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ORIGINAL PAPER

Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson

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Abstract Bumblebees (*Bombus* spp.) have been declining rapidly in many temperate regions of the Old World. Despite their ecological and economic importance as pollinators, North American bumblebees have not been extensively surveyed and their conservation status is largely unknown. In this study, two approaches were used to determine whether bumblebees in that region were in decline spatially and temporally. First, surveys performed in 2004–2006 in southern Ontario were compared to surveys from 1971 to 1973 in the same sites to look at changes in community composition, in one of the most bumblebee diverse areas of eastern North America. Second, the extent of range decline for a focal species (*Bombus affinis* Cresson) was estimated by surveying 43 sites throughout its known native range in eastern Canada and the United States. Our study documents an impoverishment of the bumblebee community in southern Ontario over the past 35 years. *Bombus affinis* in particular was found to have declined drastically in abundance not only in southern Ontario but throughout its native range. The loss of any bumblebee species may result in cascading impacts on native fauna and flora and reduce agricultural production. Implications for the conservation of this important group of pollinators are discussed.

Keywords Bee conservation · Bumblebees · Pollinator decline · *Bombus affinis* · Species diversity · Species range · Relative abundance

Introduction

The decline of pollinators has become a global issue of concern in recent decades (Buchmann and Nabhan 1996; Allen-Wardell et al. 1998; Kearns et al. 1998; Cox and Elmqvist 2000; Steffan-Dewenter et al. 2005; Biesmeijer et al. 2006). The population dynamics, behavioural ecology and status in the wild for pollinator species are understudied in conservation biology (Buchmann and Nabhan 1996). The loss of native pollinators would likely have far-reaching, cascading effects on plant communities (Corbet

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et al. 1991; Bond 1994; Vamosi et al. 2006) and on organisms that depend on native plants for shelter and sustenance (Buchmann and Nabhan 1996). Additionally, the projected economic costs associated with pollinator decline as a result of decreased crop yield are substantial (Pimentel et al. 1997; Allen-Wardell et al. 1998; Kevan and Phillips 2001). However, the lack of information on the statuses of insect pollinator populations has hindered conservation efforts, especially in North America. In this study we focus on assessing the conservation status of the native North American bumblebee species found in southern Ontario, Canada.

Bumblebees (*Bombus* Latreille) (Hymenoptera: Apidae, Bombini) are more vulnerable to extinction than most other animal taxa for a variety of reasons. Their long colony cycles with the production of reproductives primarily towards the end means even slight changes in resource acquisition could have large cumulative impacts on colony development and reproductive success. Another feature that makes these bees very susceptible to extinction is that they require three types of habitats (for foraging, nesting and hibernating) in proximity to each other. In addition, they may require specific flowers for foraging (Harder 1985) and specific substrates for nesting (Macfarlane 1974). The combination of haplodiploidy along with their eusocial colony organization (Packer and Owen 2001; Zayed and Packer 2005) and complex habitat requirements makes bumblebees more susceptible to extinction than most other organisms.

In parts of Europe, many bumblebee species have been observed to be undergoing drastic decline while others remain abundant (Williams 1982; Rasmont 1995; Westrich 1996; Goulson 2003; Sarospataki et al. 2005; Goulson et al. 2006; Fitzpatrick et al. 2007). For example, of the 25 species known in the UK, three are considered extinct and at least seven have undergone significant declines (Williams 1982; Goulson et al. 2005; Benton 2006). The causes for the decline of European bumblebee species diversity are not fully understood, but have been attributed to agricultural intensification (Williams 1986; Osborne and Corbet 1994; Goulson 2003; Carvell et al. 2006; Rasmont et al. 2006) and pesticide use (Williams 1986; Thompson and Hunt 1999; Rasmont et al. 2006).

In North America, the lack of long-term monitoring and baseline data have hindered efforts to determine the conservation status of native bumblebees (Berenbaum et al. 2007). Nevertheless, there is some evidence of decline in four species, all of which are members of the subgenus *Bombus* Latreille (*Bombus franklini* Frison and *B. occidentalis* Greene in the west and *B. affinis* Cresson and *B. terricola* Kirby in the east). As a result, the Xerces Society for Invertebrate Conservation has placed these species on its Red List of pollinator insects (Thorp and Shepherd 2005). *Bombus franklini* is thought to be at the brink of extinction because its small range has been extensively searched in recent years and very few specimens have been observed (Thorp 2005). *Bombus terricola, B. affinis* and *B. occidentalis* have much larger ranges but have disappeared from many sites where they were previously common (Thorp and Shepherd 2005). There is even less evidence for declines in populations of species in other subgenera. Consequently, hypotheses to explain patterns of decline have not been as adequately formulated or tested in North America as they have in parts of Europe.

In this study, we first aim to determine whether eastern North American bumblebees show evidence of decline. We do this by quantifying current *Bombus* community composition using various measures of richness and abundance in a region of eastern North America and comparing our data to those obtained by a similar study performed over 30 years ago at the same sites (Macfarlane 1974). Secondly, we use *Bombus affinis* as a focal species to determine extent of decline throughout its historical range. This species was chosen for two reasons. First, it is most closely related to *B. franklini* (Cameron et al.

2007) which is the only North American bumblebee considered to be a "species of concern" by the US Fish and Wildlife Service (Thorp 2005). Second, it seems to have declined rapidly throughout its range over the past decade (Berenbaum et al. 2007), despite numerous studies which suggest it was historically common and ubiquitous in eastern North America (Leonard 1928; Macior 1966; Macfarlane 1974; Fisher 1983; Bregazzi and Laverty 1992; Schiestl and Barrows 1999).

Methods

Natural history

Our chosen focal species, *Bombus affinis* is found in eastern North America west to the Dakotas, north to southern Ontario and south to Georgia (Thorp and Shepherd 2005). This species has one of the longest colony cycles of all native social bees; it is one of the earliest to emerge in the spring and one of the last to cease foraging in the fall (Macfarlane 1974). According to museum holdings from the Canadian National Collection, University of Guelph and Royal Ontario Museum, specimens of *B. affinis* have been collected in a wide variety of habitats including mixed farmland, marshes and wooded areas throughout its range. Macfarlane (1974) observed *B. affinis* on at least 65 plant genera, many of which are ecologically and economically important. *Bombus affinis* has also been observed biting holes (i.e. nectar-robbing) in flowers with long corolla tubes such as *Impatiens capensis* Meerb (Jewelweed), *Linaria vulgaris* Mill (Yellow Toadflax) (R. Gegear, pers. comm.) and *Vicia cracca* L. (Cow Vetch) (Harder 1983). Furthermore, *B. affinis* is an important host for the social parasite *Bombus (Psithyrus) ashtoni* (Cresson) (Laverty and Harder 1988).

Assessing changes in *Bombus* community composition

Southern Ontario is within the historical range of the majority of eastern North American *Bombus* species (Laverty and Harder 1988) and was thus chosen to perform a comparative study to determine changes in species richness and abundance patterns. An extensive study performed between 1971 and 1973, in the city of Guelph and surrounding area, examined various aspects of bumblebee ecology and diversity (Macfarlane 1974) providing baseline data for comparison. That study sampled all bumblebee species in three areas; the main study area was in the southern region of Guelph, the other areas were near the towns of Arkell and Belwood. At each site, foraging bumblebees were opportunistically collected (using insect nets) while foraging. In 1972 and 1973, queens, workers and males were collected approximately three times a week from mid-April until first frost in October. In 1971, bees were collected less frequently. The specimens were later identified in the laboratory.

During our survey, we collected foraging bumblebees from two sites (the southern region of Guelph and Belwood) over three summers (2004–2006) using insect nets. These sites were chosen based on detailed descriptions in the previous survey (Macfarlane 1974). The town of Arkell was omitted because the landscape has undergone substantial changes over the past 30 years and sampling in the same areas would not have been possible. Queens were not caught to reduce the impact of this study on current populations. The bees were either identified in the field and released or brought back to the lab to be identified morphologically (Laverty and Harder 1988). Released bees were marked with non-toxic fluorescent powder to prevent recapture.

In 2004 and 2005, the sites were sampled approximately once a month from May to September. In 2006, a general protocol for a direct capture line transect method to determine bee species diversity and abundance in complex flower communities was used (Dafni et al. 2005). Within each site, two belt transects approximately 1 km in length and 2 m wide were slowly paced once a week from April until first frost in October, and all foraging male and worker bumblebees were collected. To be consistent with the previous study, the Guelph site was the main area surveyed; Belwood was only sampled every five weeks. Surveys were only performed on days without precipitation or strong winds and with temperatures between 15 and 30°C. Data were compiled from 2004 to 2006 and compared with appropriate subsets of the data presented in the Macfarlane (1974) study.

The extent of decline of *Bombus affinis* throughout its historical range

We used *B. affinis* as a focal species to determine extent of range decline of a previously common bumblebee species. Foraging bees were collected using insect nets from 43 sites, 18 in Canada, and 25 in the United States (Table 1), throughout the native range for *B. affinis* from March 2005 to July 2007. Of these sites, 28 were chosen from locality information for specimens obtained between 1904 and 2003 in various collections (Table 1). Fifteen additional sites within its historical native range (Mitchell 1962) were also selected. Within each site, three different habitats (roadside ditch, old field and wetland) were sampled when possible to allow collecting from a diversity of plant species. Efforts were made to find similar sites for sampling if food plant, elevation and habitat type were described on the original specimen labels.

Using ComRAND randomization software (Zayed and Grixti 2005) on the historical data set (Macfarlane 1974), it was determined that by collecting 150 individuals, the probability of missing *B. affinis* if it was present at a given site at previous abundances was less than 5%. To increase our chances of finding the species, we collected 200 bumblebees and determined the presence or absence of *B. affinis* at each site. Again, bees were either identified in the field and marked and released, or brought back to the laboratory to be identified. Voucher specimens can be found in the L. Packer Bee Collection at York University, Toronto, Ontario, Canada.

Data analysis

For the comparison of our survey to that of Macfarlane (1974), we only considered data collected by R. Macfarlane on worker and male bumblebees in Guelph and Belwood. To determine changes in the abundance of each species between the two 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. We quantified biodiversity levels for all sampling periods using the Shannon-Weiner diversity (H') and Pielou's Evenness (E) indices. These indices were applied in this study as they are widely used metrics in biodiversity studies (Magurran 2003, 1988).

Table 1 Locations of historical and additional sites for presence/absence surveys of *Bombus affinis*. Historical sites were chosen based on specimen locality information at various insect collections. Additional sites were chosen within the species historical range according to Laverty and Harder (1988) and Mitchell (1962)

Historical sites	Collection containing specimen	Additional survey sites
Macomb County, MI, USA	Ohio State University	St. Clair Co. MI, USA
Clingman's Dome, Great Smoky Mountains National Park, TN, USA	Canadian National Collection	Lake Junaska, NC, USA
Highlands 3800 ft, NC, USA	Canadian National Collection	Grandfather Mountain, NC, USA
Mt. Rogers, Jefferson National Forest, VA, USA	Ohio State University	Elk Creek, VA, USA
Watoga State Park, WV, USA	Ohio State University	Bryson City, NC, USA
Walhalla, SC, USA	Canadian National Collection	Charlotte, NC, USA
Meredith, NH, USA	Canadian National Collection	Wake County, NC, USA
Ithaca, NY, USA	Cornell University	Cuyahoga National Pk, OH, USA
Amherst, MA, USA	Canadian National Collection	
Framingham, MA, USA	Canadian National Collection	
Casco, ME, USA	Cornell University	
Tuckasegee, NC, USA	Canadian National Collection	
Tompkins County, NY, USA	Canadian National Collection	
Macon Co. 3500' NC, USA	Canadian National Collection	
6 Mile Creek, NY, USA	Canadian National Collection	
Mercer Co. PA, USA	Ohio State University	
Okefenokee, GA, USA	Cornell University	
London, ON, CAN	T. Laverty Collection	Edwards Gardens, ON, CAN
Amherst Island, ON, CAN	T. Laverty Collection	Exeter, ON, CAN
Pinery Provincial Park, ON, CAN	Royal Ontario Museum	Leamington, ON, CAN
Hamilton, ON, CAN	Royal Ontario Museum	King City, ON CAN
G. Ross Lord Park, ON, CAN	Royal Ontario Museum	High Park, ON, CAN
Guelph, ON, CAN	University of Guelph	Kingston, ON, CAN
Arkell, ON, CAN	University of Guelph	St. Catherines, ON, CAN
Belwood, ON, CAN	University of Guelph	
Gatineau Provincial Park, QC, CAN	Canadian National Collection	
Parkhill, ON, CAN	Canadian National Collection	
Manester Tract, Norfolk Co. ON, CAN	York University	

We used BioDiversity Pro software (McAleece et al. 1997) to generate rarefaction curves in order to determine whether the sampling effort was adequate. To compare species richness and diversity to the previous survey, we generated the mean number of species collected and the Shannon-Wiener diversity index for our sample size from 1,000 iterations of samples randomly drawn from the larger historical dataset, producing 95% confidence intervals using EcoSim software (Gotelli and Entsminger 2006). In addition, we used Species Diversity and Richness software (Seaby and Henderson 2006) to produce a clustering dendrogram using the Jaccard similarity index to show the degree of similarity between time periods and sites. We chose the Jaccard similarity index due to its widespread use on presence–absence data and its ability to provide a more conservative similarity measure than indices which take into account species abundance (Magurran 2003, 1988).

Results

A total of 1,195 bumblebees belonging to 11 species were collected during 2004–2006; 11 in Guelph and 9 in Belwood (Fig. 1). These results differ from the previous study (Macfarlane 1974) where a total of 14 bumblebee species were found (13 at each site). The Shannon-Weiner and Pielou's Evenness indices were higher in the previous study ($H' = 2.163$, $E = 0.820$) than the recent study ($H' = 1.504$, $E = 0.627$). No bumblebee species were found during our survey that had not been collected in the previous study. The species present in the earlier survey but absent from both sites in our survey were *B. affinis*, *B. pensylvanicus* DeGeer and *B. ashtoni* (Fig. 1). Species exhibiting significantly lower relative abundances than those observed in the previous survey were *B. fervidus* Fabricius, *B. terricola*, *B. vagans* Smith and *B. citrinus* Smith (Fig. 1, Table 2). Declines were thus observed for both long and short-tongued *Bombus* species (Laverty and Harder 1988). Conversely, four species (*B. bimaculatus* Cresson, *B. impatiens* Cresson, *B. rufocinctus* Cresson and *B. ternarius* Say) exhibited significant increases in relative abundances than those observed in the previous study (Fig. 1, Table 2); *Bombus impatiens* and *B. bimaculatus* were especially numerous with relative abundances over twice that of the historical dataset.

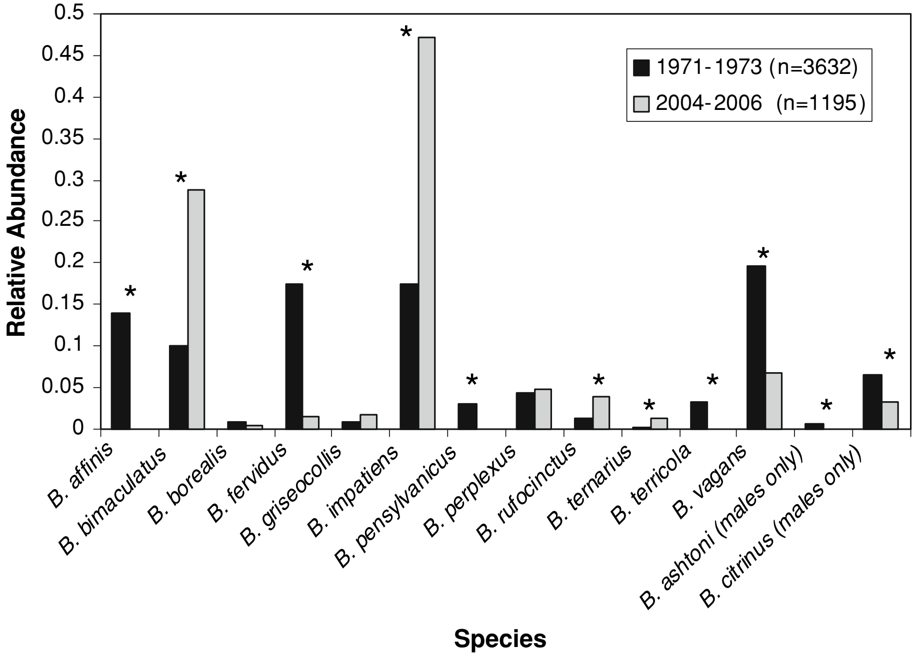

Fig. 1 Comparison of the relative abundance of each bumblebee species collected in Southern Ontario from 1971–1973 (black) (Macfarlane 1974) and 2004–2006 (grey) (* indicates $P < 0.001$, z statistics are presented in Table 2)

Table 2 Values for z-tests of equal proportions for the relative abundances of each *Bombus* species between the two survey periods (1971–1973 and 2004–2006) where the null hypothesis is that the proportion for each species is equal during both time periods. The first proportion was calculated from a subset of data presented in Macfarlane (1974). Indicated species tongue lengths were obtained from Laverty and Harder (1988)

Species/tongue length [S(hort), M(edium) and L(ong)]	$z_1 = \frac{\hat{p}_1-\hat{p}_2}{\sqrt{\frac{\hat{p}_1(1-\hat{p}_1)}{n_1}+\frac{\hat{p}_2(1-\hat{p}_2)}{n_2}}}$	P value	Direction of change
B. affinis (S)	24.991	<0.001	Decrease
B. bimaculatus (M)	−13.483	<0.001	Increase
B. borealis (L)	1.277	=0.102	No change
B. fervidus (L)	21.842	<0.001	Decrease
B. griseocollis (M)	−1.921	=0.978	No change
B. impatiens (M)	−18.800	<0.001	Increase
B. pensylvanicus (L)	10.750	<0.001	Decrease
B. perplexus (M)	−0.518	=0.699	No change
B. rufocinctus (S)	−4.146	<0.001	Increase
B. ternarius (S)	−3.185	<0.001	Increase
B. terricola (S)	10.400	<0.001	Decrease
B. vagans (M)	12.970	<0.001	Decrease
B. ashtoni (S)	5.216	<0.001	Decrease
B. citrinus (S)	5.013	<0.001	Decrease

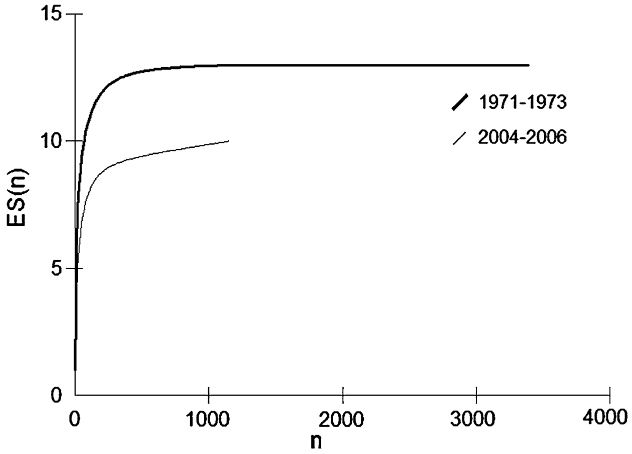

Fig. 2 Rarefaction curves for the two sampling periods (1971–1973 and 2004–2006) at Guelph, ON and Belwood, ON combined generated using BioDiversity Pro software (McAleece et al. 1997)

Rarefaction curves indicated that differences in species richness and diversity were not due to the differences in sample size (Fig. 2). Random samples of 1,195 individuals (i.e., our sample size) drawn from the historical dataset show an expected mean species richness of 13.968 ± 0.031 and mean H' of 2.160 ± 0.000 for the two sites combined. Our observed values of 11 and 1.504 fall well below the 95% confidence intervals determined from the simulations of the historical dataset demonstrating a significant reduction in diversity over time. Performing the same analysis on each site independently showed our observed values (Guelph species richness = 11, $H' = 1.317$; Belwood species richness = 9) were below the 95% confidence intervals of the expected values generated from the historical dataset. Only our observed diversity index for Belwood ($H' = 1.979$) was not

Fig. 3 Clustering dendrogram based on the Jaccard similarity index generated using Species Diversity and Richness software (Seaby and Henderson 2006). The differences between bumblebee communities based primarily on the presence or absence of species for the two sampling periods are illustrated

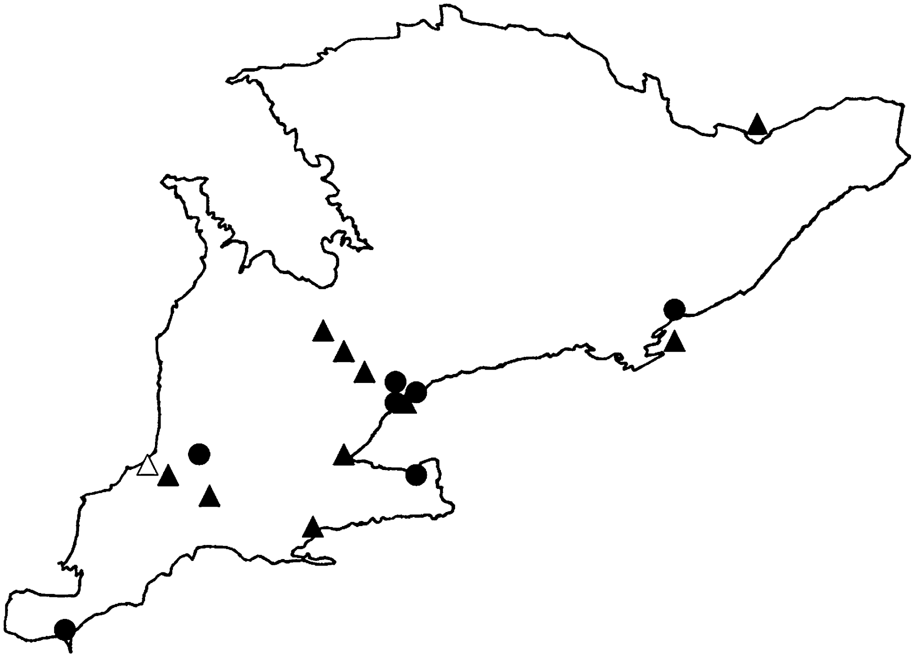

Fig. 4 Historical and additional sites sampled during the summers of 2005 and 2006 for the presence or absence of *Bombus affinis* throughout its Canadian range. The only site where the species was found was Pinery Provincial Park, ON. Triangles represent historical sites and circles represent additional sites. Closed triangles and circles indicate locations where *B. affinis* was absent and open figures represent sites where the species was present

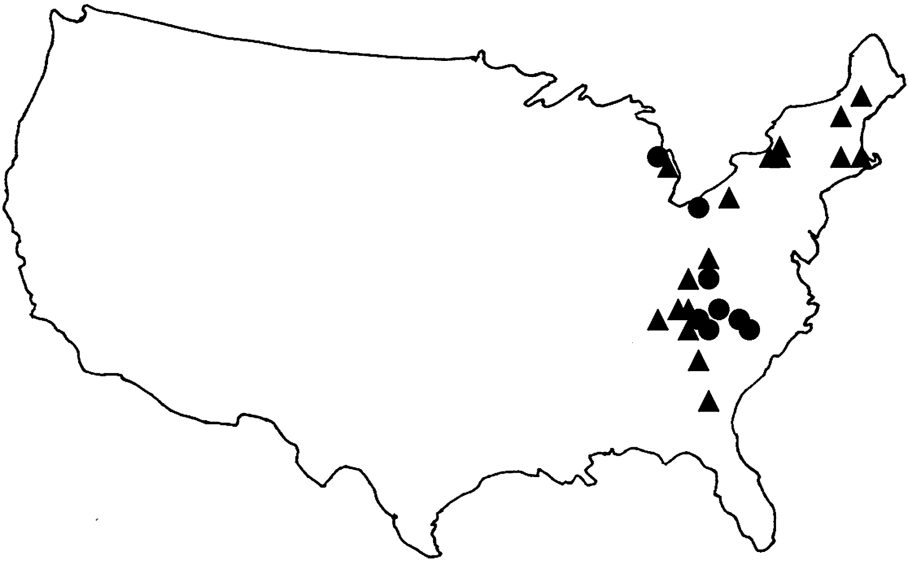

Fig. 5 Historical and additional sites sampled during the summer of 2006 for the presence or absence of *Bombus affinis* throughout its eastern US range. No individuals belonging to this species were found

found to be below the expected value for that site ($H' = 1.734 + 0.004$). The cluster analysis revealed that the bumblebee communities clustered more closely by time period than locality (Fig. 3).

After surveying at 43 sites (approx. 9000 *Bombus* individuals), only one *B. affinis* individual was collected (Pinery Provincial Park, Ontario, Canada) (Fig. 4); while foraging on *Helianthus divaricatus* L. (Woodland Sunflower). No individuals belonging to this species were found during surveys of sites in the United States (Fig. 5).

Discussion

This study provides the first quantitative evidence that a historically bumblebee diverse region of Eastern North America has undergone declines in bumblebee species richness, evenness, diversity and relative abundance in recent decades. By looking at changes in community composition between two time periods, our study supports suggestions that the North American members of the subgenus *Bombus* (*B. affinis, B. franklini, B. occidentalis* and *B. terricola*) and a social parasite which specializes on members of this group (*B. ashtoni*) are declining (Giles and Ascher 2006; Berenbaum et al. 2007). We also show evidence of decline among the members of the subgenera *Fervidobombus* (*B. fervidus* and *B. pensylvanicus*) and the other species of *Psithyrus* found in this region (*B. citrinus*). Additionally, by surveying numerous sites for *B. affinis*, we demonstrate that this previously widespread and common species has undergone drastic decline and has likely been extirpated throughout much of its range.

Of the 14 species collected in the first survey by Macfarlane (1974), we found seven to be either absent or decreasing in relative abundance while four species exhibited increases in relative abundance. This pattern is similar to that observed in Europe where approximately half of the bumblebee species have been shown to be in decline, and only a few species are increasing (Berezin et al. 1995; Sarospataki et al. 2005; Benton 2006; Kosior et al. 2007). The reasons for declines in the North American fauna over the past few decades are not well understood but likely include multiple stressors such as pathogen spillover from commercial colonies, pesticide use and habitat loss (Berenbaum et al. 2007). The distributions and abundances of the social parasites *B. citrinus* and *B. ashtoni* are likely influenced by these factors directly, as well as by effects upon the population dynamics of their hosts.

Pathogen spillover has been implicated in the significant declines of many animals (Morton et al. 2004; Power and Mitchell 2004) but is a poorly understood threat for pollinators. The use of commercial bumblebees with a high prevalence of parasites for greenhouse pollination has been shown to cause pathogen spillover into populations of wild bumblebees foraging nearby (Colla et al. 2006). Although the effects of certain parasites on species native to eastern North America have been found to be mostly sub-lethal, studies have been performed only on the common species *B. impatiens* (Macfarlane et al. 1995; Otterstatter et al. 2005; Gegear et al. 2006). Parasites found in commercial colonies have been found in species other than *B. impatiens* (Macfarlane 1974; Macfarlane et al. 1995; Colla et al. 2006) but the extent of their lethal and sublethal effects in other *Bombus* species remains unknown. Nonetheless, the increased use of bumblebees in greenhouse operations in recent decades has been implicated in the decline of members of the subgenus *Bombus*, including *B. affinis* and *B. terricola* (Thorp and Shepherd 2005; Berenbaum et al. 2007).

Another recent change in North America possibly implicated in the observed bumblebee declines is the extensive use of novel pesticides. In particular, one group of persistent pesticides (the neonicotinoids) has been shown to be highly toxic to bees (EPA 1994; Marletto et al. 2003) and has been implicated in bee declines in various regions in Europe (Tasei et al. 2001). Its use in North America began in the early 1990s, before members of the subgenus *Bombus* were noted to be in decline, and thus this group of pesticides may be a substantial threat. The neonicotinoids are now a commonly used systemic insecticide in many regions of eastern North America for crop and turf pest control (Cox 2001). A member of this group (Imidacloprid) is non-lethal to bumblebees when used as directed; however, studies of its effects on bumblebees only tested one species, *B. impatiens*, as the representative for species in eastern North America (Gels et al. 2002; Morandin and Winston 2003). The lethal and sub-lethal effects of this group of pesticides urgently need to be determined for other North American bee species to understand their potential impact on pollinator decline.

Habitat loss due to intensive agriculture and urbanization provides another significant threat to native pollinator populations (Kearns and Inouye 1997). While *B. impatiens* and *B. bimaculatus* seem to have adapted well to nesting in urban and agricultural areas and remain abundant throughout their ranges (Bartholomew et al. 2006; Colla et al. 2006; Giles and Ascher 2006), the declines noted in other species may be reversed if native ecosystems are restored. In particular, *Bombus fervidus, B. pensylvanicus* and *B. vagans* are long-tongued species and may be more susceptible to decline due to their increased specialization on flowers with long corollas (Harder 1983). Whether reduced availability of appropriate food plants contributes to the declines of these species remains to be determined.

Understanding differential responses within a community subject to the same environmental changes is an important issue when considering bumblebee conservation. In parts of Europe, habitat loss due to agricultural intensification is the main threat to the bumblebee fauna (Williams 1986; Goulson et al. 2005; Benton 2006; Rasmont et al.

2006). In Britain, where the best data on bumblebee population dynamics and natural history exists, two main hypotheses have been put forward to explain the different responses of different species to habitat loss. Firstly, the loss of food plants with long corollas (such as legumes) has been implicated in the decline of long-tongued species (Williams 1988, 1989; Goulson et al. 2005; Carvell et al. 2006; Rasmont et al. 2006). In addition, the climatic specializations of the different species may interact with food-plant availability to make species more vulnerable where they are near their range edges (Williams 1985, 1988; Williams et al. 2007). The data presented in this study suggest neither hypothesis completely explains the observed pattern of decline: both long and short-tongued species were shown to be in decline, and a previously common species, *B. affinis*, has rapidly declined not only at the edge of its range, but throughout. These results support the suggestion by Williams et al. (2007) that the causes of bumblebee decline likely differ between Europe and North America.

In the UK, adequate baseline data has allowed for the mechanism of decline to be studied further: as a result, species-specific conservation plans have been designed and implemented (Edwards 1998, 2002; Benton 2006). However, little is known in North America about the habitat requirements for each species, and therefore designing species-specific conservation programs is problematic. It may not be fruitful to search for a single reason for the decline of numerous species of bumblebees worldwide: reasons for the decline likely differ among species within a habitat and among bumblebee communities across the landscape. Nonetheless, given the importance of bumblebees as pollinators and as indicators of ecosystem health, it is essential that we obtain a better understanding of this subject.

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