most abundant genus (520 specimens) followed closely by *Lasioglossum* (506 specimens). The most abundant species collected were *Bombus impatiens* (423 specimens), *Agapostemon virescens* (410 specimens), *Halictus ligatus* (309 specimens) and *Augochlorella aurata* (161 specimens). Conversely, we also collected 46 single occurrence species. Of the 118 bee species we collected, 17 species represent new state records for New Hampshire and seven are
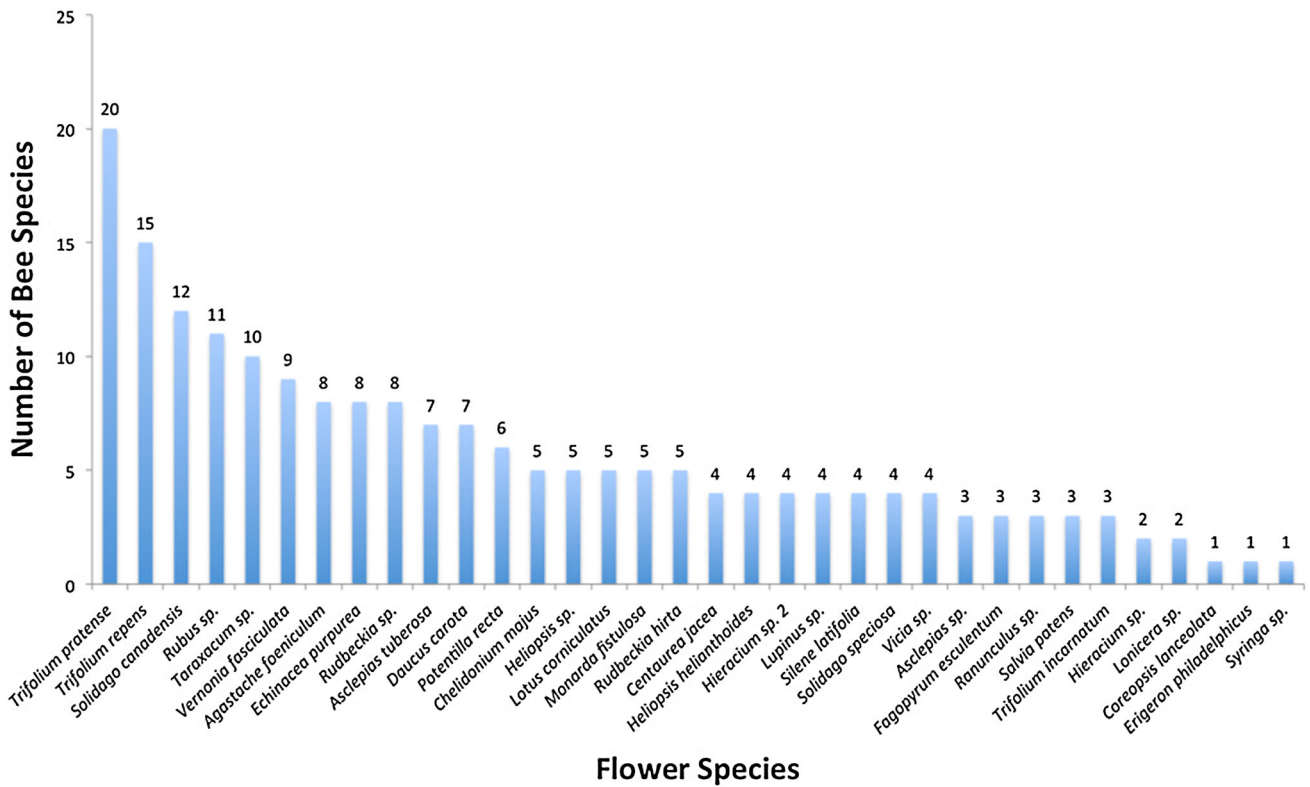
Fig. 1 Abundance of each bee species collected during this study. Bee species are colored by family and each species is labeled with total specimen counts

introduced species (Supplementary Table 1). *Trifolium repens* (white clover) supported the largest abundance of bees (Fig. 2), however, *Trifolium pratense* (red clover) supported the highest diversity of bees (Fig. 3) while *Monarda fistulosa* and *Solidago canadensis* also supported a rich diversity of bee species (Fig. 2).

Plant–pollinator interactions

A plant–pollinator network for the entire collection period (full) was constructed in addition to networks for three separate seasons (early, mid, late). There are a total of 34 flower species (Table 1), 63 bee species (Table 2) and 197 unique species interactions included in the full network (Fig. 4). Community composition changed drastically throughout the collection season, varying in size, weighted nestedness, and connectance (Table 2). The community composition was largest in the middle of summer (77 taxa) in both bee and plant species, but neither weighted nestedness nor connectance showed the same pattern (Table 3). Weighted nestedness (species co-occurrence) was highest late in the season (0.57), even higher than the full community network weighted nestedness (0.51). This indicates the plant–pollinator community is at its most complex at this time, despite only containing about a third (34 taxa) of the potential taxa (97) in the full network. Although the early season was composed of the fewest taxa (20), it measured highest in connectance (0.24). This is strikingly higher than the connectance of the full network (0.09) as well as the mid season network (0.11), which contained the

most possible taxa at any one point in time (77). These results indicate that while the community at its largest mid season and most complex during the late season, it is most robust and resilient to species loss in the early season.

We used three species level network measures to assess the importance of individual bee species in the full network: degree, normalized degree and PSI (Table 2), and two species level network measures to assess the plant species importance: degree (bee species associated) and normalized degree (Table 1). For the pollinators, both *B. impatiens* and *H. ligatus* had the broadest floral host breadth with the highest number (20) of unique flower species interactions. Within the community almost half (49 %) of the contributing pollinators were generalists (categorized herein as a species associated with more than one flower species). By sheer abundance, *B. impatiens* had the greatest number of interactions (388) with flowering plants in the community. The Pollinator Service Index was highest for *H. ligatus* (0.74) with *B. impatiens* almost as high (0.70). For the flowering plants, *T. pratense* (red clover) provided services to the greatest number of bee species (20), but *T. repens* (white clover) had the highest abundance of pollinators (184). Most of the flower species sampled (91 %) appear to be generalists providing floral resources to multiple bee species, however three specialist flowers were only serviced by one bee species, *Coreopsis lanceolata* (lance-leaved coreopsis) and *Erigeron philadelphicus* (Philadelphia fleabane) both visited by *H. ligatus*, and a species of *Syringa* (Lilac) visited by *Lasioglossum cressonii* (Table 1). PSI was very low (0.01) for

Fig. 2 Bee species diversity for each flower species sampled using sweep netting. Flower species are in order of greatest bee diversity supported
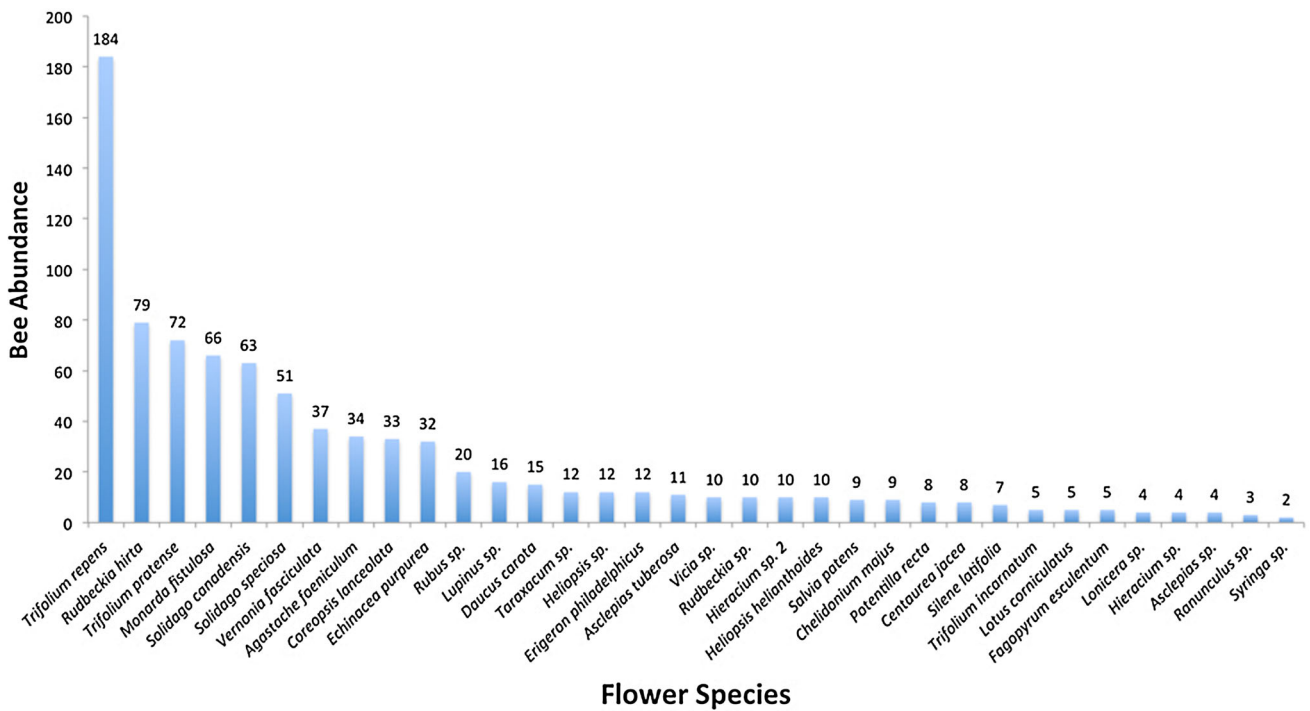

Fig. 3 Abundance of bee specimens collected from each flower species during sweep netting. Flower species are in order of greatest abundance of bees

Table 1 Flower species, common names, and bee associations

Flower	Common name	Native	Bee species associations	Bee abundance	Normalized degree	Node duration
Apiaceae						
Daucus carota	Wild carrot	No	7	16	0.11	0.18
Apocynaceae						
Asclepias sp.	Milkweed	Yes	3	4	0.05	0.09
Asclepias tuberosa	Butterfly weed	Yes	7	9	0.11	0.09
Asteraceae						
Centaurea jacea	Brown knapweed	No	4	8	0.06	0.09
Coreopsis lanceolata	Lance-leaved coreopsis	Yes	1	33	0.02	0.18
Echinacea purpurea	Eastern purple coneflower	Yes	8	32	0.13	0.18
Erigeron philadelphicus	Philadelphia fleabane	Yes	1	12	0.02	0.09
Heliopsis helianthoides	False sunflower	Yes	4	10	0.06	0.09
Heliopsis sp.	Oxeye	Yes	5	12	0.08	0.09
Hieracium sp.	Hawkweed	Probably	2	4	0.03	0.09
Hieracium sp. 2	Hawkweed	Probably no	4	10	0.06	0.09
Rudbeckia hirta	Black-eyed-susan	Yes	5	79	0.08	0.18
Rudbeckia sp.	Coneflower	Yes	8	10	0.12	0.09
Solidago canadensis	Canadian goldenrod	Yes	12	59	0.18	0.27
Solidago speciosa	Showy goldenrod	Yes	5	51	0.08	0.27
Taraxacum sp.	Dandelion	Probably	10	12	0.15	0.09
Vernonia fasciculata	Prairie ironweed	Yes	9	37	0.14	0.09
Caprifoliaceae						
Lonicera sp.	Honeysuckle	Probably no	2	4	0.03	0.09
Caryophyllaceae						
Silene latifolia	White champion	No	4	7	0.06	0.09
Fabaceae						
Lotus corniculatus	Bird's-foot trefoil	No	5	5	0.08	0.09
Lupinus sp.	Lupine	Probably	4	16	0.06	0.09
Trifolium incarnatum	Crimson clover	No	3	5	0.05	0.18
Trifolium pratense	Red clover	No	20*	72	0.31	0.18
Trifolium repens	White clover	No	15	184*	0.23*	0.45*
Vicia sp.	Vetch	Probably	4	10	0.06	0.27
Lamiaceae						
Agastache foeniculum	Anise hyssop	Yes	1	34	0.12	0.09
Monarda fistulosa	Bee balm	Yes	5	66	0.08	0.27
Salvia patens	Gentian sage	No	3	9	0.05	0.09
Oleaceae						
Syringa sp.	Lilac	No	1	2	0.02	0.09
Papaveraceae						
Chelidonium majus	Greater celandine	No	5	9	0.08	0.09
Polygonaceae						
Fagopyrum esculentum	Buckwheat	No	3	5	0.05	0.09
Ranunculaceae						
Ranunculus sp.	Buttercup	Probably	3	3	0.05	0.09
Rosaceae						
Potentilla recta	Sulphur cinquefoil	No	6	8	0.09	0.09
Rubus sp.	Berry brambles	Probably	11	20	0.17	0.09

Flower family names are in bold and species within each family are listed below

* Highest values for each network metric

eight bee species (*Andrena hilaris*, *A. regularis*, *Calliopsis andreniformis*, *Heriades carinata*, *Lasioglossum paradmirandum*, *L. tegulare*, *Protandrena bancrofti*, *Osmia inspergens*), indicating their relatively small contribution to the larger network during 2014. Floral host breadth for 31 bee species was extremely narrow (only one flower interaction), although 30 of those bee species are represented by single occurrence data, which may not accurately represent breadth of floral hosts.

Phenology

Violin plots were produced to depict phenologies of bee and flower species included in the network analysis (Fig. 4). These plots show species presence or absence throughout the collection year from sweep net samples. There were no flower species present through the entire collection period, although at least one representative of the clover genus, *Trifolium*, was present at most sampling periods (April to August). *T. repens* had the highest node duration and was sampled from mid May into August. While bees were collected from a number of flowers two to three times during the season, 68 % of the flowers (23 taxa) on which bees were collected were from single time periods. No bee species was present through the entire collection period, although *B. impatiens* came close and was only absent mid June (Fig. 4). Node duration was highest for *B. impatiens* (0.82). The family Colletidae was rare in sweep samples and consequently three *Hylaeus* species were represented by single floral associations, twice in May and once in August. At least one species in the family Apidae is present throughout the season. Members of Halictidae were present in all but April and members of Andrenidae were present in all but September. Species from the family Megachilidae were collected from April to July.

A violin plot was produced showing all bee species (pan and sweep samples) flight duration and abundance (Supplementary Figure 1). The bee community appears relatively complex with an overlapping combination of long and short duration bees. All bee families were represented by at least one species at every time period. *A. aurata* was common throughout the season and was the only species found to have a perfect node duration of 1.00 through combined pan and sweep sampling. Six other members of Halictidae (*A. virescens*, *H. ligatus*, *L. coriaceum*, *L. pilosum*, *L. tegulare* and *L. versatum*) were present in all but one collection period (node duration =0.91). Most genera appear to be relatively evenly spread throughout the collection season, with the exception of the Megachilidae. Within Megachilidae, most species and genera were collected in June or later except members of the genus *Osmia*. All but one *Osmia* species were sampled early in the

season, from early April to mid May. The one exception, *O. inspergens*, was collected from mid May to mid June. Fifty-four species, with representative from all families, were only represented in a single collection period. Bees were both most abundant (Supplementary Figure 2) and diverse (Supplementary Figure 3) mid collecting season and both least abundant and diverse in the early collecting season.

Discussion

Abundance and diversity

New Hampshire has a high bee species richness compared to similar faunistic surveys conducted in eastern North America. In a 1-year period we found 118 bee species compared to that of 54 species in Illinois (Burkle et al. 2013) and 64 species in Pennsylvania over 2 years (Russo et al. 2013), 54 species in New York over a 4-year period (Matteson et al. 2008), and 124 species in Ontario over a 1-year period (Richards et al. 2011). While our estimated species capture rate of 80 % is slightly below the 83 % that Richards et al. (2011) reported, it is higher than other diversity studies such as Russo et al.'s (2013) capture rate of 61 %. In a detailed survey of 140 years of museum specimens of northeastern US, 438 bee species were recorded (Bartomeus et al. 2013). Our bee collection efforts recorded 118 species, more than a quarter of the species currently present in northeastern America, if not more considering recent bee declines (Burkle et al. 2013).

While most of the species we collected in high abundance are from the family Halictidae, the most abundant species was *B. impatiens* (Apidae). *B. impatiens* is a significant pollinator of many greenhouse crops and is often used as a managed bee. Historically, *B. impatiens* has been a common species, hence the name 'common eastern bumble bee', but since the new millennium this species has become even more widespread doubling and sometimes even tripling in abundance across North American bee surveys (Tripodi and Szalanski 2015; Colla et al. 2012; Cameron et al. 2011; Colla and Packer 2008). Similar studies also report *B. impatiens* as the most abundant species (Russo et al. 2013; Matteson et al. 2008), with increased population levels likely influenced by propagation of this species to supplement commercial agricultural pollination (Tripodi and Szalanski 2015). Recent population increases might also be attributable to this species' range extending northward with climate change (Kerr et al. 2015). On the low end of the abundance spectrum, 46 of the bee species collected were single occurrences, which are well distributed over all five represented families. This indicates the New Hampshire bee community may be a

Table 2 Species level network statistics for wild bees collected from sweep net samples

Bee family	Bee species	Abundance	Degree/floral hosts	Normalized degree	PSI	Node duration
Andrenidae	*Andrena braccata*	2	1	0.03	0.03	0.09
	Andrena carlini	1	1	0.03	0.08	0.09
	Andrena commoda	3	3	0.09	0.03	0.27
	Andrena confederata	1	1	0.03	0.11	0.09
	Andrena crataegi	2	1	0.03	0.10	0.09
	Andrena cressonii	7	5	0.15	0.04	0.45
	Andrena dunningi	3	3	0.09	0.10	0.27
	Andrena erigeniae	2	2	0.06	0.20	0.18
	Andrena hilaris	1	1	0.03	0.01	0.09
	Andrena imitatrix	1	1	0.03	0.05	0.09
	Andrena krigiana	1	1	0.03	0.08	0.09
	Andrena miserabilis	4	2	0.06	0.25	0.18
	Andrena nivalis	4	3	0.09	0.04	0.18
	Andrena perplexa	5	3	0.09	0.06	0.18
	Andrena regularis	1	1	0.03	0.01	0.09
	Andrena sigmundi	2	2	0.06	0.07	0.18
	Andrena simplex	1	1	0.03	0.02	0.09
	Andrena vicina	2	2	0.06	0.13	0.18
	Andrena wilkella	11	4	0.12	0.11	0.18
	Calliopsis andreniformis	3	2	0.06	0.01	0.18
	Calliopsis nebraskensis	2	1	0.03	0.03	0.09
	Protandrena bancrofti	1	1	0.03	0.01	0.09
Apidae	*Anthophora terminalis*	3	3	0.09	0.03	0.18
	Bombus bimaculatus	44	8	0.24	0.30	0.55
	Bombus griseocollis	3	2	0.06	0.05	0.27
	Bombus impatiens	388*	20*	0.59*	0.70	0.82*
	Bombus perplexus	1	1	0.03	0.13	0.09
	Bombus vagans	38	15	0.44	0.19	0.55
	Ceratina calcarata	5	4	0.12	0.13	0.27
	Ceratina dupla	5	3	0.09	0.03	0.27
	Ceratina mikmaqi	4	3	0.09	0.06	0.18
	Melissodes subillata	3	2	0.06	0.14	0.18
	Mellita eickworti	1	1	0.03	0.02	0.09
	Xylocopa virginica	24	9	0.26	0.14	0.64
Colletidae	*Hylaeus affinis*	1	1	0.03	0.02	0.09
	Hylaeus mesillae	1	1	0.03	0.05	0.09
	Hylaeus modestus	3	1	0.03	0.15	0.09
Halictidae	*Agapostemon virescens*	14	10	0.29	0.13	0.36
	Augochlorella aurata	5	4	0.12	0.24	0.27
	Augochloropsis metallica	1	1	0.03	0.33	0.09
	Halictus confusus	8	6	0.18	0.09	0.27
	Halictus ligatus	175	20*	0.59*	0.74*	0.55
	Halictus rubicundus	2	2	0.06	0.13	0.09
	Lasioglossum abanci	1	1	0.03	0.11	0.09
	Lasioglossum albipenne	3	2	0.06	0.18	0.18
	Lasioglossum cinctipes	2	2	0.06	0.06	0.18
	Lasioglossum coriaceum	1	1	0.03	0.13	0.09
	Lasioglossum cressonii	19	6	0.18	0.38	0.27

Table 2 continued

Bee family	Bee species	Abundance	Degree/floral hosts	Normalized degree	PSI	Node duration
	Lasioglossum fuscipenne	1	1	0.03	0.03	0.09
	Lasioglossum imitatum	1	1	0.03	0.07	0.09
	Lasioglossum leucozonium	4	1	0.03	0.40	0.09
	Lasioglossum lineatulum	1	1	0.03	0.07	0.09
	Lasioglossum paradmirandum	1	1	0.03	0.01	0.09
	Lasioglossum pectorale	1	1	0.03	0.03	0.09
	Lasioglossum pilosum	7	5	0.15	0.17	0.27
	Lasioglossum tegulare	1	1	0.03	0.01	0.09
	Lasioglossum versatum	17	7	0.21	0.10	0.45
Megachilidae	*Anthidium oblongatum*	1	1	0.03	0.20	0.09
	Heriades carinata	1	1	0.03	0.01	0.09
	Hoplitis spoliata	1	1	0.03	0.03	0.09
	Megachile centuncularis	1	1	0.03	0.10	0.09
	Megachile inermis	2	2	0.06	0.09	0.18
	Osmia inspergens	1	1	0.03	0.01	0.09

* Highlight the highest values for each factor

reserve of rare species and that long-term sampling is necessary to capture an accurate representation of local diversity. The collection of many new state records in this study also supports the need for continued sampling of bees in New Hampshire. Among the new records, we found a specimen of *Halictus tectus*, a species introduced from southern Europe as recently as year 2000 (Droege 2015). It appears that *H. tectus* is expanding its range with additional records from Pennsylvania (2005; bison.usgs.ornl.gov) and Maryland (2006–2013; www.discoverlife.org), and here we present the northern most record of this species in New Hampshire (2014; this study).

Plant–pollinator interactions

Although we found a higher bee and flower species richness in New Hampshire (Total Richness, TR = 97) than similar studies in Pennsylvania (TR = 89) and Illinois (TR = 80), we found fewer unique interactions (197, compared to 261 and 246 respectively; Russo et al. 2013; Burkle et al. 2013). The network weighted nestedness in the New Hampshire community was low, indicating that while diverse, this system is likely unstable and could be negatively impacted by disturbances. Connectance for this community is also very low, suggesting that this network is not robust and might lack the interaction complexity necessary for a stable ecosystem. Surprisingly, both weighted nestedness and connectance were at the lowest in the middle of the collection season when there was the highest diversity of both bees and flowering plants (Table 3). This may be due to the high number of specialist pollinators or possibly indicates that while more diverse, the floral resources available mid season may not be as broadly utilized as those available early or late in the season.

Our network analyses show that there is a large portion of specialists comprising the bee community (49 %) although the specialists' total interactions within the community are small (5 %) in comparison to the generalists. The most abundant pollinators in the community are *H. ligatus* and *B. impatiens*, which have the highest number of interactions as well as widest floral host breadth. Both of these species are native to North America, have wide distributions, and visit both native and introduced floral species (Richards et al. 2011). While neither species visits the entire floral suite sampled in this study, the loss of one or both species could cause serious changes to the New Hampshire ecosystem and as such should be considered keystone species. Unlike the abundance of specialist bee documented, there were relatively few specialist flowers (15 %) with both native and introduced representatives. Two introduced species of the genus *Trifolium* (clovers) supported both the highest number of unique interactions within the community as well as the highest abundance of bees. The number of bees supported by *T. repens* (white clover) was more than double any other flower species and it, along with *T. pratense* (red clover), appear to be key floral resources. Despite the importance of *Trifolium* and the large representation of other introduced flower species (39 %), overall the native flower species support the majority (52 %) of the bee population (the remaining 9 % are from flowers only determined to genus).
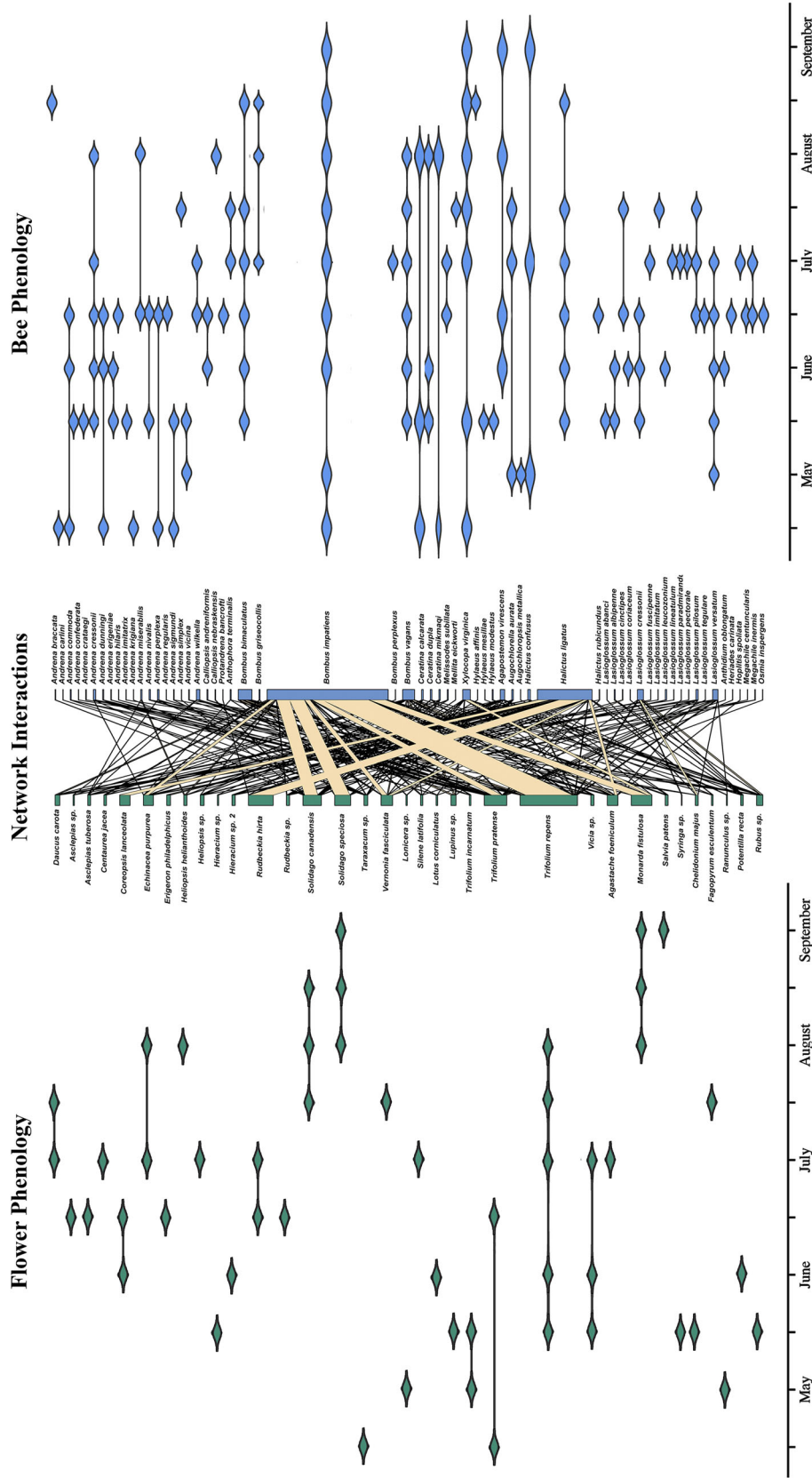
Fig. 4 Interaction network, bee and flower phenology duration. Flower phenology duration in *green* (*left*), bee phenology duration in *blue* (*right*). Plant–pollinator association network in *yellow* (*center*) with interaction line width proportionate to species abundance. (Color figure online)

Table 3 Full and seasonal community network statistics

	Weighted nestedness	Connectance	Number of bee species	Number of plant species	Total community size
Early	NA	0.24	15	5	20
Mid	0.49	0.10	53	24	77
Late	0.57	0.20	24	10	34
Full	0.51	0.08	63	34	97

Weighted nestedness could not be calculated for the early season due to the small size of the total community (denoted NA). Early = April and May; Mid = June and July; Late = August and September; Full = April to September

Phenology

In accordance with supporting the highest abundance of bees, *T. repens* had the longest bloom duration through most of the mid season and into the late season. However, despite supporting the high diversity of bee species, *T. pratense* had a relatively short bloom duration with bee specimens only collected early in the season and once at the onset of the mid season. Bloom duration does not appear to directly correlate with either diversity or abundance of bee visits as bloom duration can be very short and still support a wide diversity or abundance of bees. For example, *Rubus* sp. only has a brief bloom duration (sampled in a single collection event), but provided floral resources for 11 different bee species and 20 individuals. Many of the flower species have similar results. This indicates that even a brief appearance of a particular flower is import to bee foraging if it is a preferred floral resource.

Based on the full network (Fig. 4), it does not appear that any bee phenology follows a specific flower phenology. During the early part of the season both bee and flower species were at their lowest diversity (Supplementary Figure 3) and as flower variety increased towards the middle of the season so did bee diversity (Supplementary Figure 2). These data support the need for mixed forage of early-mid-late blooming flowers to sustain bee diversity. In the plant–pollinator network phenology (Fig. 4), *B. impatiens* had by far the longest foraging duration with *B. bimaculatus*, *B. vagans*, *H. ligatus* and *Xylocopa virginica* making significant contributions as well. The total bee phenology including both pan and sweep net sampling characterizes a greater number of bee species than the network phenology based on floral sweep net sampling alone. While there were no bee species present through the entire year in the total bee phenology, representatives of bees from all five families, even the least abundant Colletidae, were present throughout the entire season. By a narrow margin *A. aurata* had the longest flight duration with *A. virescens*, *H. ligatus*, *Lasioglossum coriaceum*, *L. tegulare*, *L. pilosum*, and *L. versatum* collected almost as frequently.

Conclusion

The conservation of wild bees is essential for the pollination services they provide to natural ecosystems and agricultural systems. Yet in order to implement conservation procedures, we must have a basic understanding of what species are present and in what habitat and functional role. Here we report a broad diversity of bee species in eastern New Hampshire and their floral associations across the foraging season. Many of the bee species documented in this study represent new state records for New Hampshire. There are likely many more species to be discovered as indicated by our species rarefaction test. Previous long-term studies also support this notion, as 1 year of intensive sampling cannot fully represent the bee community due to considerable species composition turnover in most ecosystems (Minckley et al. 1999; Grixti and Packer 2006). In addition to the broad diversity of bee species, we also found at least one introduced species that appears to be expanding its range. We identified potential keystone species in both the bee and floral community and determined that introduced floral species are an important component of the current ecosystem. We also found flower diversity is important for supporting the bee community throughout the season. These data suggest that increasing the diversity of early season blooming flowers may have a positive impact on the bee community and possibly strengthen stability of network interactions early in the season. As might be expected, New Hampshire has unique plant–pollinator interactions and community diversity compared to similar studies conducted elsewhere in the northeast.

Bee species diversity is crucial for ecosystem functioning and stability of agricultural production (Cardinale et al. 2012; Bommarco et al. 2013). In order to conserve species diversity and richness it is necessary to understand the components and interactions within the ecosystem we aim to protect. This study is the first step in ongoing efforts to document the bee community, plant–pollinator networks, and respective phenologies in northern New England.

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