



Decline of bumble bees in northeastern North America, with special focus on *Bombus terricola*



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ABSTRACT

Concerns about the rapid and severe declines of many bumble bee (*Bombus* spp.) species in Europe, and more recently North America, have spurred research into the extent and possible causes for these losses. Drawing conclusions has been difficult due to a lack of long-term data, especially for specific regions that may have different factors at play than the global trend. In this study, 150 years of *Bombus* records in the state of New Hampshire from the University of New Hampshire Insect Collection were examined. This allowed for changes in abundance and distribution to be tracked over time, with focus on species designated of greatest conservation need by NH Fish & Game Department. Floral records also provided insight into the diet breadth of these species, which may affect their vulnerability. Evidence of drastic decline was found in *Bombus affinis*, *Bombus fervidus*, and *Bombus terricola*, as well as significant decline in *Bombus vagans* with data suggesting it has been ecologically replaced by *Bombus impatiens* over time. We suggest *Bombus vagans* receive future conservation consideration. Our analyses found a severe constriction of the geographic range of *Bombus terricola* to high elevation regions in the latter half of the 20th century, and its role as pollinator of several alpine plants necessitates immediate conservation action.

1. Introduction

Wild bee declines, particularly in bumble bees (*Bombus* spp.), have been documented worldwide (Freitas et al., 2009; Bartomeus et al., 2013; Senapathi et al., 2015). The majority of these losses have occurred in the second half of the 20th century, coinciding with the general timeframe of the global industrialization of agriculture and the resulting conversion and degradation of bee habitat (Donovan, 1980, Kosior et al., 2007, Williams and Osborne, 2009, Potts et al., 2010, Meeus et al., 2011, Bommarco et al., 2012, Vanbergen and Insect Pollinators Initiative, 2013, Goulson et al., 2015). Wild bees rely on temporally staggered food sources throughout their flight season, and for social species such as bumble bees, to support a colony. Present day agriculture consists mainly of mass-flowering monocultures that offer few benefits for wild bees outside of their short blooming period, which provides a pulse of resources but only for a small fraction of the growing season (Mandelik et al., 2012; Vanbergen and Insect Pollinators Initiative, 2013). Many bumble bees also require subterranean nesting sites, and the disturbance of these sites through mowing, tilling, or paving can be detrimental to their ability to establish persisting populations (Kremen and Ricketts, 2000, Goulson et al., 2008, Williams and Osborne, 2009, Goulson et al., 2015). At the same

time, this reduces or eliminates wild forage that bees could use to supplement their diet before and after crops have bloomed (Goulson et al., 2009, Williams and Osborne, 2009). In the past, leguminous cover crops, particularly clover, were used to return nitrogen to the soil between growing seasons; this was an extremely valuable food source for species of long-tongued bumble bees specializing on legumes. However, with the advent of nitrogenous fertilizers, this practice has all but disappeared (Carvell et al., 2006; Grixti et al., 2009; Williams and Osborne, 2009). The extensive conversion of natural land to agriculture that occurred in the 20th century, and in many parts of the world continues unabated, has resulted in the degradation or total loss of massive amounts of bee habitat.

Although some of the documented gradual *Bombus* declines can be traced back to the changes in land use during the mid-20th century, several historically common species have been experiencing severe rapid declines within only the last few decades (Colla and Packer, 2008; Grixti et al., 2009; Cameron et al., 2011; Colla et al., 2012). The causes are likely numerous and cumulative; there is evidence that pesticides, parasites, genetics, inbreeding, climate change, and diet simplification among other factors are contributing to recent bumble bee losses (Goulson et al., 2009, Goulson et al., 2015). The increased use of pesticides due to agricultural expansion has been implicated as a main

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driver of honey bee decline (Goulson et al., 2015; Tison et al., 2016; Tsvetkov et al., 2017). Herbicides kill weeds and wildflowers used as bee forage, making them unavailable for bees (Goulson et al., 2015, Potts et al., 2010). The invention of neonicotinoid insecticides in the 1990s coincides with the beginning of many bumble bee declines (Goulson et al., 2009). The acute toxicity of neonicotinoids is high, and can affect the richness and abundance of bee communities exposed to them (Mallinger et al., 2015). However, studies now show they cause many lasting effects as well, such as reduced queen and worker production, impaired social behavior and foraging efficiency, and suppressed immunity to parasites (Feltham et al., 2014; Goulson et al., 2015; Mallinger et al., 2015; Tison et al., 2016). Bees can be exposed not only via contact with airborne insecticides, but also in the nectar and pollen of contaminated plants, which can occur some distance away from sprayed fields due to drift or persistence in soil and water (Goulson et al., 2015, Hladik et al., 2016).

The spread of parasites from commercially raised bumble bees is also strongly implied as a factor in recent declines. In the early 1990s colonies of *Bombus occidentalis*, a widely distributed western species bred for commercial greenhouse pollination, were shipped to Europe to be raised alongside another popular pollinator, *B. terrestris*. It is believed that during this period of contact, *B. occidentalis* picked up a new strain of the parasite known as *Nosema bombi* (Goulson et al., 2009, Brown, 2011, Cameron et al., 2011, Meeus et al., 2011). Commercially managed bumble bee colonies can be perfect breeding grounds for parasites, due to high host density and plentiful food sources that allow infected bees to survive with loads that would be lethal in the wild (Meeus et al., 2011). This lack of host die-off may foster greater parasite virulence as well (Meeus et al., 2011; Cameron et al., 2016). Though this pathogen is found in North America, it has been suggested that bringing these managed colonies back into the country acted as a re-introduction, expanding its numbers and intensifying pressure on native bees (Cameron et al., 2016). After only a few years, the industry for *B. occidentalis* collapsed when the colonies were overwhelmed by parasites, and *B. impatiens*, a species native to the eastern U.S., is now used in its place (Winter et al., 2006). Evidence from numerous studies points towards pathogen spillover from these colonies into wild populations of *B. occidentalis* and other native species, likely through contact with escaped bees on flowers during foraging (Goulson et al., 2009, Otterstatter and Thomson, 2008, Meeus et al., 2011, Graystock et al., 2014). The prevalence of *N. bombi* in several now-declining native bumble bees, including *B. affinis* and *B. terricola*, increased in the years immediately following the *B. occidentalis* importation event and these species continue to harbor high parasite loads today (Cameron et al., 2011, 2016).

In the state of New Hampshire, four bumble bee species have been designated in the NH Fish & Game Department's 2015 Wildlife Action Plan as being of greatest conservation need: *Bombus affinis* (rusty-patched bumble bee), *B. terricola* (yellow-banded bumble bee), *B. fervidus* (golden northern or yellow bumble bee), and *B. pensylvanicus* (American bumble bee). *Bombus affinis* has suffered possibly the most drastic declines, with an estimated range retraction of at least 87% (Cameron et al., 2011). Only a few populations of *B. affinis* are now known from the Midwest, and it has been absent from recent surveys in Pennsylvania, Maine, Massachusetts, and New Hampshire, where it was known historically (Donovall and van Engelsdorp, 2010; Bushmann and Drummond, 2015; Goldstein and Ascher, 2016; Tucker and Rehan, 2016). *Bombus pensylvanicus* was once one of the most widespread bumble bee species in North America, however, now it appears absent from the northern and eastern portions of its range, a 23% range reduction (Cameron et al., 2011). Currently, it primarily persists in the Gulf States and parts of the Midwest (Gixti et al., 2009, Lozier and Cameron, 2009, Warriner, 2011, Warriner, 2012, Figueroa and Bergey, 2015). *Bombus terricola*, on the other hand, only remains known in high-elevation refuges in the northeast and Appalachian Mountains, its range having shrunk 31% (Gixti et al., 2009; Cameron et al., 2011;

Bushmann and Drummond, 2015; Tucker and Rehan, 2017). The decline of *Bombus fervidus* has been estimated at 50%, and its disappearance has been noted in multiple studies (Colla and Packer, 2008, Colla et al., 2012, Bushmann and Drummond, 2015, Bartomeus et al., 2013). Concurrent with these losses, a small number of generalist species have tolerated or even benefited from agriculture and urban development, expanding their ranges, becoming more abundant, and possibly coming to dominate ecosystems (Colla and Packer, 2008; Goulson et al., 2008; Bommarco et al., 2012; Colla et al., 2012; Morales et al., 2013). In New England, the most notable of these is *Bombus impatiens* (Colla and Packer, 2008; Colla et al., 2012; Tucker and Rehan, 2016).

The lack of information pertaining to bumble bee declines, particularly in New England, has been a roadblock to prescribing and justifying conservation action for these species of concern. Data on native bumble bee ecology and floral associations, as well as historical abundances and distributions, are all vital to informing current and future management action. Obtaining this information for regionally specific populations will allow a better understanding of overall trends and drivers of decline, along with what measures can be taken to preserve these species across their range. Thus, the aims of this study are to, 1) track shifts in abundance and distribution over the past 150 years for *Bombus* species of greatest conservation need in the state of New Hampshire, and, 2) determine habitat requirements through plant-pollinator interactions for the state's bumble bee species and document changes therein over time.

2. Methods

2.1. Specimens and records

Bombus specimens for this study were made available from the University of New Hampshire Insect Collection (UNHC), as well as from field collections performed by the Rehan lab during summers of 2014–2016 (Tucker and Rehan, 2016, 2017). All specimens were identified to species using the interactive identification guides on DiscoverLife.org and recent taxonomic literature (Mitchell, 1962; Williams et al., 2014) and are retained at the UNHC. Specimens were labeled with available metadata pertaining to location, date, collection method, and floral host. Floral records, particularly for historical specimens, were cross-referenced for accuracy with original journal entries from collectors and contemporary databases. A small number of floral hosts were recorded with a common name identifiable only to the family level and were excluded from floral association analyses. All specimen records and distribution data are available for download from the University of New Hampshire Insect Collection web portal: <https://unhcollection.unh.edu/database/>. The multiple datasets were compiled into a single New Hampshire *Bombus* database, and each record was sorted into one of five periods, determined by the earliest and latest records: 1867–1896, 1897–1926, 1927–1956, 1957–1986, and 1987–2016. Specimens missing collection date data were excluded from analyses. Thirty years was chosen as the time frame for each period as the majority of severe *Bombus* declines have occurred in the last three decades, and much of the agricultural development in the United States falls into these designations. Data in the 1897–1926 period are referred to as “historical” while data in the 1987–2016 period are referred to as “recent” here forward. These two periods had the most records with 1544 and 1548 bumble bee specimens respectively (Table S1).

2.2. *Bombus* population trends

Relative abundance of *Bombus* species across time periods was used as the metric of determining status for each bumble bee to avoid bias due to periods of low sample size. Some *Bombus* species had insufficient records for reliable conclusions on population status. These were classified as ‘Data Deficient’ in Table 1. Species defined as data deficient

Table 1
Status of northeastern *Bombus*.

	Stable/no change	Increasing	Declining	Data deficient
<i>Bombus affinis</i>			1,2,3,4,5,6 ^a	
<i>Bombus ashtoni</i>			1,3,4,5	^a
<i>Bombus bimaculatus</i>	2,3,4,5	1,4 ^a		
<i>Bombus borealis</i>	3,5		1,4	^a
<i>Bombus citrinus</i>	4,5	1	3	^a
<i>Bombus fernaldae</i>	5		4	1 ^a
<i>Bombus fervidus</i>			1,3,4,5,6 ^a	
<i>Bombus griseocollis</i>	3,4,5	1		^a
<i>Bombus impatiens</i>	2,5	1,3,4 ^a		
<i>Bombus pensylvanicus</i>			1,2,3,4,5,6	^a
<i>Bombus perplexus</i>	3,5 ^{a,b}	1		
<i>Bombus rufocinctus</i>	5	3,4		1 ^a
<i>Bombus sandersoni</i>	1,5 ^{a,b}		4	
<i>Bombus ternarius</i>	4,5	3 ^a	1	
<i>Bombus terricola</i>			1,2,3,5,6 ^a	
<i>Bombus vagans</i>	4,5		1,3 ^a	

1 Bartomeus et al. (2013). [Northeast U.S.] – note this study used a subset of the UNHC records.

2 Cameron et al. (2011). [Eastern U.S.]

3 Colla and Packer (2008). [Ontario, Canada].

4 Colla et al. (2012). [Eastern U.S.]

5 IUCN Red List. [North America].

6 New Hampshire Fish & Game Wildlife Action Plan 2015. [NH].

^a This study.

^b Limited data.

comprised < 1% of total *Bombus* collected and were present in fewer than three of five time periods. This eliminated seven species: *B. ashtoni*, *B. borealis*, *B. citrinus*, *B. fernaldae*, *B. griseocollis*, *B. pensylvanicus*, and *B. rufocinctus*. These species were still used in plant-pollinator analyses if they had associated floral records.

To estimate the species richness of the bee communities sampled and determine how well the community was sampled a rarefaction test was conducted with ACE and ACE-1 (Chao and Lee, 1992), Chao-1 (Chao, 1984, 1987; Colwell and Coddington, 1994), and Jackknife (Burnham and Overton, 1978, 1979) estimates using the R ‘SPECIES’ package (Wang, 2011). To determine changes in the abundance of each species between historic (1891–1926) and recent (1987–2016) time periods, we calculated the relative abundance as the number of individuals collected for each species divided by the total collected in that sampling period. We used Z-tests of equal proportions to determine whether the relative abundance of each species differed significantly between the two-time periods. Z-test values were generated using `z.test` in R version 3.2.2.

2.3. Network analysis

Analyses of plant-pollinator interactions for bumble bee records with associated floral data were performed in R 3.3.2 using the package “bipartite” (Dormann et al., 2008). Interaction networks were generated for each time period apart from 1927 to 1956, as well as for all floral records combined, with the `plotweb` function. The 1927–1956 period was excluded because it contained only one floral record; however, it was incorporated into the combined network for all collection years. The `networklevel` function was used to examine community structure by creating indices of weighted nestedness and connectance. Weighted nestedness considers not only presence or absence of interactions, but also their frequencies in order to evaluate the overlap in interactions between generalist and specialist species; in a nested system, the diet of specialist pollinators is a subset of that of the generalists (Galeano et al., 2009; Delmas et al., 2017). Thus, a value of 1 = perfectly nested and 0 = no overlap. Connectance determines the resiliency of the system to species loss by measuring the proportion of utilized plant-pollinator interactions to all possible associations (Dunne

et al., 2002). In this case, 1 = a system where all flowers are pollinated by all bees, and thus individual species loss is inconsequential, and 0 = a system in which each flower is pollinated only by one bee and each bee visits only one flower, rendering the system highly vulnerable should any species be lost. The function `specieslevel` was used to examine the contributions of individual species to the system and identify participants playing unique or important roles, through degree, normalized degree, and Pollination Service Index (PSI). Degree is a basic measure of the number of unique interactions for each bee (how many floral hosts) or plant (how many pollinators), while normalized degree adjusts this value against the total number of possible interactions in the system, allowing for unbiased comparisons between species (Dormann et al., 2016). PSI determines the importance of a pollinator species to all other plant species in the ecosystem, or vice versa; it is effectively a measure of ecological role, where 1 = a species which provides a highly unique specialized service, or interacts with an immense number of other species, either of which are critical to the persistence of the system, and 0 = a species that is functionally irrelevant to the system, where its role is redundant and its loss would be inconsequential.

2.4. Geographic distribution analysis

Shifts in distribution and abundance of four *Bombus* species over time were mapped using QGIS 2.18.3. Three species, *Bombus affinis*, *B. fervidus*, and *B. terricola*, were chosen for analysis due to their status as Species of Greatest Conservation Need. For comparison, *Bombus impatiens*, a species thought to be increasing, was also analyzed. Background layers included a 100-meter resolution natural earth of the United States layer obtained from the USGS, and 1:1,000,000-scale county boundaries of the United States from The National Map (TNM). Specimens lacking a collection date were excluded from the maps, but were utilized in the network analysis for all years.

3. Results

3.1. Status of *Bombus*

A total of 3333 bumble bee specimens comprising 16 *Bombus* species were analyzed (Table S1). Three species were collected across all sampling periods: *B. impatiens*, *B. fervidus*, and *B. vagans*. *Bombus impatiens* was the most frequently collected with 1209 specimens, followed by *B. terricola* with 583 specimens. The five least collected species were *B. rufocinctus* (1 specimen between 1987 and 2016), *B. pensylvanicus* (6 specimens), *B. fernaldae* (8 specimens), *B. ashtoni* (15 specimens), and *B. sandersoni* (37 specimens). Two of the Species of Greatest Conservation Need, *B. affinis* and *B. fervidus*, were represented by 140 and 308 specimens, respectively. Rarefaction point estimates of sampling completeness indicate a highly representative species sampling for most time periods (Jackknife = 67–100%), and had similar sampling completeness estimates from all test types (Table S3).

Four *Bombus* species were found to be in decline: *Bombus affinis*, *B. fervidus*, *B. terricola*, and *B. vagans* (Tables 1 & S2). The relative abundance of *B. affinis* has decreased over time, beginning in the 1950s and declining rapidly thereafter. It comprised 5.8% of specimens historically, but only 0.01% in recent years represented by one specimen in 1992 and one in 1993 (Table S1). While *B. fervidus* is one of only three species to be collected in all time periods, it too decreased in both relative and raw abundance. Historically, *B. fervidus* highest relative abundance was 14.4% of total *Bombus*, but it has steadily fallen to its lowest point recently with a relative abundance of only 0.05%. The majority of *B. terricola* were collected historically, with 366 specimens and a relative abundance of 23.7%. In contrast, 105 specimens were collected recently, with the lowest relative abundance of 6.8%. *Bombus vagans* experienced its highest raw counts historically (287) with its highest relative abundance (37.8%) in the 1867–1896 time period. There were substantially fewer *B. vagans* collected in recent years (166

individuals, relative abundance of 10.7%).

Three *Bombus* species were found to be increasing in both absolute and relative abundance over time: *B. bimaculatus*, *B. impatiens*, and *B. ternarius* (Tables 1 & S2). *Bombus impatiens* was common historically, but over time increased in relative abundance and became the most abundant species in recent collections. Between historic and recent periods, the relative abundance of *Bombus impatiens* rose from 23.5% to 51.6%, despite equal sample size (Table S1). Incidence of *B. bimaculatus* increased greatly between the historic and recent times periods (1897–1926 to 1987–2016, 2.7% to 11.2%). *Bombus ternarius* has experienced a more subtle population expansion from historic to recent years with increases in both relative and raw abundance (4.9% and 76 specimens, to 7.7% and 119 individuals). *Bombus perplexus* and *B. sandersoni*, while represented in multiple sampling periods, were consistently found at low numbers, and thus classified as no change (Table S2).

3.2. Plant-pollinator interactions

The total 150-year plant-pollinator network dataset was comprised of 108 flower and 13 bumble bee species, with 250 unique interspecies interactions and 1609 total interactions between species (Fig. 1). The community composition and richness of the networks varied greatly between 30-year time periods. The two time periods with the greatest number of records (1897–1926, 1987–2016) had the highest species richness (Fig. S2, 10 *Bombus* and 52 flower species; Fig. S4, 9 *Bombus* and 46 flower species), while those periods with few records (1867–1896, 1957–1986) documented fewer species (Fig. S1, 5 *Bombus* and 12 flowers; Fig. S3, 5 *Bombus* and 11 flowers). The recent time period had the greatest complexity of species interactions (Table S4), even compared with the total 150-year dataset (weighted nestedness = 0.70 compared to 0.63). Connectance within each time period was relatively low but consistent (0.24–0.3), with an even lower (0.18) connectance for the total 150-year dataset.

At the species level, *Bombus impatiens* had the most interactions (914) overall and broadest floral breadth with 61 unique interactions (Table S5). *Bombus vagans* had almost as many unique interactions (56) although only 210 total interactions. One or both of these species held the highest degrees and normalized degrees for all time periods except 1957–1986, where *Bombus terricola* represented the majority of interactions from that time period (Tables S5, S6). The PSI values revealed that *B. impatiens* was a highly important generalist in every time period it was present (Table 2). In the recent time period (1987–2016), *Bombus terricola* appears essential to the system (PSI = 1) due to its interaction with an *Aster* sp., which was not associated with any other bumble bee species. However, this record could overestimate the PSI for *B. terricola*, if *Aster* sp. is synonymous with *Aster novae-angliae*, as we have no further information to clarify the plant species identity from the specimen labels.

Four plants shared the highest count of 7 unique interactions (Tables S7, S8): *Trifolium pratense* (red clover), *Aster* sp. (aster), *Rhus glabra* (smooth sumac), and *Heliopsis helianthoides* (oxeye sunflower). None of these plants were sampled in more than two periods each. *Epigaea repens* (trailing arbutus) had the greatest number of unique interactions (3) between 1867 and 1896, while *Vaccinium* sp. had the greatest number of unique interactions between 1957 and 1986 (3). *Trifolium pratense* had the most unique interactions (7) and *Trifolium repens* (white clover) had the greatest overall number of interactions (193). Of the 108 flower species sampled, 43.5% was associated with only one bumble bee species. *Solidago latifolia* (now *Solidago flexicaulis*, zigzag golden rod) was the most important floral resource in the total 150-year system (PSI = 1; Table S8) followed by *E. repens* (0.42). *Solidago* sp. and *S. latifolia* were both critical to the community during 1957–1986, while *Aster* sp. was most fundamental between 1897–1926 and 1987–2016. Between 1867 and 1896, *E. repens* and *Solidago lanceolata* (lance-leaved goldenrod) were the most important floral

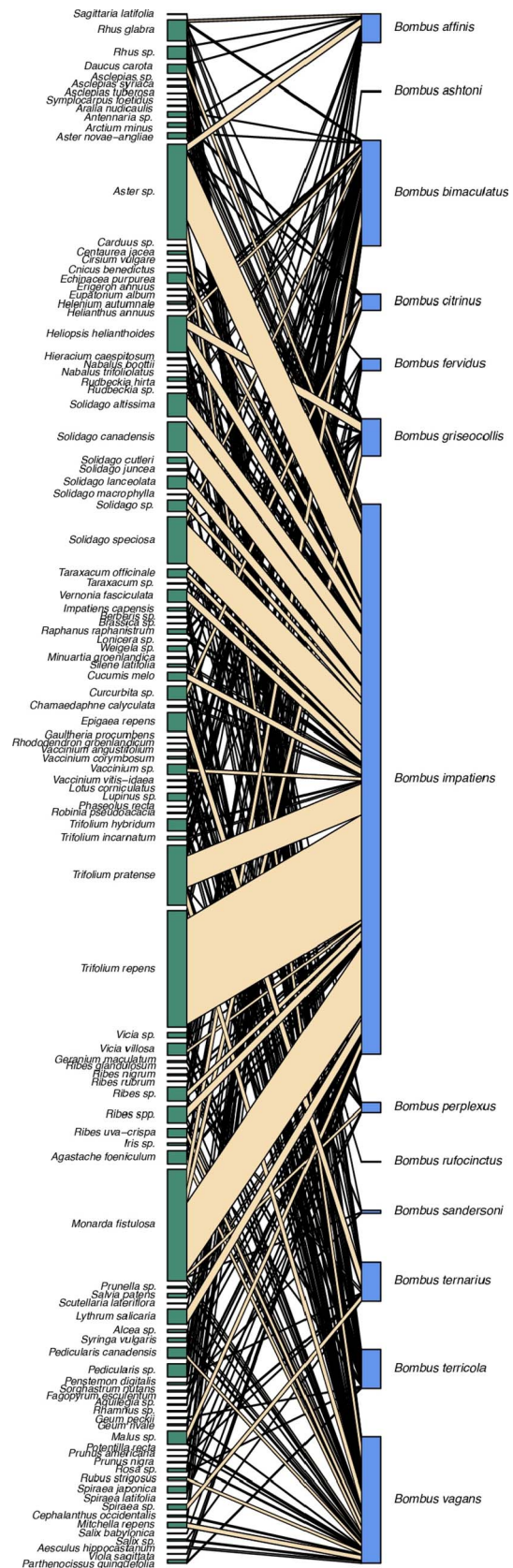


Fig. 1. Plant-pollinator network comparing relationships between bumble bees and flowers for all collection years 1867–2016 combined.

Table 2
Pollinator Service Index (PSI) for *Bombus* with documented floral associations. 1927–1956 omitted from individual analysis due to insufficient data.

	All years	1867–1896	1897–1926	1957–1986	1987–2016
<i>Bombus affinis</i>	0.17	0.73	0.20	–	–
<i>Bombus ashtoni</i>	1.00	–	–	1.00	–
<i>Bombus bimaculatus</i>	0.36	0.27	0.53	–	0.32
<i>Bombus citrinus</i>	0.41	–	0.41	–	–
<i>Bombus fervidus</i>	0.55	–	0.55	–	–
<i>Bombus griseocollis</i>	0.21	–	0.03	–	0.21
<i>Bombus impatiens</i>	0.74	0.95	0.62	–	0.80
<i>Bombus perplexus</i>	0.18	–	0.31	–	0.21
<i>Bombus rufocinctus</i>	0.07	–	–	–	0.07
<i>Bombus sandersoni</i>	0.17	–	–	1.00	0.19
<i>Bombus ternarius</i>	0.65	0.92	0.39	1.00	0.02
<i>Bombus terricola</i>	0.46	–	0.28	0.48	1.00
<i>Bombus vagans</i>	0.43	0.78	0.53	0.42	0.25

resources.

3.3. Geographic distribution analysis

Spatial mapping of bumble bee records allowed for a visualization of shifts in abundance and distribution over time. *Bombus terricola* shows a distinct declining trend over time (Fig. 2). Early records indicate it was present throughout the state. Through the mid-20th century its range constricted, with records only from northern New Hampshire. From 1987 to 2016, an intensely sampled period, only a single specimen was found in the southern half of the state, in 1997. All other recent records are restricted to the White Mountains region. This illustrates not only a constriction of its range northward, but also in recent years to higher elevations; historic specimens were from an average elevation of 61 m, while recent records are from an average of 527 m. This represents a significant shift in elevation (466 m; $Z = -13.68$, $p < 0.0001$). In contrast, *B. impatiens* shows a clear range expansion (Fig. 3). Records of *B. impatiens* were historically centered in southern New Hampshire with an average elevation of 29 m, and only in the most recent time period has this species been collected from the northern part of the state. This species remains at relatively low elevations with an average elevation of 37 m across all recent collections.

4. Discussion

In this study, records of *Bombus* collected in New Hampshire spanning a 150-year period were analyzed to evaluate the status of the state's bumble bee species through changes in abundance and distribution over time as well as to assess plant-pollinator interactions to provide valuable information for conservation efforts. Results support the listing of *B. affinis*, *B. fervidus*, and *B. terricola* as Species of Greatest Conservation Need by the New Hampshire Fish & Game Department, and propose that *B. vagans* receive future conservation status considerations. *Bombus* plant-pollinator communities were shown to be highly nested but low in connectance, indicating a vulnerability to species loss (Table S4). *Bombus impatiens* was found to be highly important to the system due to its generalist floral associations (Table 2), and *Trifolium pratense* and *T. repens* were central floral resources based on degree and quantity of interactions respectively (Table S7). The distribution of *B. terricola* has constricted over the last century, isolated at higher elevations, while *B. impatiens* has expanded its range in

addition to increasing in abundance (Figs. 2 and 3).

4.1. Status of *Bombus* in New Hampshire

Declines were found for three of the four species designated by the NH Fish & Game Department as Species of Greatest Conservation Need: *B. affinis*, *B. fervidus*, and *B. terricola* (Table 1). The fourth, *B. pennsylvanicus*, was represented by only six New Hampshire records, and thus was classified as Data Deficient. However, several other regional studies have noted its decline (Colla and Packer, 2008; Cameron et al., 2011; Colla et al., 2012; Bartomeus et al., 2013). *Bombus affinis* is experiencing severe declines and range constriction (Colla and Packer, 2008, Cameron et al., 2011, Colla et al., 2012, Bartomeus et al., 2013). It has also been found to be absent in recent surveys from other New England states (Bushmann and Drummond, 2015; Goldstein and Ascher, 2016). Based on New Hampshire records, the most severe decrease occurred between the 1957–1986 and 1987–2016 sampling periods, where relative abundance fell by 96.5% with the last specimen known from the state collected in 1993 (Table S1). Despite intensive sampling in the seacoast and White Mountains regions in the last few years, no individuals of *B. affinis* have been observed. Based on this information, its listing as federally endangered in 2017 (DOI, 2017) is well justified. *B. fervidus* and *B. terricola* were both collected within the last three years, confirming their continued, albeit much reduced, presence in the state (Tucker and Rehan, 2017). Isolated specimens of *B. fervidus* were also recorded in recent surveys from Massachusetts and Maine (Bushmann and Drummond, 2015, Goldstein and Ascher, 2016), yet its relative abundance has declined 96.4% between the 1897–1926 and 1987–2016 time periods. *B. vagans* is also experiencing a decline in New Hampshire. Bartomeus et al. (2013) observed this declining trend across the northeastern U.S., as did Colla and Packer (2008) in Canada, although it was considered stable in the eastern U.S. by Colla et al. (2012). In contrast, *B. impatiens*, as well as *B. bimaculatus* and *B. ternarius*, are increasing in New Hampshire. The expansion and growth of *B. impatiens* populations are well documented across the northeast (Colla and Packer, 2008; Colla et al., 2012; Bartomeus et al., 2013). This species is not only increasing, but also coming to dominate pollinator communities (Tucker and Rehan, 2016). *Bombus bimaculatus* has consistently been reported as stable or increasing (Table 1; Colla and Packer, 2008, Cameron et al., 2011, Colla et al., 2012, Bartomeus et al., 2013). While Bartomeus et al. (2013) found *B. ternarius* to be declining in the northeastern U.S., this species has been reported to be increasing in Canada (Colla and Packer, 2008), but stable in assessments across the broader eastern U.S. (Colla et al., 2012). Our data corroborate the Canadian assessment as we found an increase in the relative abundance of *B. ternarius* between historic and recent collections (Table S2).

4.2. Plant-pollinator communities

Analysis of floral records showed that *B. impatiens* is the dominant, generalist species, associated with 61 flower species over 150 years, although *B. vagans* provides services to a similar number of floral species (56; Table S5). Both bees were important pollinators historically; however, in recent years, the PSI value of *B. vagans* has dropped while that of *B. impatiens* has remained high (Table 2). This has led to an apparently reduced role of *B. vagans* in recent plant-pollinator systems compared to the previous century. A survey of the White Mountains National Forest in 2015 by Tucker and Rehan (2017) found 33 *B. vagans* and only 5 *B. impatiens*, whereas collections in the seacoast region (Tucker and Rehan, 2016) documented 43 *B. vagans* and 423 *B. impatiens*, further supporting the inverse relationship in the abundances of these two species observed in this study. The two species share 29 floral hosts, representing over half of the flowers recorded for *B. vagans*, suggesting competition for resources may exist. It has been proposed that the increase in abundance of *B. impatiens* can be partially attributed to the commercial rearing of this species and its subsequent escape into

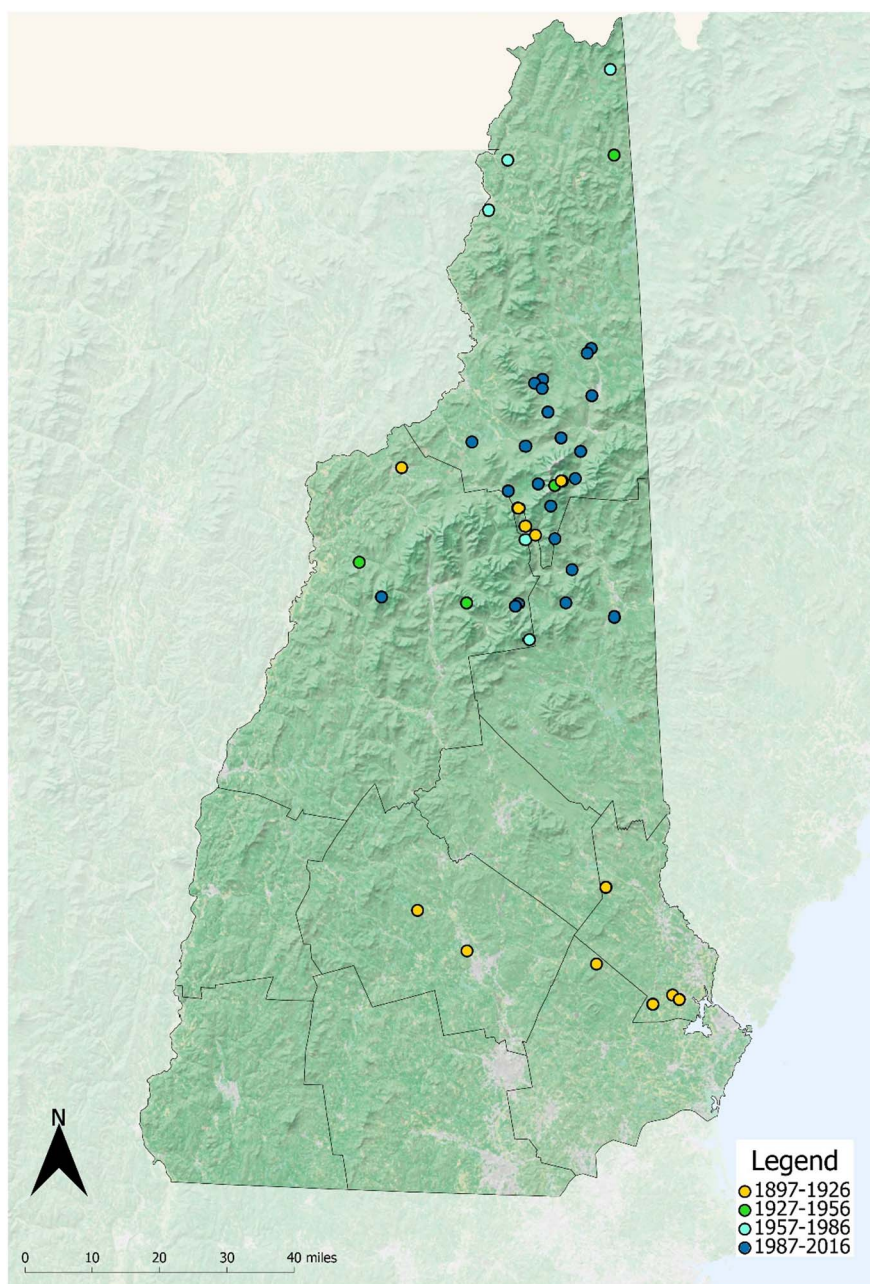


Fig. 2. Map of historical distributions of *Bombus terricola* in New Hampshire.

the wild (Tripodi and Szalanski, 2015; Cameron et al., 2016). Its higher tolerance of neonicotinoids, broad diet, early emergence, and long flight season likely has allowed it to take advantage of many types of floral resources, adapt to urbanization and shifting phenologies of floral resources (Colla and Packer, 2008; Scott-Dupree et al., 2009; Cameron et al., 2016). Taken together, both physiological and phenological factors are likely contributing to the spread of *B. impatiens* and perhaps equipping it to outcompete *B. vagans* when in such high abundances.

A high diversity of 108 flower species was documented in New Hampshire plant-pollinator communities, associated with 13 *Bombus* species (Fig. 1). Their abundance, richness, and composition differed greatly between time periods, as a function of sample size and collection location. Clover (namely *T. pratense* and *T. repens*) had some of the greatest unique and total interactions, with *T. repens* considered moderately important to the total 150-year community (PSI = 0.18) due to the large quantity of pollinators it serviced. Sumac, aster, and goldenrod were also commonly utilized by many species of *Bombus* (Table S7). Nearly half of the flower species recorded however were associated

with only one bee, and while much of this was influenced by quantity of historical records based on sample size, it is evident that plant-pollinator networks contain numerous complex, and possibly specialized interactions. This is supported by a high overall weighted nestedness value. Networks experienced consistently low connectance values across time periods, suggesting that while New Hampshire's bumble bee communities may be diverse and complex, they could be vulnerable to species loss. However, its consistency over time despite the declines of some species and changes in community composition suggest that while the state's bumble bee communities are not robust, they are stable.

4.3. Impacts of climate change and land use on New Hampshire *Bombus*

The shifting of *Bombus* ranges to higher elevations is not unique to *B. terricola*; this trend has been observed in other North American and European species as well, where bumble bees have lost portions of their southern range but have failed to expand to more northern latitudes, instead finding refugia at higher elevations (Ploquin et al., 2013; Kerr

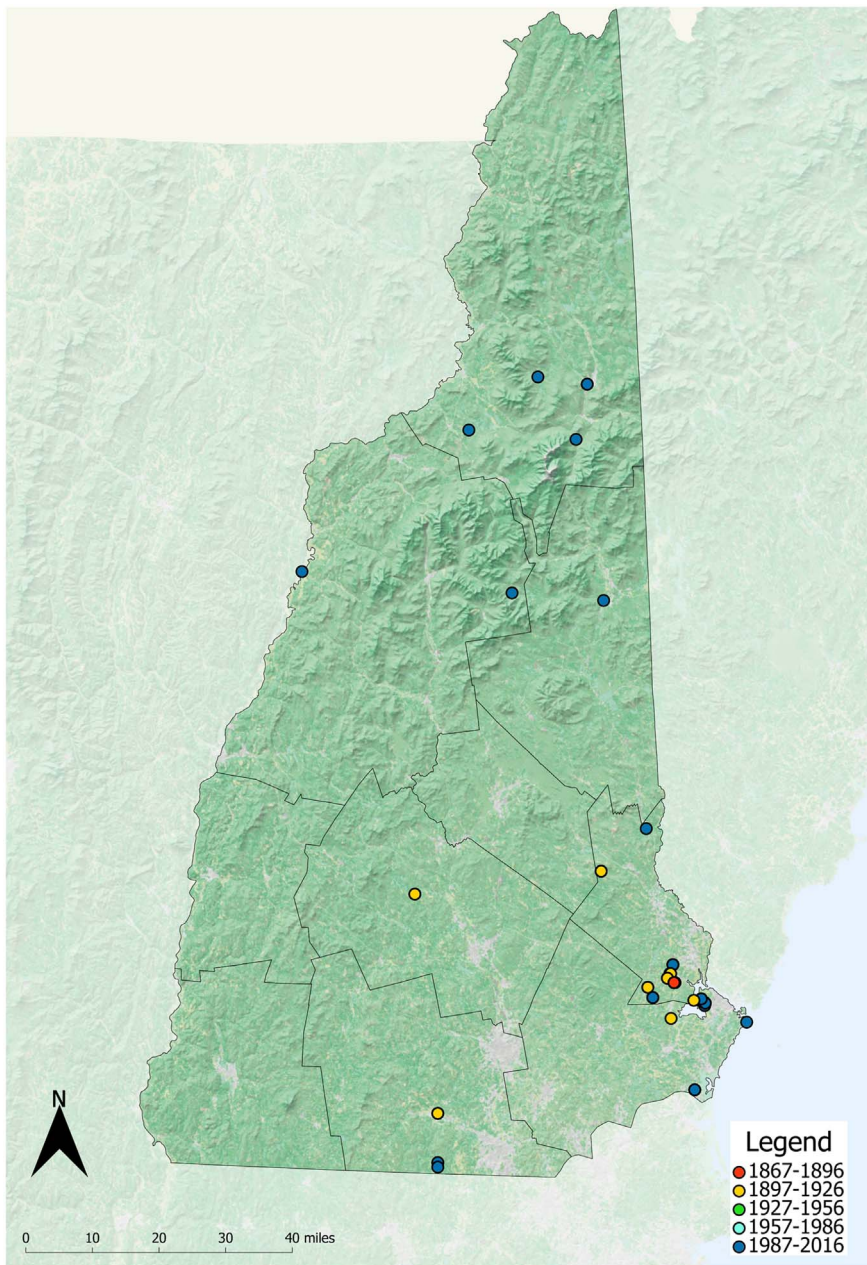


Fig. 3. Map of historical distributions of *Bombus impatiens* in New Hampshire.

et al., 2015; Pyke et al., 2016).

Network-level statistics indicate that New Hampshire plant-pollinator communities have low resilience to species loss, and this is consistent throughout all time periods (Table S4). A low connectance value was also observed by Tucker and Rehan (2016), further suggesting that bumble bee declines may be having unforeseen impacts on native flora. While historic host plants of *Bombus terricola* in southern New Hampshire are pollinated by other bees, it is possibly the main pollinator of a number of alpine, forest, and bog-dwelling species, some of which are very uncommon. The loss of *B. terricola* from New Hampshire may have negative consequences for plants like *Minuartia groenlandica* (Greenland stitchwort; Levesque and Burger, 1982) which is absent in the south (RI, CT, MA), but present across northern New England states (NH, VT, ME; <https://gobotany.newenglandwild.org>). *Geum peckii* (mountain avens) had not been recorded as a host plant for this bumble bee prior to examination of these records and is a threatened species endemic to the White Mountains of New Hampshire (<https://gobotany.newenglandwild.org>). When threatened by habitat loss and climate

change, ecological communities have shown to favor common generalists over specialists, leading to a homogenization of natural systems (Warren et al., 2001; Tschardt et al., 2002; Bommarco et al., 2010; Rowe et al., 2011; Carvalheiro et al., 2013). While species like *B. impatiens* may pollinate a large proportion of New England native plants, the loss of functionally redundant species can lead to greater vulnerability to disturbance and species loss in the future (Kaiser-Bunbury et al., 2017), and losing diet specialists can lead to possible detrimental impacts to rare or specialized flowering plants that can have ramifications for other taxa and trophic levels. While climate change is a long-term and large-scale issue, habitat loss, fragmentation, and degradation resulting from agricultural practices and urban development, particularly in the southern and southeastern portions of New Hampshire, can be mitigated or minimized to improve bumble bee population persistence, plant-pollinator system function, and increase resiliency (Carvell et al., 2017; Kaiser-Bunbury et al., 2017).

5. Conclusions

Wild bees, particularly bumble bees, are highly important pollinators for both agriculture and unmanaged ecosystems. They have experienced alarming declines in recent decades, and in order to effectively work towards their protection, information about their life histories, ecological roles, and distributional changes on a more local scale is needed. This study identified declines in four *Bombus* species in the state of New Hampshire, including a new species for consideration of greatest conservation need, and tracked these declines over 150 years with shifts in relative abundance and distribution. Plant-pollinator network associations of New Hampshire natural communities revealed the complexity of these ecosystems. Climate and land use change may be playing significant roles in the losses of northeastern bumble bees, with many effects still unknown with continued alterations to precipitation patterns, temperature, phenology and availability of native flora. Studies on bumble bee declines are time-sensitive and crucial to understanding how wild bees are being affected by anthropogenic changes to the planet. These data are needed so that we may prevent vulnerable pollinators from going extinct with far-reaching ramifications within ecosystems. This study adds critical floral associations and demographic data for New England bumble bees and those undergoing national decline, to better inform management decisions and conservation efforts going into the future.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2017.11.026>.

References

- Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M., Winfree, R., 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proc. Natl. Acad. Sci. U. S. A.* 110 (12), 4656–4660.
- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I., Öckinger, E., 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. B* 277 (1690), 2075–2082.
- Bommarco, R., Lundin, O., Smith, H.G., Rundlöf, M., 2012. Drastic historic shifts in bumble-bee community composition in Sweden. *Proc. R. Soc. B* 279 (1727), 309–315.
- Brown, M.J.F., 2011. The trouble with bumblebees. *Nature* 469, 169–170.
- Burnham, K.P., Overton, W.S., 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika* 65, 625–633.
- Burnham, K.P., Overton, W.S., 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology* 60, 927–936.
- Bushmann, S.L., Drummond, F.A., 2015. Abundance and diversity of wild bees (Hymenoptera: Apoidea) found in lowbush blueberry growing regions of downeast Maine. *Environ. Entomol.* 44 (4), 975–989.
- Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F., Griswold, T.L., Robinson, G.L., 2011. Patterns of widespread decline in North American bumble bees. *Proc. Natl. Acad. Sci. U. S. A.* 108 (2), 662–667.
- Cameron, S.A., Lim, H.C., Lozier, J.D., Duenns, M.A., Thorp, R., 2016. Test of the invasive pathogen hypothesis of bumble bee decline in North America. *Proc. Natl. Acad. Sci. U. S. A.* 113 (16), 4386–4391.
- Carvalho, L.G., Kunin, W.E., Keil, P., Aguirre-Gutiérrez, J., Ellis, W.N., Fox, R., Groom, Q., Henekens, S., Van Landuyt, W., Maes, D., Van de Meutter, F., Michez, D., Rasmont, P., Ode, B., Potts, S.G., Reemer, M., Roberts, S.P.M., Schaminée, J., WallisDeVries, M.F., Biesmeijer, J.C., 2013. Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants. *Ecol. Lett.* 16, 870–878.
- Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D., Goulson, D., 2006. Declines in forage availability for bumblebees at a national scale. *Biol. Conserv.* 132, 481–489.
- Carvell, C., Bourke, A.F.G., Dreier, S., Freeman, S.N., Hulmes, S., Jordan, W.C., Redhead, J.W., Sumner, S., Wang, J., Heard, M.S., 2017. Bumblebee family lineage survival is enhanced in high-quality landscapes. *Nature* 543, 547–549.
- Chao, A., 1984. Nonparametric estimation of the number of classes in a population. *Scand. J. Stat.* 11, 265–270.
- Chao, A., 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43, 783–791.
- Chao, A., Lee, S.M., 1992. Estimating the number of classes via sample coverage. *J. Am. Stat. Assoc.* 87, 210–217.
- Colla, S.R., Packer, L., 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodivers. Conserv.* 17, 1379–1391.
- Colla, S.R., Gadalla, F., Richardson, L., Wagner, D., Gall, L., 2012. Assessing declines of North American bumble bees (*Bombus* spp.) using museum specimens. *Biodivers. Conserv.* 21, 3585–3595.
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. B* 345, 101–118.
- Delmas, E., Besson, M., Brice, M., Burkle, L., Riva, G.V.D., Fortin, M., Gravel, D., Guimarães, P., Hembray, D., Newman, E., Olesen, J.M., Pires, M., Yeakel, J.D., Poisot, T., 2017. Analyzing ecological networks of species interactions. *bioRxiv*. <http://dx.doi.org/10.1101/112540>.
- Department of the Interior [DOI], 2017. Endangered and threatened wildlife and plants; endangered species status for rusty patched bumble bee. *Fed. Regist.* 82 (7), 3186–3188.
- Donovall III, L.R., van Engelsdorp, D., 2010. A checklist of the bees (Hymenoptera: Apoidea) of Pennsylvania. *J. Kansas Entomol. Soc.* 83 (1), 7–24.
- Donovan, B.J., 1980. Interactions between native and introduced bees in New Zealand. *N. Z. J. Ecol.* 3, 104–116.
- Dormann, C.F., Gruber, B., Freund, J., 2008. Introducing the bipartite package: analysing ecological networks. *R News* 8, 8–11.
- Dormann, C.F., Freund, J., Gruber, B., 2016. Visualising Bipartite Networks and Calculating Some (Ecological) Indices.
- Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Food-web structure and network theory: the role of connectance and size. *Proc. Natl. Acad. Sci. U. S. A.* 99 (20), 12917–12922.
- Feltham, H., Park, K., Goulson, D., 2014. Field realistic doses of pesticide imidacloprid reduce bumblebee foraging efficiency. *Ecotoxicology* 23, 317–323.
- Figuerola, L.L., Bergey, E.A., 2015. Bumble bees (Hymenoptera: Apoidea) of Oklahoma: past and present biodiversity. *J. Kansas Entomol. Soc.* 88 (4), 418–429.
- Freitas, B.M., Imperatriz-Fonseca, V.L., Medina, L.M., Kleinert, A.M.P., Galetto, L., Nates-Parra, G., Quezada-Euán, J.J.G., 2009. Diversity, threats and conservation of native bees in the Neotropics. *Apidologie* 40, 332–346.
- Galeano, J., Pastor, J.M., Iriondo, J.M., 2009. Weighted-interaction nestedness estimator (WINE): a new estimator to calculate over frequency matrices. *Environ. Model. Softw.* 24 (11), 1342–1346.
- Goldstein, P.Z., Ascher, J.S., 2016. Taxonomic and behavioral composition of an island fauna: a survey of bees (Hymenoptera: Apoidea: Anthophila) on Martha's vineyard, Massachusetts. *Proc. Entomol. Soc. Wash.* 118 (1), 37–92.
- Goulson, D., Lye, G.C., Darvill, B., 2008. Decline and conservation of bumble bees. *Annu. Rev. Entomol.* 53, 191–208.
- Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347 (6229). <http://dx.doi.org/10.1126/science.1255957>.
- Graystock, P., Goulson, D., Hughes, W.O.H., 2014. The relationship between managed bees and the prevalence of parasites in bumblebees. *PeerJ* 2, e522. <http://dx.doi.org/10.7717/peerj.522>.
- Grixti, J.C., Wong, L.T., Cameron, S.A., Favret, C., 2009. Decline of bumble bees (*Bombus*) in the American Midwest. *Biol. Conserv.* 142, 75–84.
- Hladik, H.L., Vandever, M., Smalling, K.L., 2016. Exposure of native bees foraging in a landscape to current-use pesticides. *Sci. Total Environ.* 542, 469–477.
- Kaiser-Bunbury, C.N., Mougial, J., Whittington, A.E., Valentin, T., Gabriel, R., Olesen, J.M., Blüthgen, N., 2017. Ecosystem restoration strengthens pollination network resilience and function. *Nature* 542, 223–227.
- Kerr, J.T., Pindar, A., Galpern, P., Packer, L., Potts, S.G., Rober, S.M., Rasmont, P., Schweiger, O., Colla, S.R., Richardson, L.L., Wagner, D.L., Gall, L.F., Sikes, D.S., Pantoja, A., 2015. Climate change impacts on bumblebees converge across continents. *Science* 349 (6244), 177–180.
- Kosior, A., Celary, W., Olejniczak, P., Fijał, J., Król, W., Solarz, W., Plonka, P., 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apoidea: Bombini) of western and central Europe. *Oryx* 41 (1), 79–88.
- Kremen, C., Ricketts, T., 2000. Global perspectives on pollinator disruptions. *Conserv. Biol.* 14 (5), 1226–1228.
- Levesque, C., Burger, J.F., 1982. Insects (Diptera, Hymenoptera) associated with *Minuartia groenlandica* (Caryophyllaceae) on Mount Washington, New Hampshire, U.S.A., and their possible role as pollinators. *Arct. Alp. Res.* 14 (2), 117–124.
- Lozier, J.D., Cameron, S.A., 2009. Comparative genetic analyses of historical and contemporary collections highlight contrasting demographic histories for the bumble bees *Bombus pensylvanicus* and *B. impatiens* in Illinois. *Mol. Ecol.* 18, 1875–1886.
- Mallinger, R.E., Werts, P., Gratton, C., 2015. Pesticide use within a pollinator-dependent crop has negative effects on the abundance and species richness of sweat bees, *Lasioglossum* spp., and on bumble bee colony growth. *J. Insect Conserv.* 19, 999–1010.
- Mandelik, Y., Winfree, R., Neeson, T., Kremen, C., 2012. Complementary habitat use by wild bees in agro-natural landscapes. *Ecol. Appl.* 22 (5), 1535–1546.

- Meeus, I., Brown, M.J.F., De Graaf, D.C., Smagge, G., 2011. Effects of invasive parasites on bumble bee declines. *Conserv. Biol.* 25 (4), 662–671.
- Mitchell, T.B., 1962. Bees of the eastern United States. In: Technical Bulletin No 152. vol 2 North Carolina Agricultural Experiment Station, Raleigh, North Carolina.
- Morales, C.L., Arbetman, M.P., Cameron, S.A., Aizen, M.A., 2013. Rapid ecological replacement of a native bumble bee by invasive species. *Front. Ecol. Environ.* 11 (10), 529–534.
- Otterstatter, M.C., Thomson, J.D., 2008. Does pathogen spillover from commercially reared bumble bees threaten wild pollinators? *PLoS One* 3 (7), e2771. <http://dx.doi.org/10.1371/journal.pone.0002771>.
- Ploquin, E.F., Herrera, J.M., Obeso, J.R., 2013. Bumblebee community homogenization after uphill shifts in montane areas of northern Spain. *Oecologia* 173 (4), 1649–1660.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts, and drivers. *Trends Ecol. Evol.* 25 (6), 345–353.
- Pyke, G.H., Thomson, J.D., Inouye, D.W., Miller, T.J., 2016. Effects of climate change on phenologies and distributions of bumble bees and the plants they visit. *Ecosphere* 7 (3). <http://dx.doi.org/10.1002/ecs2.1267>.
- Rowe, R.J., Terry, R.C., Rickart, E.A., 2011. Environmental change and declining resource availability for small-mammal communities in the Great Basin. *Ecology* 92 (6), 1366–1375.
- Scott-Dupree, C.D., Conroy, L., Harris, C.R., 2009. Impact of currently used or potentially useful insecticides for canola agroecosystems on *Bombus impatiens* (Hymenoptera: Apidae), *Megachile rotundata* (Hymenoptera: Megachilidae), and *Osmia lignaria* (Hymenoptera: Megachilidae). *J. Econ. Entomol.* 102 (1), 177–182.
- Senapathi, D., Carvalheiro, L.G., Biesmeijer, J.C., Dodson, C.A., Evans, R.L., McKerchar, M., Morton, R.D., Moss, E.D., Roberts, S.P.M., Kunin, W.E., Potts, S.G., 2015. The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proc. R. Soc. B* 282 (1806). <http://dx.doi.org/10.1098/rspb.2015.0294>.
- Tison, L., Hahn, M.L., Holtz, S., Rösner, A., Greggers, U., Bischoff, G., Menzel, R., 2016. Honey bees' behavior is impaired by chronic exposure to the neonicotinoid thiacloprid in the field. *Environ. Sci. Technol.* 50, 7218–7227.
- Tripodi, A.D., Szalanski, A.L., 2015. The bumble bees (Hymenoptera: Apidae: *Bombus*) of Arkansas, fifty years later. *J. Melittology* 50, 1–17.
- Tscharntke, T., Steffann-Dewenter, I., Kruess, A., Thies, C., 2002. Characteristics of insect populations on habitat fragments: a mini review. *Ecol. Res.* 17, 229–239.
- Tsvetkov, N., Samson-Robert, M., Sood, K., Patel, H.S., Malena, D.A., Gajiwata, P.H., Maciukiewicz, P., Fournier, V., Zayed, A., 2017. Chronic exposure to neonicotinoids reduces honeybee health near corn crops. *Science* 356, 1395–1397.
- Tucker, E.M., Rehan, S.M., 2016. Wild bee pollination networks in northern New England. *J. Insect Conserv.* 20 (2), 325–337.
- Tucker, E.M., Rehan, S.M., 2017. High elevation refugia for *Bombus terricola* (Hymenoptera: Apidae) conservation and wild bees of the White Mountain National Forest. *J. Insect Sci.* 17 (1), 1–10.
- Vanbergen, A.J., Insect Pollinators Initiative, 2013. Threats to an ecosystem service: pressures on pollinators. *Front. Ecol. Environ.* 11 (5), 251–259.
- Wang, J.P., 2011. SPECIES: an R package for species richness estimation. *J. Stat. Softw.* 40, 1–15.
- Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D., Thomas, C.D., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414, 65–69.
- Warriner, M.D., 2011. Bumblebees (Hymenoptera: Apidae) of remnant grasslands in Arkansas. *J. Kansas Entomol. Soc.* 84 (1), 43–50.
- Warriner, M.D., 2012. Bumble bees (Hymenoptera: Apidae) of Texas: historical distributions. *Southwest. Nat.* 57 (4), 442–445.
- Williams, P.H., Osborne, J.L., 2009. Bumblebee vulnerability and conservation worldwide. *Apidologie* 40, 367–387.
- Williams, P.H., Thorp, R.W., Richardson, L.L., Colla, S.R., 2014. Bumble Bees of North America: An Identification Guide. Princeton University Press, New Jersey.
- Winter, K., Adams, L., Thorp, R., Inouye, D., Day, L., Ascher, J., Buchmann, S., 2006. Importation of Non-native Bumble Bees Into North America: Potential Consequences of Using *Bombus terrestris* and Other Non-native Bumble Bees for Greenhouse Crop Pollination in Canada, Mexico, and the United States. North American Pollinator Protection Campaign.