

Status changes in the wild bees of north-eastern North America over 125 years revealed through museum specimens

MINNA E. MATHIASSEN and SANDRA M. REHAN  Department of Biological Sciences, University of New Hampshire, Durham, NH, USA

Abstract. 1. Though recent literature highlights widespread bee declines, detailed information on local communities and individual species remains scarce. In order to accurately direct conservation initiatives and to evaluate the status of wild bees, regional long-term data on these populations are critical.

2. This study analysed 119 wild bee species within New Hampshire, USA, over 125 years (1891–2016) using museum data. Examining pollinator communities across regional spatial scales has the power to highlight small-scale changes that go undetected in larger investigations. In the light of unknown effects of introduced species and cumulative range expansions of exotic taxa, monitoring wild communities closely and extensively over time is becoming increasingly important.

3. The composition of the New Hampshire wild bee community has changed between the historical and contemporary time periods with 14 species found to be statistically significantly declining and eight species found to be statistically significantly increasing. Over half of the species found to be in statistically significant decline experienced a significant elevational or latitudinal range shift, many are regionally important crop pollinators, and all are native New Hampshire taxa.

4. Guild affiliations were not found to be indicators of change, suggesting that the requirements and behaviour of individual species must be examined in order to evaluate the current and future stability of the wild bee community. Many of these species occur in varied landscapes, climates, and habitats; thus, monitoring changes at regional scales is critical to informing conservation recommendations broadly and focusing future research directions.

Key words. Apoidea, bee declines, biodiversity, climate change, range shifts, species at risk.

Introduction

Wild bees provide fundamental pollination services to most angiosperms, ensuring their reproductive success and endurance in both managed and unmanaged ecosystems globally (Ollerton *et al.*, 2011). Yet, the effects of continuous land development, pathogen spread, and climate shifts on the wild bee community remain

understudied (Russo, 2016). In order to support the health of bee pollination and to direct conservation policymakers, evaluating and monitoring temporal, spatial, and taxonomic characteristics of bee communities within specific regions and over time are essential (Lebuhn *et al.*, 2012). In tandem with agricultural expansion and land-use change, there have been notable bee and pollinator declines in recent decades documented across Europe and North America, further signalling the importance of comparing changes within the community before and throughout this period (Wenzel *et al.*, 2006; Goulson *et al.*, 2008).

Correspondence: Sandra M. Rehan, Department of Biological Sciences, University of New Hampshire, 38 Academic Way, Durham, NH 03824, USA. E-mail: sandra.rehan@gmail.com

Much of the research on the bee community is focused on managed bees such as honey bees (*Apis mellifera*, Linnaeus) and bumble bees (*Bombus* spp., Latreille). Recent declines in both have been widely recorded across Europe and North America (Goulson *et al.*, 2008; vanEngelsdorp *et al.*, 2009; Colla *et al.*, 2012; Bartomeus *et al.*, 2013). These notable declines in addition to recent evidence that wild bees are often more effective pollinators than managed bees have prompted investigation into possible declines beyond these well-studied species to the rest of the bee community (Garibaldi *et al.*, 2013; Winfree *et al.*, 2018). The global wild bee community is represented by over 20 000 described species, almost all of which are unmanaged (Goulson, 2003; Winfree, 2010; Ascher & Pickering, 2018). North America alone hosts an estimated 4000 of those species, each of which has nuanced requirements for reproduction and survival (Cane & Tepedino, 2001; Ascher & Pickering, 2018). In order to more fully understand species' individual needs in addition to their pollination and ecosystem contributions, long-term assessments are necessary, particularly for rare and poorly studied species (Bartomeus *et al.*, 2013; Burkle *et al.*, 2013).

Due to the disproportionate funding and agricultural support for honey bees, the importance of unmanaged wild bee research and conservation is often underestimated (Colla & MacIvor, 2017). In particular, long-term data on regional North American wild bee communities are lacking. Museum collections, however, are powerful sources of insight into historical communities of flora and fauna (Suarez & Tsutsui, 2004; Bartomeus *et al.*, 2013; Jacobson *et al.*, 2018), and utilising museum data is an important step towards generating fundamental information on wild bee populations and the status of individual species within these communities.

Wild bees face many threats currently, including climate change, habitat loss due to anthropogenic land-use change, and invasive species competition. Increasing fluctuation in temperatures poses a serious threat to ectothermic organisms such as bees (Blanford *et al.*, 2013). Even slight temperature changes have been shown to impact bee flight activity and foraging patterns (Heard & Hendrikz, 1993; Stone, 1994; Rader *et al.*, 2013). Phenological mismatches between plant-pollinator pairings as a result of climate change could reduce the diet breadth of bee species and hinder the mutualistic relationship between bees and host plants (Memmott *et al.*, 2007; Robbirt *et al.*, 2014). It is predicted by climate change models that latitudes in the northern hemisphere are more likely to experience diminished seasonality and weakening temperature gradients (La Sorte *et al.*, 2014). Non-migratory organisms, such as wild bees, that persist in these regions could be strongly affected by these temperature changes (Roth *et al.*, 2014; Pyke *et al.*, 2016).

Investigating individual bee species and the overall community composition over time is furthermore important to identifying trends and to monitoring interactions between native and introduced species. Introduced bee species comprise approximately 40 of the bee species in

North America and, apart from the few species introduced for crop pollination such as honey bees, most were introduced unintentionally (Droege, 2015). Introduced species are widely believed to threaten biodiversity and compete with native taxa (Vanbergen *et al.*, 2018), yet they merit conservation value due to their ability to persist in unpredictable climates and supplement lost ecosystem services of extinct taxa (Schlaepfer *et al.*, 2011). A 2018 simulation study revealed that introduced species with high foraging efficiency are the most likely to succeed and have the greatest impact on native plant-pollinator network structure (Valdovinos *et al.*, 2018). Given the difficulties inherent in assessing the possible competition between such mobile organisms, however, conclusive evidence that exotic bee introductions have negative consequences requires more thorough evaluation (Goulson, 2003). To further understand the effects of introduced species and to detect potential ecological invasions, the proportion of each species within regional communities should be compared over time (Grixti & Packer, 2006). All of these aforementioned effects are likely to affect particular bee taxa more intensely due to variable traits such as body size, diet breadth, sociality, and habitat preference. It is therefore important to investigate the combined effects of these threats on individual species and the entire community, which has the overarching potential to weaken ecosystem function.

In this study, we evaluate the wild bee community in New Hampshire over 125 years in order to assess changes in species composition by comparing historical (1891–1987) and contemporary (1988–2016) samples. Analyses are based on taxonomy, habitat preferences, range, geography, and nesting biology. New Hampshire's diverse assortment of habitats and its northern temperate climate make it an ideal location to fundamentally assess a local wild bee community. The establishment of regional baseline data of the wild bee community in New Hampshire is important to the evaluation of anthropogenic impacts and to direct conservation policy. The aims of this work were twofold: first, to assess the changes in status and range of the wild bee community over the past 125 years and second, to determine the long-term stability of the wild bee community through individual species assessments.

Methods

Bee specimen database

A total of 17 036 non-*Bombus* wild bee specimens collected over 125 years spanning from 1891 to 2016 were included in this study. A recent study (Jacobson *et al.*, 2018) evaluated changes in New Hampshire *Bombus* over 150 years; thus, this study focused on the remainder of New Hampshire's wild bee community. All bee specimens were identified using taxonomic keys (Mitchell, 1960, 1962; Gibbs, 2011; Rehan & Sheffield, 2011; Ascher & Pickering, 2018) and confirmed to species by professional

taxonomists (John Ascher – American Museum of Natural History, Don Chandler – University of New Hampshire, Sam Droege – USGS, Jason Gibbs – University of Manitoba, Joan Milam – UMass Amherst, Erika Tucker – University of Michigan, and Michael Veit – Lawrence Academy), given a unique UNH barcode ID, and entered into the database. Specimens are housed in the University of New Hampshire Insect Collection. Only specimens that had the following information were included in the final data set: collection date, collection location, and species-level identification. Record locations ranged statewide from 42.72° to 45.19° N latitude and –72.42° to –70.933° W longitude. Specimens were databased with geographic coordinates and repository information. Specimen record data can be downloaded through the search collection option in the online portal: <https://www.gbif.org/publisher/154da9ab-c010-422d-8fef-dbc54d10a3c6>.

Collection periods and rarefaction

In order to evaluate changes in the bee community composition, species richness, and abundance over time, the data were divided into equally represented bins based on the entire data set. Given the uncertainty of sampling effort in museum collections (Bartomeus *et al.*, 2013), partitioning the data into equal time periods that each span an equal number of years would not be suitable. Rarefaction curves and statistics were calculated using species richness and specimen abundance as metrics for the binning scheme. Based on these curves and considering the unknowns of historical collection effort, species richness proved most suitable for a primary regulator of equalisation so that each bin contained roughly the same number of species and a rarefaction curve was generated with the ‘rarecurve’ function from the VEGAN package (Jari Oksanen *et al.*, 2017) in R 3.3.2. The following two periods were established: 1891–1987 (historical) and 1988–2016 (contemporary). These two periods were additionally selected to reflect different temporalities: pre-urbanisation and industrialisation before the late 1980s compared with increasing roadways, and urbanisation and population gain between the 1980s and the present (U.S. Census Bureau 2012) as well as to allow for an evaluation of long-term changes over the past 125 years (Colla *et al.*, 2012; Jacobson *et al.*, 2018).

Species richness indices and community sampling effectiveness

A species richness analysis determined how well the bee community sampled in any given individual collection period captured the estimated true diversity of the community. Species diversity indices were generated for each time period using the SPECIES package (Wang, 2011) in R 3.3.2. The following species richness estimates were calculated: Chao and Chao-1 with the function ‘chao1984’

(Chao, 1984), ACE and ACE-1 with the function ‘chao1992’ (Chao & Lee, 1992), and Jackknife with the function ‘jackknife’ (Burnham & Overton, 1978). Each of these tests uses abundance data to calculate a lower and upper bound estimate of species richness through which the effectivity of community sampling can be calculated by comparing the species richness of each sample to the species richness of the total assemblage (Gotelli & Colwell, 2009).

Bee abundance and community composition

After sorting the specimens into their respective collection time periods, the status of each bee species was evaluated using a relative abundance measurement to account for possible disparity in sampling effort, especially during periods of low collection in the early 1900s (Colla & Packer, 2008; Jacobson *et al.*, 2018). The relative change in each genera was examined proportionally within family between the two periods. Analyses were conducted for individual species both within the total sample and within each genus. As many species were represented by only a few specimens overall or inconsistently over time, species were categorised as ‘data deficient’ if they did not meet the following requirements: species is recorded in each time period, species is represented by >14 total specimens (mean number of specimens per species = 52.9 ± 9.7 SE), and species represents >1% of total collections within its genus. A relative abundance measurement was made for each qualified species using the following equation to weight each time period by its total number of specimens collected:

Relative Abundance

$$= \frac{\# \text{specimens collected of species within time period}}{\# \text{total specimens collected in total or genus within time period}}$$

Z-tests were performed using the functions ‘z.prop’ and ‘prop.test’ in R 3.3.2 comparing qualified specimens in the historical and contemporary samples, using the following equation with a 95% confidence interval:

$$Z = \frac{\hat{p}_1 - \hat{p}_2}{\sqrt{\frac{\hat{p}_1 \cdot \hat{q}_1}{n_1} + \frac{\hat{p}_2 \cdot \hat{q}_2}{n_2}}}$$

\hat{p}_1 = proportion of species within total or genus in historical sample; \hat{p}_2 = proportion of species within total or genus in contemporary sample; $\hat{q}_1 = 1 - \hat{p}_1$; $\hat{q}_2 = 1 - \hat{p}_2$; n_1 = total specimens or total specimens within genus in historical sample; n_2 = total specimens or total specimens within genus in contemporary sample.

Using the relative abundance measurements and z-score calculations, each species was given a status determination based on any significant change ($P < 0.05$) classified as one of the following: increase, decrease, or no change. To

ensure that species status evaluations were as conservative as possible, classifications were determined from significant change that was consistent between the total and genus analyses for a species.

Habitat, range, and behavioural characteristics

For each species that was found to be either decreasing or increasing in proportion, additional information on nesting habit (ground, stem, cavity), range (native or introduced), social behaviour (solitary, eusocial, cleptoparasitic), and degree of floral specialisation (generalist or specialist) was compiled. Nesting habitat, range, social behaviour, and floral specialisation data were taken from former species lists and online repositories providing these data (Ascher *et al.*, 2014; Selfridge *et al.*, 2017; Ascher & Pickering, 2018). Average elevation and latitude were calculated for each species found in decline comparing the two samples. Descriptive statistics (mean and standard error) were calculated using the 'describe' function in the package PSYCH in R 3.3.2 (Revelle, 2017) for both elevation and latitude. A heteroscedastic Welch's two-sample *t*-test for unequal variances was run using the 't.test' function.

Results

Bee specimen database and collection periods

The 17 036 wild bee specimens in the database represent six families, 36 genera, and 322 species (Table S1). As expected, the frequency distribution of bee species across the 125-year period (1891–2016) is uneven due to variation in population sizes of common and rare species and the unknowns of historical sampling effort (Bartomeus *et al.*, 2013). Of the entire collection, 150 species were represented by more than 10 independent records, 26 species were represented by over 100 independent records, and 46 species were represented by single specimen records. The collection location of specimens in both samples ranged widely across New Hampshire (Fig. 1). A total of 89 bee species met all requirements to be included in status assessment analyses (Table S1). Another 56 species that did not meet the requirements for status assessment analyses but that underwent notable change were examined additionally (Tables S3 and S10).

Species richness indices and community sampling effectiveness

The species richness analysis indicated a high bee species richness in New Hampshire that has increased from the historical period to the present (Table S4). The number of species comprising the New Hampshire wild bee community during the 1891–1987 historical time period was estimated to be 233 by the ACE test lower bound

value with 202 observed species, translating to a 90% sampling effectiveness. The other species richness indices calculated yielded similar results (Chao: 235 lower bound (lb), 89% effectiveness; ACE-1: 241 lb, 87% effectiveness; Jackknife-1: 257 lb, 87% effectiveness). The number of species comprising the New Hampshire wild bee community during the 1988–2016 contemporary time period was estimated to be 333 by the ACE test lower bound value with 308 observed species, translating to a 97% sampling effectiveness. The other species richness indices calculated yielded similar results (Chao: 335 lb, 92% effectiveness; ACE-1: 319 lb, 97% effectiveness; Jackknife-1: 360 lb, 90% effectiveness).

Bee abundance and community composition

Analysing the relative proportion of particular genera within family revealed significant change in 16 of 36 genera based on z-score calculations (Fig. S2). The following seven genera were found to be decreasing: *Andrena* (Fabricius), *Nomada* (Scopoli), *Hylaeus* (Fabricius), *Halictus* (Latreille), *Sphecodes* (Hübner), *Coelioxys* (Latreille), and *Megachile* (Chelostomoda). The following nine genera were found to be increasing: *Calliopsis* (Smith), *Pseudopanurgus* (Cockerell), *Ceratina* (Latreille), *Melissodes* (Latreille), *Colletes* (Latreille), *Agapostemon* (Smith), *Lasioglossum* (Curtis), *Anthidium* (Fabricius), and *Osmia* (Panzer).

The 89 species that were conserved between both status analyses were assigned status determinations based on significant z-score calculations (Tables S2, S3, S5, & S6). A total of 14 species were found to be in significant decline: *Andrena carlini* (Cockerell), *A. erythrogaster* (Ashmead), *A. forbesii* (Robertson), *A. imitatrix* (Cresson), *A. miserabilis* (Cresson), *A. salictaria* (Robertson), *A. vicina* (Smith) (Andrenidae), *Nomada bella* (Cresson), *N. depressa* (Cresson) (Apidae), *Halictus rubicundus* (Christ), *Lasioglossum imitatum* (Smith), *L. quebecense* (Crawford) (Halictidae), *Megachile brevis* (Say), and *M. montivaga* (Cresson) (Megachilidae; Table S5, Fig. 2). In contrast, eight species were found to be increasing significantly: *Andrena commoda* (Smith) (Andrenidae), *Ceratina mikmaqi* (Rehan & Sheffield) (Apidae), *Agapostemon virescens* (Fabricius), *Lasioglossum cressonii* (Robertson), *L. leucocomum* (Lovell), *L. leucozonium* (Schränk), *L. pilosum* (Smith) (Halictidae), and *Osmia pumila* (Cresson) (Megachilidae; Table S6). The remaining 67 species were found to have experienced no significant proportional change, likely including a combination of stable species and species that could be undergoing undetected changes and thus should be a focus of further research (Table S7).

Habitat, range, and behavioural characteristics

All species found to be in decline are native to New Hampshire. Out of the declining species, 13 are ground

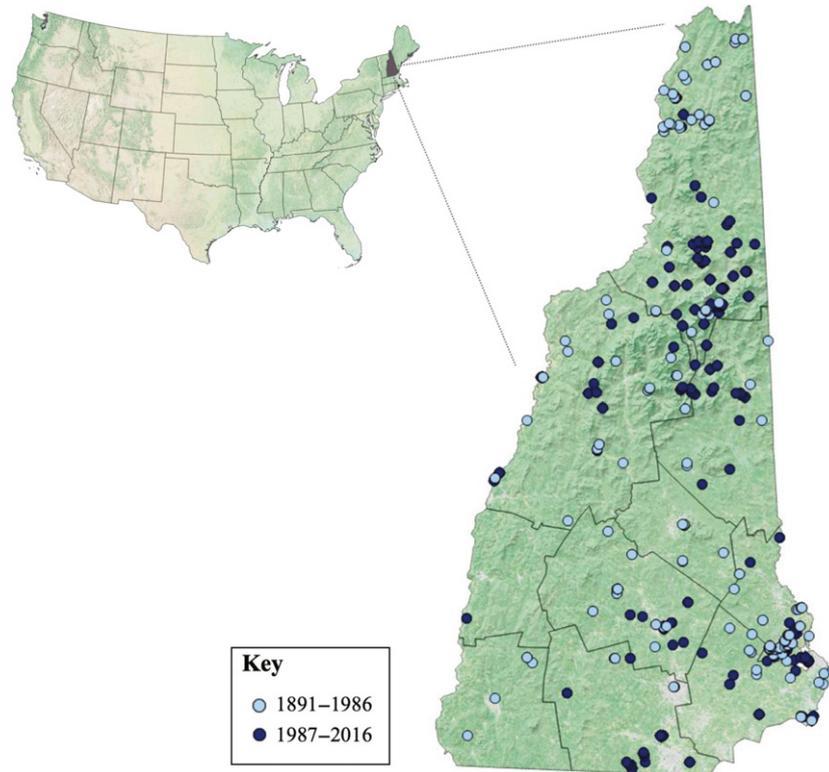


Fig. 1. Map of study database specimen locations across New Hampshire, U.S.A. (generated using QGIS 2.18.13 Las Palmas). [Colour figure can be viewed at wileyonlinelibrary.com]

nesters and one is cavity-nesting. Two specialist pollinators (*Andrena erythrogaster*, *A. salictaria*) and 12 generalist pollinators were found to be in decline. Most declining species are solitary nesters except for two eusocial species (*Halictus rubicundus* and *Lasioglossum imitatum*; Table 1).

Out of the eight species found to be increasing, six species are ground nesters and two are stem or cavity-nesting species (*Ceratina mikmaqi* and *Osmia pumila*). One increasing species (*Lasioglossum leucozonium*) is introduced, and the remaining increasing species are native to New Hampshire. All increasing species are generalists. Five increasing species are solitary nesters and three are eusocial species (*Lasioglossum cressonii*, *L. leucocomum*, and *L. pilosum*; Table S8).

Comparisons between the historical and contemporary samples of the average collection elevation revealed significant differences for half of the declining species (Welch's *t*-tests, $P < 0.05$; Table 2) and four increasing species (Table S9). The following seven declining species experienced a significant increase in elevation: *Andrena forbesii*, *A. imitatrix*, *A. miserabilis*, *Halictus rubicundus*, *Lasioglossum imitatum*, and *Megachile montivaga*. Two declining species experienced a significant decrease in elevation: *Andrena vicina* and *Lasioglossum quebecense*, and five declining species experienced no significant change in elevation: *Andrena carlini*, *A. erythrogaster*, *Nomada bella*,

N. depressa, and *Megachile brevis*. The following three increasing species experienced a significant increase in elevation: *Lasioglossum leucozonium*, *L. pilosum*, and *Osmia pumila*. One increasing species (*Lasioglossum cressonii*) experienced a significant decrease in elevation, and four increasing species experienced no significant change in elevation (Table S9).

Comparisons between the historical and contemporary samples of the average collection latitude revealed significant differences for more than half of the species found to be in decline (Welch's *t*-tests, $P < 0.05$; Table 2) and a third of the species found to be increasing (Table S8). The following six declining species experienced a significant increase in collection latitude: *Andrena forbesii*, *A. imitatrix*, *A. miserabilis*, *Halictus rubicundus*, *Lasioglossum imitatum*, and *Megachile montivaga*. The following two declining species experienced a significant decrease in collection latitude: *L. quebecense* and *Megachile brevis*, and six declining species experienced no significant change in latitude (Table 2). The following three increasing species experienced a significant increase in collection latitude: *Lasioglossum leucozonium*, *L. pilosum*, and *Osmia pumila*. One increasing species (*Lasioglossum cressonii*) experienced a significant decrease in collection latitude. Three increasing species experienced no significant change in latitude (Table S8).

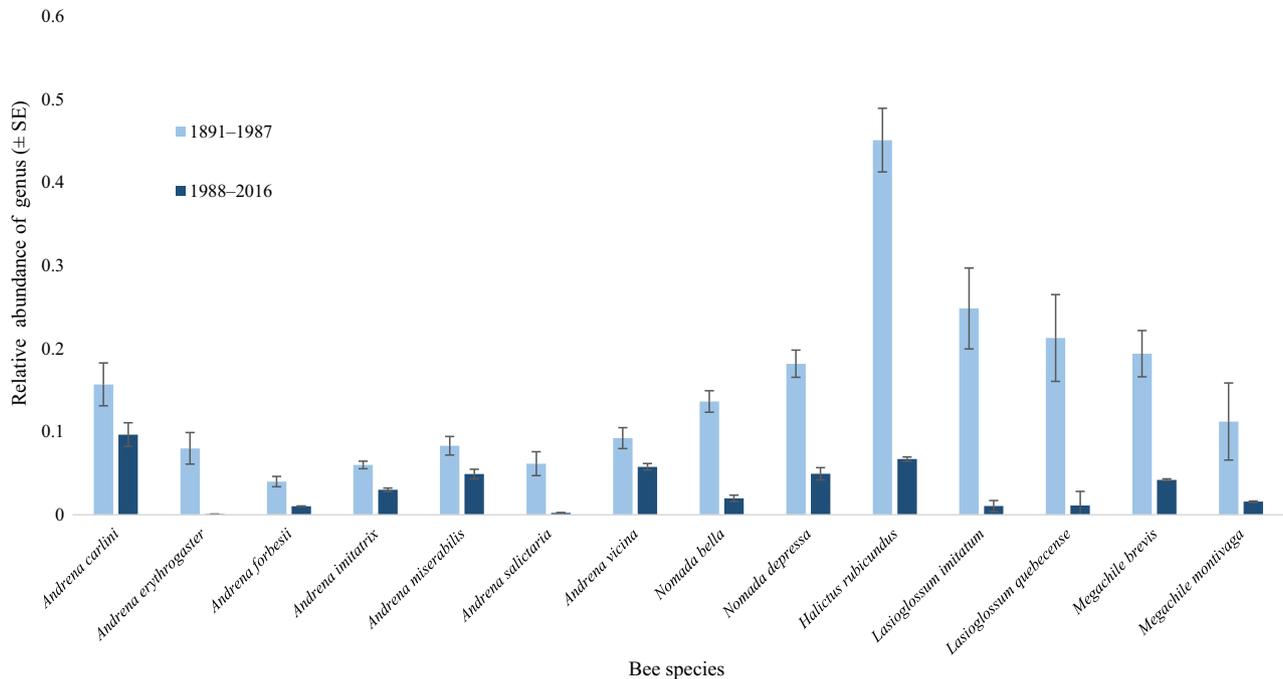


Fig. 2. Relative abundance (proportion of species within genus) of New Hampshire wild bee species found to be in decline based on significant ($P < 0.05$) z-scores compared between historical (1891–1987) and contemporary (1988–2016) periods. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Declining New Hampshire wild bee species with traits.

Family	Species	Subgenus	Nesting Habit	Social Behaviour	Range (North-east)	Forage Behaviour
Andrenidae	<i>Andrena carlini</i> *	<i>Melandrena</i>	Ground	Solitary	Native	Generalist
Andrenidae	<i>Andrena erythrogaster</i> *	<i>Tylandrena</i>	Ground	Solitary	Native	Specialist
Andrenidae	<i>Andrena forbesii</i>	<i>Trachandrena</i>	Ground	Solitary	Native	Generalist
Andrenidae	<i>Andrena imitatrix</i>	<i>Scapteropsis</i>	Ground	Solitary	Native	Generalist
Andrenidae	<i>Andrena miserabilis</i>	<i>Larandrena</i>	Ground	Solitary	Native	Generalist
Andrenidae	<i>Andrena salictaria</i> *	<i>Micrandrena</i>	Ground	Solitary	Native	Specialist
Andrenidae	<i>Andrena vicina</i>	<i>Melandrena</i>	Ground	Solitary	Native	Generalist
Apidae	<i>Nomada bella</i>	None	Ground†	Cleptoparasite	Native	–
Apidae	<i>Nomada depressa</i>	None	Ground†	Cleptoparasite	Native	–
Halictidae	<i>Halictus rubicundus</i> *	<i>Halictus</i>	Ground	Eusocial & Solitary	Native	Generalist
Halictidae	<i>Lasioglossum imitatum</i> *	<i>Dialictus</i>	Ground	Eusocial	Native	Generalist
Halictidae	<i>Lasioglossum quebecense</i>	<i>Sphexodogastra</i>	Ground	Solitary	Native	Generalist
Megachilidae	<i>Megachile brevis</i> *	<i>Litomegachile</i>	Cavity	Solitary	Native	Generalist
Megachilidae	<i>Megachile montivaga</i>	<i>Megachile</i>	Ground and cavity	Solitary	Native	Generalist

*Found to be in decline in north-east United States by Bartomeus *et al.*, 2013 (note: this study used a subset of UNHC bee specimens).

†Associated with nesting habit, but did not construct nest.

Discussion

This study examined changes in the wild bee community over the span of 125 years (1891–2016) and potential correlates of change across taxonomic levels. Status assessment analyses that compared historical (1891–1987) and contemporary (1988–2016) samples revealed 14 declining

and eight increasing wild bee species. The ecological and agricultural consequences of wild bee species declines and community composition require further investigation in the habitat necessary to sustain these most important pollinators and the valuable services they provide (Potts *et al.*, 2010). Explanatory characteristics such as habitat preferences, range, social behaviour, elevation, and

Table 2. Average elevation and latitude for declining New Hampshire wild bee species comparing historical (1891–1987) and contemporary (1988–2016) samples (elevation data found with Geoplaner V2.7).

Family	Species	Average latitude					Average elevation (m)								
		1891–1987	SE	1988–2016	SE	T	df	P	1891–1987	SE	1988–2016	SE	T	df	P
Andrenidae	<i>Andrena carlini</i> †	43.20	0.02	43.15	0.02	1.87	123.9	0.06	53.25	10.55	48.14	7.27	0.40	99.5	0.69
Andrenidae	<i>Andrena erythrogaster</i> †	43.13	0.00	44.65	–	–	–	–	20.76	1.56	420.3	–	–	–	–
Andrenidae	<i>Andrena forbesii</i>	43.14	0.01	43.54	0.17	–2.32	12.0	0.04*	28.02	6.26	129.21	44.47	–2.25	12.5	0.04*
Andrenidae	<i>Andrena imitatrix</i>	43.13	0.00	43.31	0.08	–2.10	31.04	0.04*	152.31	73.2	129.28	33.62	–2.84	35.5	0.008*
Andrenidae	<i>Andrena miserabilis</i>	43.26	0.09	43.68	0.07	–3.54	60.6	<0.001*	44.94	15.23	249.60	24.94	–7.00	86.7	<0.001*
Andrenidae	<i>Andrena salictaria</i> †	43.14	0.00	43.43	0.31	–0.96	2	0.44	19.20	0.00	63.23	28.81	–1.53	2.0	0.27
Andrenidae	<i>Andrena vicina</i>	43.40	0.09	43.21	0.04	1.95	40.7	0.06	365.3	118.81	102.70	28.09	2.15	32.3	0.04*
Apidae	<i>Nomada bella</i>	43.34	0.21	42.95	0.10	1.69	10.9	0.11	106.59	68.93	92.82	20.10	0.19	9.3	0.85
Apidae	<i>Nomada depressa</i>	43.66	0.24	43.32	0.11	1.29	15.6	0.22	229.64	82.31	133.51	41.03	1.05	14.9	0.31
Halictidae	<i>Halictus rubicundus</i> †	43.28	0.04	43.55	0.06	–3.88	167.6	<0.001*	78.33	12.79	175.36	24.17	–3.55	142.5	<0.001*
Halictidae	<i>Lasius lossum imitatus</i> †	43.18	0.05	44.09	0.05	–12.52	78.1	<0.001*	32.98	19.51	307.37	19.36	–9.98	77.3	<0.001*
Halictidae	<i>Lasius lossum quebecense</i>	44.11	0.10	43.59	0.09	3.89	63.6	<0.001*	1298.22	152.75	231.02	31.88	6.84	31.54	<0.001*
Megachilidae	<i>Megachile brevis</i> †	43.16	0.01	43.08	0.03	2.57	10.5	0.03*	36.03	12.04	19.59	6.12	1.22	24.3	0.24
Megachilidae	<i>Megachile montivaga</i>	43.38	0.05	44.37	0.00	–19.19	10	<0.001*	165.36	16.32	318.70	0.00	–9.39	10	<0.001*

*P < 0.05.

†Found to be in decline in north-east United States by Bartomeus *et al.* (2013) (note: this study used a subset of UNHC bee specimens).

– data insufficient to conduct a *t*-test.

latitude were compiled for each species that experienced significant change. Most species that experienced significant change in abundance also revealed significant elevational or latitudinal range shifts. Most latitudinal shifts were northward and most elevational shifts were upward, which parallels regional shifts in temperature and climate, and indicates that these species may be experiencing phenological mismatch or competition for habitat and forage within their former ranges (Parmesan *et al.*, 1999; Grixti & Packer, 2006). Change was not experienced among species sharing traits such as nesting habit or degree of floral specialisation, which suggests multiple drivers of change. The baseline information on the species analysed in this study is fundamental to generating regionally specific status recommendations for the northern New England wild bee community and highlights the individual importance of these species for future-focused study across North America.

Bartomeus *et al.* (2013) used a subset of the specimens from this study as well as historical records covering a broad section of the north-eastern United States and found corresponding declines in six species: *Andrena carlini*, *A. erythrogaster*, *A. salictaria*, *Halictus rubicundus*, *Lasioglossum imitatum* (also found to be notably declining by Grixti & Packer, 2006), and *Megachile brevis*. Consistent increases were found in two species: *Agapostemon virescens* and *Lasioglossum cressonii*. This study revealed significant population changes in 14 additional species in New Hampshire, which indicates the importance of historical museum collections as well as the power that regionally specific studies have to detect finer-scale changes in the wild bee community. Many of the species in this study are widespread across North America, yet are likely undergoing change at varying rates within each regional community. Due to small sample sizes or rarity, many species were excluded from analyses in this study but warrant future study (Bartomeus *et al.*, 2013). Developing additional techniques to utilise museum data in further analyses will be important to continued monitoring across all scales of the wild bee community.

Most bees examined in this study are ground-nesting, and all but one species found to be in decline are ground nesters. Though ground-nesting biology is a shared trait among these species, there is great interspecific variation in nest depth, soil type, vegetation, and nearby resources necessary for a female to build a suitable nest (Cane, 1991). Ground-nesting species, in contrast with cavity-nesting species, have been previously shown to be especially sensitive to land-use change and habitat fragmentation (Kremen & Ricketts, 2000; Cane *et al.*, 2006). Continued monitoring of after periods of general agricultural expansion will be important to future studies that focus on the effects that specific types of agricultural practices have on the composition of the wild bee community, bees with varying nesting biology, and habitat availability.

Cleptoparasitic species are particularly important as bioindicators due to their reliance on other bee species for survival (Sheffield *et al.*, 2013). *Nomada* spp., the

largest genus of cleptoparasitic bees, have been shown to decline correspondingly with host decline, which are primarily *Andrena* species (Westrich, 1996). Proportional changes in cleptoparasitic bee species could reveal changes not only in their respective host species, but also in the stability and abundance of the overall bee community (Sheffield *et al.*, 2013). This study found two *Nomada* species to be decreasing (*Nomada bella* and *N. depressa*). Declines in cleptoparasitic species could signal ecosystem instability as they are known to be community stabilisers (Sheffield *et al.*, 2013).

Poleward latitudinal range shifts of non-migratory organisms have been documented in the northern hemisphere because of warming climates (Parmesan *et al.*, 1999; Lenoir & Svenning, 2013), which contribute to range shifts in bee communities (Kuhlmann *et al.*, 2012). Northward constriction has been detected in individual *Bombus* species in the north-eastern United States (Jacobson *et al.*, 2018), yet a similar study on range shifts in *Bombus* spp. across North America and Europe detected no northward expansion (Kerr *et al.*, 2015). Of the bee species found to be in decline in this study, 50% showed northward latitudinal and upward elevational range shifts. One third of the species found to be increasing also experienced upward latitudinal range shifts over the 125-year period. Given predictions for continued climate change, continued monitoring the distributional patterns of species across regions is important. Synthesising information on regional species lists, land use, and the ecology of pollinator communities is an essential future step to generating appropriate landscape management and conservation policy recommendations. This study provides important species status assessments for northern New England for comparison to future detailed studies in other ecoregions that could reveal habitat specificity and individual species declines and expansions on a broader scale.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Rarefaction curves illustrating the species richness of the New Hampshire wild bee community sampled during historical (1891–1987) and contemporary (1988–2016) periods.

Figure S2. Relative abundance of wild bee genera (proportion within family) comparing a historical sample (1891–1987, light blue) and contemporary sample (1988–2016, dark blue) of the New Hampshire wild bee community.

Table S1. Specimen counts of each species represented in the historical and contemporary periods and whether species met all requirements to be included in status assessment analyses.

Table S2. Genus-level Z-test scores for New Hampshire wild bee species: Z-test of two proportions indicate the relative abundance of each non-Bombus species comparing a historical (1891–1987) and contemporary (1988–2016) sampling from the UNH Insect Collections.

Table S3. Z-test scores for New Hampshire wild bee species: Z-test of two proportions indicate the relative abundance of each non-Bombus species comparing a historical (1891–1987) and contemporary (1988–2016) sampling from the UNH Insect Collections.

Table S4. Species richness indices Chao, ACE, ACE-1, and Jackknife for 2 collection periods: 1891–1987 and 1988–2016.

Table S5. Decreasing New Hampshire wild bee species conserved between Z-test analyses of two proportions that indicate the relative abundance of each species within genus and the relative abundance within the total sample comparing a historical (1891–1987) and contemporary (1988–2016) sampling from the UNH Insect Collection.

Table S6. Increasing New Hampshire wild bee species conserved between Z-test analyses of two proportions that indicate the relative abundance of each species within genus and the relative abundance within the total sample comparing a historical (1891–1987) and contemporary (1988–2016) sampling from the UNH Insect Collection.

Table S7. Species that did not experience a significant proportional change conserved between all status assessment analyses.

Table S8. Increasing New Hampshire wild bee species with traits.

Table S9. Average elevation and latitude for increasing New Hampshire wild bee species comparing historical (1891–1987) and contemporary (1988–2016) samples (elevation data found with Geoplaner V2.7).

Table S10. Specimen counts of species that did not meet status assessment requirement of representation in both periods.

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