



# Wild bee declines linked to plant-pollinator network changes and plant species introductions

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**Abstract.** 1. The mutualistic interactions of plant-pollinator networks provide myriad economic, ecological, and cultural constituents without which there would be severe environmental and societal consequences. Plant-pollinator networks are becoming increasingly vulnerable to disturbance through intensifying anthropogenic land use and climate change.

2. Wild bees are central to pollination and documenting unique regional interactions between wild bees and floral hosts provides powerful insights into local ecology and biodiversity in addition to the potential to detect temporal network variation.

3. This study characterises the changes in a northern New England wild bee plant-pollinator network over the past 125 years and reveals a striking increase in exotic bee and plant taxa over time. Here we document that declining wild bee species have historic ties to threatened and endangered plant species. These data provide a rare insight into the fragile nature of plant-pollinator networks.

4. Notable specialist interactions between native taxa that were recorded in historical networks have been lost, most likely due to local extirpation of these now threatened and endangered plant species. Subsequent monitoring and conservation efforts focused on habitat restoration for declining wild bee and plant taxa are fundamental to the future preservation of regional native diversity.

**Key words.** Apoidea, climate change, exotic species introductions, landscape restoration, plant-pollinator interaction networks, wild bee conservation.

## Introduction

Plant-pollinator networks are composed of interactions among thousands of species with individualised needs for survival. It is likely that these interactions occurring between both native and introduced flora and fauna have been impacted by changes in climate, habitat availability, and exotic species introductions. Though there is speculation in existing literature of the positive or negative effects of species introductions, these effects are often un-quantified (Russo 2016). Rapid range expansions and accidental introductions of exotic species invite notions of competition-induced consequences for native species' food sources and habitat availability. Though antagonism by introduced species is difficult to observe in a natural environment, what information can be parsed of the effects of introduced species on

native species interactions is important to document as a reference point for future research.

Though the network of interactions between plants and their pollinators is a strong demonstration of mutualism and coevolution, it is likewise a complex and fragile system. Pollination is often viewed through the lens of ecosystem services, a quantification of the beneficial services provided to humans by ecosystems (Morelli 2011). In accordance, the importance of pollination to the global crop economy was recently valued at an annual \$235–577 billion (FAO 2018). Wild bees are the top contributors of pollination services (Free 1993; Javorek et al. 2002; Garibaldi et al. 2013) and are believed to pollinate 87.5% of angiosperms, approximately 308 006 species of flowering plants (Ollerton et al. 2011). Many of these species are economically important commercial crops (Klein et al. 2007) and additionally compose the diverse array of foods available to humans. In the United States alone, wild bee pollination services were estimated to be worth \$3.07 billion in 2006 (Losey & Vaughan 2006). This estimate is likely a very conservative approximation of wild bee pollination's contemporary value

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considering the increase in pollinator-dependent crop plants over the past decade (Russo et al. 2013).

Beyond the clear economic importance of wild bee, pollination lies a wealth of ecological value characterised by plant-pollinator relationships. Recent worldwide bee declines have brought attention to the stability and resistance of plant-pollinator interactions to species and habitat loss and the corresponding effects these losses may have on pollination services and consequently food security (Winfree et al. 2008; Potts et al. 2010; Brosi & Briggs 2013; Burkle et al. 2013). The subtleties of plant-pollinator relationships are extensive and subject to change. Wide gaps in knowledge surrounding these complex networks still exist, yet biodiversity has been shown to be fundamental to a functional plant-pollinator network (Blüthgen & Klein 2011; Winfree et al. 2018). Wild bees are a highly diverse group of pollinators, encompassing a wide range of morphologies, nesting habits, lifestyles (solitary–social) and foraging patterns (specialist–generalist). Bees forage in a variety of ways for pollen and nectar from flowering plants for food and nest provisions. Specialist bees are either monolectic (uncommon) or oligolectic pollinators that visit the same or related plants, whereas generalist bees are polylectic bees that visit many unrelated plant taxa (Michener 2000). Specialisation of pollinators serves an important role in the structure and evolution of insect and plant communities, yet these specialisations go far beyond the notion of linked extinction, in which case the loss of a plant species results in the loss of an animal species. Pollination interactions may be more accurately defined as well-connected ‘interaction webs’ that experience shifts due to temporal and geographic changes (Kearns et al. 1998; Memmott et al. 2004). As ectothermic organisms, pollinators are particularly susceptible to experience decreased fitness as a result of temperature variation (Paaijmans et al. 2013). In order to protect these critical plant-pollinator interactions, there is an urgent need to gain a deeper understanding of the environmental circumstances affecting these wild pollinator populations and their specialised, evolutionary relationships with plant communities. Given that plant-pollinator webs are dependent on changes in the landscape, investigating the fundamental aspects that shape these networks is of great importance and must be inclusive of all regional habitats in order to evaluate geographic variation.

A study that simulated pollinator extinction from plant-pollinator networks found solitary bees to be among the most linked pollinators and recommended they receive increased conservation attention in temperate regions (Memmott et al. 2004). A recent long-term study of the northeastern United States bee community found that wild bee declines were linked ecologically to smaller diet breadth (specialists) and shorter foraging phenologies (Bartomeus et al. 2013). Recent analyses examined relative abundances within a community comprised 119 wild bee species over 125 years and found 14 declining species and 8 increasing species (Mathiasson & Rehan 2019). All of the wild bee species found to be in decline are native taxa and over half experienced significant range (latitude and elevation) shifts. Similarly, a study of 120 years of plant-pollinator networks (Burkle et al. 2013) revealed a disproportionate loss of specialist bee species. Nevertheless, the inability to distinguish between small diet breadth and species rarity implies that species loss

could be due to specialisation, rarity, or both factors in combination (Burkle et al. 2013).

Identifying changes in the structure of these bipartite networks could clarify drivers of bee declines such as competition between native and exotic flora and fauna, phenological shifts and mismatch, pollination specialisation vs. generalisation, and habitat requirements. Bipartite networks are illustrative of the ecological relationships that have been formed within the plant-pollinator community and are able to highlight the strengths and vulnerabilities of individual species interactions (Memmott 1999; Olesen et al. 2008; Russo et al. 2013; Russo 2016). Relating the outcome of focal studies to similar comparative studies between historical and contemporary wild bee communities (Bartomeus et al. 2013; Burkle et al. 2013) have power to draw connections between temperate regions.

New England is represented by a diverse assortment of flora species and habitat to support its approximately 400 wild bee species, making it an ideal location to assess plant-pollinator communities (Tucker and Rehan 2016; Jacobson et al. 2018; Odanaka et al. 2018).

Using a 125-year collection of wild bee specimens with floral association records, we evaluate structural change in the plant-pollinator network between historical and contemporary periods taking into consideration the conservation status of native wild bee species and native flora that comprise the plant-pollinator community in this region. This study aims to fill knowledge gaps in the modes of change within plant-pollinator relationships that characterise long-term network stability or vulnerability. Here we identify plant and bee species that are critically important ecological resources to wild bee plant-pollinator networks. This study serves as an important historical assessment of the plant-pollinator networks broadly representative of northeastern North America. The aims of this study are threefold: first, to determine the plant-pollinator network over the past 125 years; second, to evaluate if changes in the network could be attributed to exotic species introductions; and third, to investigate the network changes experienced by declining wild bee species in relation to threatened or endangered plants.

## Methods

### *Bee and floral databases*

The bee specimens evaluated in this study are held in the University of New Hampshire Insect Collections (UNHC) and specimen record data can be downloaded through the search collection option in the Global Biodiversity Information Facility (GBIF) online portal: <https://www.gbif.org/publisher/154da9abc010-422d-8fef-dbc54d10a3c6>. The full database is composed of 17,043 non-*Bombus* wild bee specimens collected between 1891 and 2016 that have been expertly identified to the species level (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). All *Bombus* species status assessments, including changes in historical plant-pollinator

networks, have been previously published (Jacobson et al. 2018). Wild bee species range information was obtained from Discover Life and The Very Handy Manual (Droege 2015; Ascher & Pickering 2018). The specimens in this database contain supporting data on taxonomy, geographic coordinates, repository information, collection method, and floral associations as available. Of the total non-*Bombus* wild bee specimens, 2497 contained records of floral host associations and were included in analyses.

Prior analyses on species-level status assessments of the wild bee community documented significant change in relative abundance (Mathiasson & Rehan 2019). Accordingly, each species was given a status determination of increase, decrease, or no change (stable) based on relative comparison calculations between historical (1891–1987) and contemporary (1988–2016) sample periods. As this study builds on prior species status assessments, the same time periods are used to compare plant-pollinator networks. These time points were determined to be the most suitable binning scheme by rarefaction and a species diversity analysis. Time periods focusing on points before and after the late 1980s have been used in similar bee decline studies (Biesmeijer et al. 2006; Colla and Packer 2008) and are additionally based on the ecological and environmental differences that divide these periods. Neonicotinoid insecticides became commercially available in 1985 and gained widespread use shortly thereafter (Kollmeyer et al. 1999), annual temperatures reached a record high in 1987 and have since been consistently above average (NOAA 2018), invasive bee species introductions have increased dramatically in North America since the 1980s (Russo 2016), and the great majority of agricultural and urban expansion occurred within the past 30 years in our study region (Sundquist and Stevens 1999; USDA 2012).

All floral host entries were verified from original specimen labels and accompanying collection information. To ensure accuracy of the plant data, any floral associations that only could be determined to family based on collection notes and field surveys were excluded. Taxonomic and range information were obtained using identification keys and distribution records on The New England Wild Flower Society website (gobotany.newenglandwild.org), Flora Novae Angliae: A Manual for the Identification of Native and Naturalised Higher Vascular Plants of New England (Haines et al. 2011), the USDA PLANTS database (USDA & NRCS 2018), and The Consortium of Northeastern Herbaria portal (Consortium of Northeastern Herbaria 2018). Information on the 288 plants species of rare or imperilled status was obtained from NH Heritage records of the Native Plant Protection Act (New Hampshire Natural Heritage Bureau 2013).

#### *Plant-pollinator network construction and species-level analyses*

To evaluate change and interrelatedness in the wild bee plant-pollinator interaction network over the 125-year study period, a network analysis was conducted using the 2497 wild bee specimens with accompanying floral data. All specimens with floral information were collected by sweep net as other trapping methods do not overtly consider floral associations. Given the uncertainty of sampling effort in museum collections

(Bartomeus et al. 2013), records were broadly classified into their respective collection time periods to account for possible disparity in sampling effort, especially during periods of low collection in the early 1900s (Mathiasson & Rehan 2019). The ‘plotweb’ function from the bipartite package (Dormann et al. 2009; Memmott 1999) in R 3.3.2 was used to build interaction network figures for the historical (1891–1987) and contemporary (1988–2016) periods, as well as for the overall 125-year period and sub-sets to illustrate key groups of conservation concern. Flowering plant species and bee species were used as the two sets of nodes, with connections drawn between to evaluate the degree of assortativity: the extent to which nodes are interconnected in that network (Noldus & Miegheem 2015). The networks are weighted representations of the plant-pollinator interactions, thus the boxes representing the nodes are proportionally scaled by the abundance of unique interactions.

The function ‘networklevel’ from the bipartite package (Dormann et al. 2009) calculated measures of nestedness, weighted nestedness, and connectance for the network, all of which are considered to be descriptive of co-evolution (Bascompte et al. 2003; Dormann et al. 2008). Nestedness is an organised network-level structure in which species are organised by decreasing numbers of interactions in a community where 0 represents a total lack of nestedness (no co-occurrence) and 1 represents maximum nestedness (high co-occurrence) (Atmar & Patterson 1993; Bascompte et al. 2003; Dormann et al. 2009). Weighted nestedness weights the nestedness measurement by considering interaction frequency to determine species co-occurrence (Galeano et al. 2009). A plant-pollinator network would be considered highly nested if, within the entire network of plants that interact with generalist bees, a group of specialist bees interacted with a subset of those plants of the larger network (Bascompte et al. 2003; Nielsen & Bascompte 2007). Conversely, little overlap between generalist and specialist species would result in a network with low nestedness. Unlike other network measures, nestedness values are not affected by network size (Nielsen & Bascompte 2007). Connectance calculates the proportion of realised links in a network out of all conceivable links (Dunne et al. 2002; Dormann et al. 2008, 2009) to measure community resilience to species loss. In theory, a highly connected system (connectance = 1) is less likely to suffer from individual species loss than a poorly connected system (connectance = 0) (Jordano 1987; Kearns et al. 1998).

The function ‘specieslevel’ from the bipartite package (Dormann et al. 2009) calculated degree, normalised degree, and pollinator service index (PSI) values for each individual bee and plant species within the interaction network. Degree is a measurement of species links: the unique interactions per individual species (Jordano et al. 2003; Dormann et al. 2009). In this study, the degree value represents the diet breadth for each bee species as a measurement of the number of floral hosts visited by that individual species and vice versa. To calculate the normalised degree value, the degree value for each species is weighted relatively to the total number of conceivable links between all species (Dormann et al. 2016; Tucker & Rehan 2016). The individual importance of each pollinator species within the entire community is measured by its PSI value. This index cannot be used to evaluate the importance of each floral plant species

(Dormann et al. 2008). The PSI is calculated based on visitation rates of bee species to plant species and the diversity of visitors for each plant species. A PSI value of 1 indicates an individual bee species' critical role within the network whereas a PSI value of 0 indicates a nonessential role. Bee species were categorised as specialists (oligolectic) or generalists (polylectic) based on degree measurements. Specialists were classified as having one floral host during all collection periods whereas generalists had two or more floral hosts.

## Results

### *Plant-pollinator network communities*

The 2497 plant-pollinator interactions used in this study occurred between 40 angiosperm (flowering plant) and six bee families over the 125-year period (1891–2016) and were represented by 222 wild bee species and 124 flowering plants. Of the 222 bee species in the full network, 74 species (33%) interacted with only one floral host, likely as specialist pollinators, whereas 127 species (57%) exhibited more generalist (between 2 and 10 floral hosts) interactions. Only 21 generalist species (9%) interacted with 10 or more floral hosts (Table S1).

The historical plant-pollinator interaction network includes 110 unique interactions. Tracing these interactions to the contemporary period revealed an interaction loss of 94% (103/110). The loss of 30% (33/110) interactions is likely due to bee or plant extirpations or declines and the other 64% (70/110) lost due to other reasons including loss of spatial co-occurrence between bee species and floral hosts, phenological mismatch, competition, or sampling bias. The remaining 6% (7/110) of interactions were maintained from the historical period to the present (Fig. 1; Table S2).

At the community level, the nestedness measure, which is not affected by network size, was highest during the historical period (5.39), indicating the most co-occurrence between generalist and specialist bee and plant species at that time. The nestedness was lowest for the overall (2.25) and slightly higher for the contemporary (2.68) network. Connectance was lowest in the overall network (0.033), with a slightly higher value during the contemporary period (0.041) and the highest value during the historical period (0.047; Table S3).

### *Exotic species introductions and expansions*

Six exotic bee species are present in this network: *Andrena wilkella*, *Hylaeus leptocephalus*, *Lasioglossum leucozonium*, *Lasioglossum zonulum*, *Anthidium oblongatum*, and *Megachile sculpturalis*. During the historical period, four interactions involving exotic bee species were recorded whereas 114 interactions involving exotic bee species were documented in the contemporary plant-pollinator network (Table S4).

The status of the 124 plant hosts that are represented in the network include taxa that are native (N), introduced (E), or naturalised (N/E). Of these 124 plants, 30% (37/124) are exotic, 54% (67/124) are native, and 16% (20/124) are naturalised. The

historical network contained 112 unique interactions (207 total interactions) that were made up of associations between wild bee species and plant hosts with: 76% native (85/112), 10% exotic (11/112), and 14% naturalised plants (16/112). The contemporary network contained 841 unique interactions (2290 total interactions) that were made up of associations between wild bee species and plant hosts with: 44% native (369/841), 40% exotic (333/841), and 16% naturalised plants (39/841) (Table S4).

Eight of the native rare or imperilled plant species are present in the interactions recorded in this study (Table 1). Six of these species have not had wild bee visitations recorded since 1990: *Eutrochium fistulosum* (Joe-Pye weed), *Nabalus boottii* (Boott's rattlesnake root), *Solidago leiocarpa* (Cutler's alpine goldenrod), *Diapensia lapponica* (pincushion plant), *Rhododendron lapponicum* (Lapland rosebay), and *Cypripedium parviflorum* (yellow lady's slipper). These eight rare and endangered species were involved in 11 unique interactions that were lost between the historical and contemporary time periods (Table S2).

### *Floral hosts of critical importance*

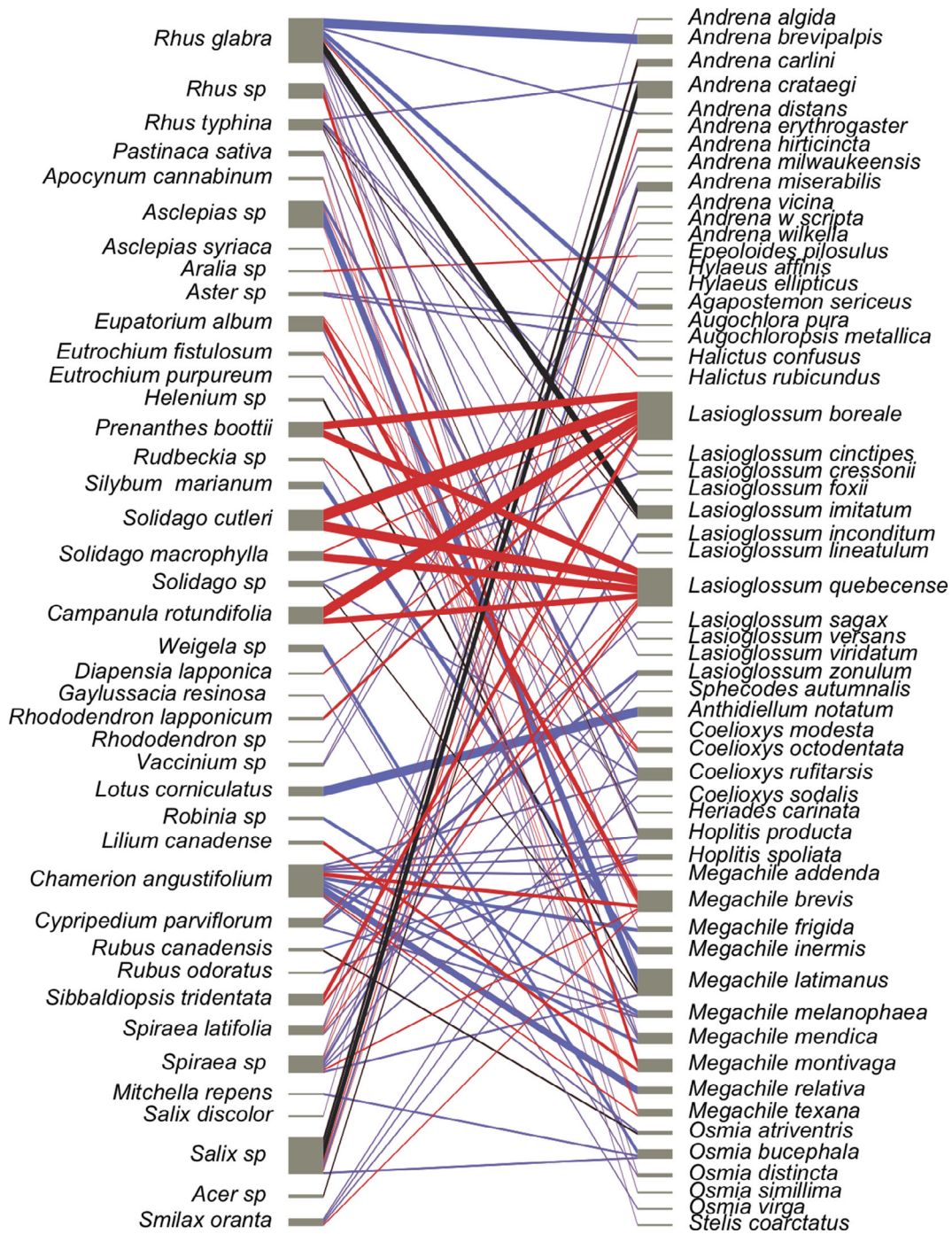
Individual floral host species importance was evaluated in each network based on node measurements of diet breadth (degree) in order to identify key species to the network. Degree measures the unique diversity of visitors to a floral host. There was no overlap in the plant species revealed to be of critical importance in the historical and contemporary networks. The average historical degree of floral hosts was 2.78 (0.047 normalised degree) and the average contemporary degree was 9.16 (0.040 normalised degree) (Tables S5 and S6).

During the historical period, four native floral plant species held the highest degree values: *Chamerion angustifolium* (narrow-leaved fireweed), *Rhus glabra* (smooth sumac), *Rhus typhina* (staghorn sumac), and *Spiraea alba* (broadleaf meadow-sweet). During the contemporary period, the four highest degree values were held by all exotic plant species: *Fagopyrum esculentum* (buckwheat), *Barbarea vulgaris* (yellow-rocket), *Trifolium repens* (white clover), and *T. pratense* (red clover).

The floral genera that supported the highest wild bee diversity and abundance also changed entirely between the historical and contemporary networks. During the historical period, the highest species diversity was supported by the following four genera: *Rhus* (sumac, N/E), *Spiraea* (spirea, N/E), *Chamerion* (fireweed, N), and *Salix* (willow, N/E). Historically, the genera that received the most bee visitations were *Rhus*, *Salix*, *Solidago* (goldenrod, N), and *Chamerion* (Table S7). During the contemporary period, the following four genera supported both the highest bee species diversity and visitor abundance: *Solidago*, *Rubus* (blackberry, N/E), *Trifolium* (clover, E), and *Fagopyrum* (buckwheat, E) (Table S7).

### *Wild bee species of critical importance*

Individual species importance was evaluated in each network based on node measurements of diet breadth (degree) and PSIs in



**Fig 1.** The historical plant-pollinator interaction bipartite network showing the 112 unique interactions and their contemporary (1988–2016) presence or absence. Black lines (7/112; 6%) represent interactions that were maintained from the historical period through the present; red lines (35/112; 31%) represent interactions that were lost due to bee or plant species extirpations or declines; blue lines (70/112; 63%) represent interactions lost due to other reasons, both plant and pollinator recorded in contemporary samples but are no longer associated. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

order to identify key species to the network. Degree measures the unique diversity of plant hosts visited by an individual species whereas PSI values synthesise visitation rates with the diversity of visitors for each plant species to reveal species contributing

essential service to the network. Aside from *Anthidiellum notatum* as an overall key species, there was otherwise no overlap in the wild bee species revealed to be of critical importance in the historical and contemporary networks. The average historical

**Table 1.** Rare plants of the wild bee plant-pollinator network. Plant conservation status obtained from NH heritage records of the Native Plant Protection act.

Family	Flower species binomial	Common name	Native New England (N) or introduced (E)	NH conservation status	Bee species associations	Bee abundance	Year of last recorded interaction
Apocynaceae							
	<i>Asclepias tuberosa</i>	Butterfly milkweed	N	Extremely rare (S1) Endangered (E)	6	8	2014
Asteraceae							
	<i>Eutrochium fistulosum</i>	Joe-Pye Weed	N	Extremely rare (S1) Endangered (E)	2	2	1990
	<i>Nabalus boottii</i>	Boott's rattlesnake root	N	Extremely rare (S1) Endangered (E)	3	8	1981
	<i>Solidago leiocarpa</i>	Cutler's alpine goldenrod	N	Rare (S2) Threatened (T)	2	11	1981
	<i>Solidago speciosa</i>	Showy goldenrod	N	Extremely rare (S1) Endangered (E)	8	24	2016
Diapensiaceae							
	<i>Diapensia lapponica</i>	Pincushion plant	N	Rare (S2) Threatened (T)	1	1	1981
Ericaceae							
	<i>Rhododendron lapponicum</i>	Lapland rosebay	N	Extremely rare (S1) Endangered (E)	1	2	1981
Orchidaceae							
	<i>Cypripedium parviflorum</i>	Yellow lady's slipper	N	Extremely rare (S1) Endangered (E)	4	5	1981

degree of bee species was 1.95 (0.048 normalised degree) and the average contemporary degree was 3.84 (0.041 normalised degree) (Table S1).

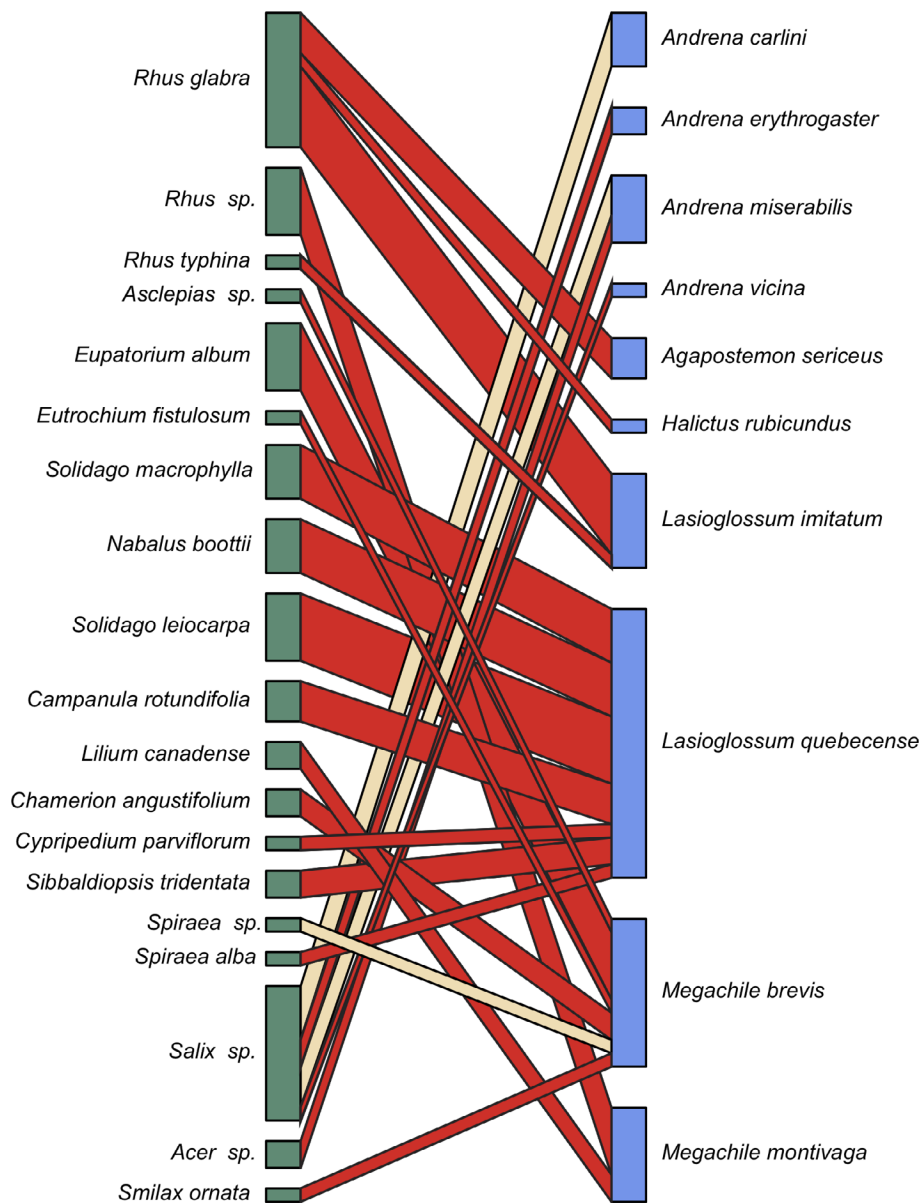
During the historical period, degree values revealed 34 species that interacted with only one floral host as specialists. Bee species in the family Megachilidae were most well represented during this period and correspondingly had the broadest diet breadth. *Megachile brevis* interacted with six unique floral hosts, and the following three species each interacted with five floral hosts: *Coelioxys rufitarsis*, *Hoplitis producta*, and *Megachile latimanus*. *Lasioglossum quebecense* (Halictidae) interacted with the most floral hosts (7) historically. Three of the seven historical floral host species visited by *Lasioglossum quebecense* that had no recorded interactions since 1981 are extremely rare and endangered specialised native flora (*Nabalus boottii*, *Solidago leiocarpa*, *Cypripedium parviflorum*). Seven bee species, all native to North America, had PSI values of 1.0 during the historical period: *Andrena algida*, *Andrena w-scripta*, *Epeoloides pilosulus*, *Anthidiellum notatum*, *Heriades carinata*, *Megachile inermis*, and *Osmia virga* (Table S1).

During the contemporary period, degree values revealed a total of 81 species that interacted with only one floral host as specialists. Bee species in the Halictidae family were most well

represented during this period and correspondingly had the greatest diet breadth. Of the nine bee species that had diet breadths of greater than 15 unique floral hosts, *Ceratina calcarata* (Apidae) is the only species that is not part of the family Halictidae. *Halictus ligatus* interacted with the most floral hosts (31), followed by *Halictus confusus* (29), *Lasioglossum versatum* (24), *Ceratina calcarata* (23), and *Agapostemon virescens* (22). Six bee species, all native to North America, had the highest PSI values: *Andrena kalmiae* (1.0), *Dufourea novaeangliae* (1.0), *Anthidiellum notatum* (1.0), *Andrena ziziae* (0.83), *Macropis ciliata* (0.80), and *Halictus ligatus* (0.65) (Table S1).

#### Floral interactions of declining wild bee species

Of the 14 wild bee species that are declining in northeastern North America (Mathiasson & Rehan 2019), eight species have records of floral interactions during both time periods, whereas six species did not and thus were excluded from further analyses. In comparing the normalised degree values, which measures the diet breadth relative to all possible interactions between bee species and floral hosts, five species experienced a decrease in diet breadth (normalised degree) from the historical to contemporary



**Fig 2.** The historical (1891–1987) plant-pollinator interaction bipartite network for declining wild bee species and the contemporary (1988–2016) presence or absence of these interactions. Yellow lines represent interactions that were maintained from the historical period through the present and red lines represent interactions that were lost. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

periods: *Andrena erythrogaster*, *Lasioglossum imitatum*, *Lasioglossum quebecense*, *Megachile brevis*, and *Megachile montivaga*. In contrast, four declining species experienced an increase in diet breadth: *Andrena carlini*, *Andrena miserabilis*, *Andrena vicina*, and *Halictus rubicundus*. The PSIs revealed that five declining species with relatively high PSI values during the historical periods experienced drastic decreases in PSI value in the contemporary period: *Andrena carlini*, *Andrena miserabilis*, *Lasioglossum quebecense*, *Megachile brevis*, and *Megachile montivaga* (Fig. 2; Table 2).

## Discussion

The overall changes in the wild bee plant-pollinator network revealed general network expansion, potential competition between native and exotic bee fauna for floral resources, and a substantial increase in exotic taxa to the network. In recent years, the network has grown to include many exotic wild bees and plants. This network expansion has likely caused certain interactions to be lost due to host plant shifts or competition. Exotic taxa are often adaptable in unfavourable environments and invade

**Table 2.** Species-level network statistics for declining wild bee species.

Family	Bee species binomial	Nesting habit	Diet breadth (degree)		Diet breadth (normalised degree)		PSI	
			Historical	Contemporary	Historical	Contemporary	Historical	Contemporary
Andrenidae	<i>Andrena carlimi</i> <sup>†</sup>	Ground	1	6	0.024	0.064	0.211	0.081
Andrenidae	<i>Andrena erythrogaster</i> <sup>†</sup>	Ground	1	-	0.024	-	0.105	-
Andrenidae	<i>Andrena forbesii</i>	Ground	-	3	-	0.032	-	0.050
Andrenidae	<i>Andrena imitatrix</i>	Ground	-	6	-	0.064	-	0.075
Andrenidae	<i>Andrena miserabilis</i>	Ground	2	11	0.049	0.117	0.495	0.127
Andrenidae	<i>Andrena salictaria</i> <sup>†</sup>	Ground	-	-	-	-	-	-
Andrenidae	<i>Andrena vicina</i>	Ground	1	8	0.024	0.085	0.053	0.079
Apidae	<i>Nomada bella</i>	Ground*	-	-	-	-	-	-
Apidae	<i>Nomada depressa</i>	Ground*	-	1	-	0.011	-	0.017
Halictidae	<i>Halictus rubicundus</i> <sup>†</sup>	Ground	1	16	0.024	0.170	0.043	0.048
Halictidae	<i>Lasioglossum imitatum</i> <sup>†</sup>	Ground	2	4	0.049	0.043	0.247	0.274
Halictidae	<i>Lasioglossum quebecense</i>	Ground	7	12	0.171	0.128	0.477	0.105
Megachilidae	<i>Megachile brevis</i> <sup>†</sup>	Cavity	6	1	0.122	0.011	0.389	0.111
Megachilidae	<i>Megachile montivaga</i>	Ground and cavity	2	1	0.049	0.011	0.732	0.033

\*Associated with nesting habit, but did not construct nest.

<sup>†</sup>Found to be in decline in Northeast United States by Bartomeus et al. (2013) (note: this study used a subset of UNHC bee specimens).

areas opportunistically (Goulson 2003; Richards et al. 2006; Crawford et al. 2009). Exotic plants spread fast and in domineering fashion to extensively cover areas; yet, when given a choice, it has been shown that bee species prefer native to exotic co-occurring flora (Williams et al. 2011; Morandin & Kremen 2013). Combined with environmental and anthropogenic disturbance, range expansions of exotic taxa could be a driver of network instability. A nested network is characterised by specialist interactions as a subset of generalist interactions and corresponds to stability in mutualistic networks (Bascompte et al. 2003; Valdovinos et al. 2016). The nestedness value was significantly highest in the historical network, indicating that the contemporary network will be more vulnerable to disturbance. Related studies have similarly found interaction network weakening in response to current anthropogenic climate change (Memmott et al. 2007; Burkle et al. 2013). This study is important as an assessment using long-term museum data to reveal changes in the wild bee plant-pollinator community.

#### *Effects of specialisation and exotic species introductions*

Two recent studies on long-term wild bee communities (Bartomeus et al. 2013; Burkle et al. 2013) found a disproportionate loss of specialist species and species with smaller diet breadths over time. This study did not find interaction loss to be overtly tied to specialisation, yet the specialist bees that lost interactions were more likely to be in decline than the generalist bees that lost interactions. We found interactions with rare and imperilled native flora were more likely to be lost with specialist pollinators

than generalist pollinators. Most of these floral species are also specialised either in morphology (*Asclepias tuberosa*, butterfly milkweed; *Cypripedium parviflorum*, yellow lady's slipper) or by alpine habitat requirements (*Nabalus boottii*, Boott's rattlesnake root; *Solidago leiocrapa*, Cutler's alpine goldenrod; *Dianthus laponicus*, pincushion plant; *Rhododendron lapponicum*, Lapland rosebay) (Haines et al. 2011).

Loss of generalist species has been proven to constitute dire imperilment to an interaction network (Memmott et al. 2004). *Megachile brevis* has not been observed in the contemporary network since 2011 and experienced a decline in both abundance and floral host interactions since the historical period. The unique floral hosts that *Megachile brevis* interacted with decreased from primarily native floral hosts (*Chamerion angustifolium*, N; *Smilax ornata*, E; *Asclepias* sp., N; *Eupatorium album*, N; *Eutrochium fistulosum*, N.; *Spiraea* sp., N/E) to one exotic floral host (*Vicia* sp., E). In previous recent studies, this species was found to be in decline in the northeastern United States (Bartomeus et al. 2013) and extinct in Illinois (Burkle et al. 2013).

The introduction of the notorious *Anthidium oblongatum*, an exotic megachilid with a rapidly expanding range, in to the plant-pollinator network appears to have induced a host plant shift for native *Anthidiellum notatum*. During the historic network, *Anthidiellum notatum* exclusively foraged on *Lotus corniculatus* (birdsfoot trefoil) whereas during the contemporary period, *Anthidium oblongatum* was the sole visitor to this plant species. *Anthidium oblongatum* was first found in the northeastern United States in 1994 (Hoebeke and Wheeler 1999; Maier 2009) and has been consistently linked to *Lotus*



*corniculatus* in this region (Ascher 2001; Maier 2009). In *Lotus corniculatus* was introduced to the United States in the 1800s as cattle forage and was found in New England as early as 1880 (Consortium of Northeastern Herbaria 2018). Though the behaviour of *Anthidium oblongatum* has not yet been well studied, its congener *Anthidium maculatum* exhibits extremely aggressive territorial behaviour and is known to attack and kill intruders that attempt to visit flowers within their territory (Wirtz et al. 1988; Hicks 2011).

The range expansions and integration of exotic species is evidenced by the increase in exotic wild bee and floral hosts in network interactions. In this study, exotic bee species comprised only four of the network interactions during the historical period in contrast to 114 exotic bee species interactions in the contemporary network. The historical interactions of exotic bee species occurred with native plant taxa, yet the contemporary exotic bee species interactions were dominated by exotic plant taxa (Table S2). Previous studies have similarly detected exotic bee preferences for exotic flora (Goulson 2003; Hanley & Goulson 2003; MacIvor et al. 2014). Congruently with the increased presence of exotic bee species, exotic plant taxa involved in network interactions increased dramatically between the two sampling periods with only 10% of unique interactions involving exotic floral hosts during the historical period compared with 40% of unique interactions in the contemporary period. This increase in interaction frequency for exotic plant taxa corresponded to a decrease for native plant taxa, with 76% of historical unique interactions involving native flora falling to only 44% of unique interactions during the contemporary period (Table S2). In terms of abundance, however, native plant taxa are strongly represented in the contemporary network with 60% of total interactions involving native plant taxa and 34% involving exotic plant taxa. Similarly, the most important genus to the contemporary network is *Solidago* (goldenrod, native), comprising 19% of total contemporary interactions. *Solidago* has additionally been shown to be an incredibly important floral resource to *Bombus* species (Jacobson et al. 2018) as well as generally to the wild bee fauna of the northeastern North America (Ginsberg 1983; Fowler 2016).

## Conclusion and future research recommendations

Consistent future monitoring of changes in these wild bee plant-pollinator networks is of vital importance to their stability and endurance. Climate change and an increase in disturbed habitat due to agricultural expansion over the past 30 years are likely drivers of these changes and are expected to continue in future (Tylianakis et al. 2008; La Sorte et al. 2014; Oakleaf et al. 2015). Increased habitat restoration combined with native floral enhancement of agricultural landscapes has been proven critical to wild bee biodiversity (Williams et al. 2015; Tonietto & Larkin 2017). The findings of this study provide additional support for focus on landscape restoration and promoting native flora plantings as a promising amelioration for the health of the wild bee community. Future studies are also much needed to examine broader plant-pollinator networks including plants that may be pollinated by non-bee pollinators.

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## Conflict of interest

The authors declare no potential conflict of interest.

## Data availability statement

The data that support the findings of this study are openly available in the Global Biodiversity Information Facility (GBIF) online portal: [<https://www.gbif.org/publisher/154da9ab-c010-422d-8fef-dbc54d10a3c6>].

## Supporting information

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

**Table S1** The number of floral associations for each wild bee species in the total New Hampshire plant-pollinator network and respectively during the historical and contemporary periods

**Table S2.** The number of floral associations weighted by total possible interactions for each wild bee species in the total New Hampshire plant-pollinator network and respectively during the historical and contemporary periods

**Table S3.** The pollinator service index for each wild bee species in the total New Hampshire plant-pollinator network and respectively during the historical and contemporary periods

**Table S4.** The number of bee associations for each floral plant species in the total New Hampshire plant-pollinator network and respectively during the historical and contemporary periods

**Table S5.** The number of bee associations for each floral plant species weighted by the total possible interactions in the total New Hampshire plant-pollinator network and respectively during the historical and contemporary periods

**Table S6.** Flowering plant species of the New Hampshire wild bee plant-pollinator network with relevant ecological information

**Table S7.** New Hampshire plant-pollinator wild bee x flower interactions compared between historical (1891–1987) and contemporary (1988–2016) periods

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