



# Historical changes in bumble bee body size and range shift of declining species

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## Abstract

Bumble bees are declining worldwide, their vital ecosystem services are diminishing and underlying mechanisms are species specific and multifaceted. This has sparked an increase in long-term assessments of historical collections that provide valuable information about population trends and shifts in distributions. However, museum specimens also contain important ecological information, including rarely measured morphological traits. Trait-based assessments of museum specimens provide additional information on underlying mechanisms of population trends, by tracking changes over time. Here, we used museum specimens of four *Bombus* species, spanning a timeframe of 125 years to: (i) compare body size of declining and increasing species, (ii) assess intra-specific trends over the last century, and (iii) investigate shifts in geographical distribution over time. We found that declining *Bombus* species were larger than increasing ones. All four species were smaller in current time than a century ago. Intra-specific size declines were more pronounced for larger-bodied species. With our sampling, declining and increasing species showed an upward shift in elevation, and declining species showed an additional geographic shift in recent times as compared to historic records. Intra-specific body size declines may represent species adaptation to unfavorable environmental conditions, and may be a useful metric to complement traditional species vulnerability assessments. We highlight the utility of incorporating trait-based assessments into future studies investigating species declines.

**Keywords** *Bombus* · Body size · Long-term data · Historic status assessments · Museum collections · Range shifts

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## Introduction

Pollinators are declining on a global scale, whereby diminishing vital ecosystem services with considerable economic (Breeze et al. 2016; Kleijn et al. 2015; Klein et al. 2007) and biodiversity value (Aguilar et al. 2006; Goulson et al. 2015; Potts et al. 2010). These declines are caused by a multitude of human induced factors, such as climate change, large-scale landscape modifications, increased use of agrochemicals and the spread of parasites and pathogens (Brown et al. 2016; Goulson et al. 2015; Winfree et al. 2009). Long-term assessments of museum specimens are particularly informative to track wild bee population trends and shifts in distribution (Bartomeus et al. 2018). Historic records reveal severe wild bee declines over the last few decades, concordant with the loss of floral resources (Bartomeus et al. 2013; Burkle et al. 2013; Scheper et al. 2014) and global agricultural intensification (Bommarco et al. 2012; Goulson et al. 2015; Kosior et al. 2007; Potts et al. 2010).

Wild bee declines are not uniform but species specific, with bumble bees showing some of the most notable declines on a global scale (Arbetman et al. 2017; Bartomeus et al. 2013; Cameron et al. 2011; Colla et al. 2012; Goulson et al. 2008; Williams et al. 2009). In Europe, 46% of the bumble bee species have suffered substantial population declines (Potts et al. 2010) and about half of the North American bumble bee fauna have severely decreased in numbers and many have experienced range contractions (Colla et al. 2012). Recent effects of climate warming exasperate these declines in cold adapted bumble bees (Cameron et al. 2007; Williams 1998). Bumble bees have shown opposite range responses in Europe and America as compared to other taxa (Sunday et al. 2012). They failed to shift into cooler regions while suffering contractions at the warmer end, resulting in losses of their historically occupied ranges (Kerr et al. 2015). Southern species have also experienced an elevational upwards shift by up to 300 m in the last 50 years (Kerr et al. 2015). In addition, projected bumble bee dispersal rates are low and areas of species losses are high at the eastern parts of America (Sirois-Delisle and Kerr 2018). Thus, assessments on a more regional scale can provide crucial information on species trends, by revealing severe local declines (Colla and Packer 2008; Jacobson et al. 2018) and extinctions (Grixti et al. 2009). This elucidates the need to complement large-scale species trends with regional scale assessments.

Declining bee species are characterized by certain life history traits, which include late spring emergence, nest location, sociality, climate and habitat specialization (Colla et al. 2012; Potts et al. 2010; Williams et al. 2009, 2010). Decline susceptible bees also show narrower dietary and phenological breadth and larger body size (Bartomeus et al. 2013; Oliveira et al. 2016; Scheper et al. 2014). Body size is a key functional trait that responds rapidly to changing environmental conditions, such as resource availability and climate (Chown and Gaston 2010). In bees, body size heritability between generations is low (Tepedino et al. 1984). Size is plastic, being mainly determined by food provisioning to the offspring (Helm et al. 2017; Radmacher and Strohm 2009; Roulston and Cane 2002). Large size can also be selected against, as more resources are required for larger bees (Müller et al. 2006), making them especially susceptible to habitat degradation through large-scale agricultural intensification (Larsen et al. 2005; Persson and Smith 2011). Population trends over the last century in the Netherlands showed a negative relationship with body size (Scheper et al. 2014). Similarly, large bees have suffered severe declines in northeast US, while some small bee populations increased (Bartomeus et al. 2013). These community level body size trends in the Netherlands are further complemented by intra-specific

patterns: bees of all sizes became smaller over the last century, and rates were especially high for large-bodied bees (Oliveira et al. 2016). However, there is little information on long-term intra-specific body size trends in wild bees in northeast US. Intra-specific changes in bee body size can result in morphological mismatches between flower and pollinator and may negatively affect pollination services (Schweiger et al. 2010). These trends in body size are likely to continue in the future as a response to further habitat degradations, urging for a detailed comparison of body size among and within species with declining and increasing populations.

The present study aims to assess changes in bumble bee body size over the last 125 years in the northeastern US, in the state of New Hampshire (NH). We addressed the following three questions. (i) Are declining species larger than increasing ones? (ii) Is there an intra-specific shift in body size through time? (iii) Are there changes in geographical distribution throughout NH during the last century? Based on previous assessments using museums specimens to describe bee declines over the last century, we expect that bees suffering population declines and range contractions are larger-bodied than those with stable or increasing population trends (Bartomeus et al. 2013; Jacobson et al. 2018; Oliveira et al. 2016; Scheper et al. 2014). Furthermore, we expect an intra-specific decrease in body size, i.e. bees collected in current time are smaller than those from a century ago (Oliveira et al. 2016); and that bees with declining status have experienced distributional changes (Colla et al. 2012; Kerr et al. 2015; Jacobson et al. 2018; Mathiasson and Rehan 2019).

## Methods

### Bee species selection and museums specimen records

Four species within the genus *Bombus* Latreille 1802, were selected based on previous studies showing consistent declining or increasing species status (Bartomeus et al. 2013; Cameron et al. 2011; Colla et al. 2012; Colla and Packer 2008; Jacobson et al. 2018), having an entire coverage in New Hampshire, and the availability of specimens for morphometric assessments from the University of New Hampshire Insect Collection (UNHC). Two representatives for increasing species were selected: first, the orange-belted bumble bee *Bombus ternarius*, which is native to and frequently found in northeastern United States and parts of Canada (Williams et al. 2014). This bee has increased in relative abundance during the last few decades (Colla and Packer 2008; Jacobson et al. 2018). Second, the common eastern bumble bee *B. impatiens*, which is currently the most abundant bumble bee species across North America, is widely used as a managed pollinator in agricultural greenhouses and has greatly expanded its range throughout North America during the last decades (Colla and Packer 2008; Jacobson et al. 2018; Williams et al. 2014). Declining species were: third, the yellow-banded bumble bee *B. terricola*, which is native to southern Canada and east to Midwest US (Williams et al. 2014). This once common bee has suffered severe population declines, with more than 30% reduction in range and population size, since the late 1990s (Bartomeus et al. 2013; Cameron et al. 2011; Hatfield et al. 2015a). Fourth, the half-black bumble bee *B. vagans*, which is distributed throughout North America from Ontario to Nova Scotia and southward to Georgia (Williams et al. 2014). It has declined in relative abundance throughout this region since the early 2000s (Colla and Packer 2008; Williams et al. 2009), and has lost about 37% of its historically occupied ranges (Colla et al.

2012). Museum specimen identification was confirmed using the identification guide for North American bumble bees by Williams et al. (2014). Notably, specimen identification for *B. vagans*, which can be confused with *B. perplexus*, was checked in accordance with characters described by Williams et al. (2014).

Specimen records of the four selected *Bombus* species cover a period of 125 years (1891–2016), an elevational gradient of 1717 m a.s.l. (2–1719 m) and the geographical extent of the state of New Hampshire (NH) in northeastern United States: covering approximately 260 km north–south, from Pittsburg to Brookline (45.0511 to 42.732 N) and 135 km east–west, from Hanover to Portsmouth (–72.29 to –70.801 W). Specimens without species level identification, geographical location information or date were excluded. Historical records were complemented with specimens from recent sampling events (Tucker and Rehan 2016, 2017a, b, 2018).

In concurrence with earlier work on the assessment of *Bombus* declines within NH (Jacobson et al. 2018) specimen records were sorted into two time bins, determined by earliest and latest collection year (1867–1926 and 1987–2016). Due to uncertain sampling efforts in museum collections (Bartomeus et al. 2013), we generated individual- and sample-based rarefaction curves (Fig. S1). These time bins reflect major agricultural and urban intensifications throughout the US (U.S. Census Bureau 2012) and allow for assessments of long-term trends throughout the last century (Colla et al. 2012; Jacobson et al. 2018). Severe pollinator declines in Europe, the UK and North America have occurred since the late 1980s (Biesmeijer et al. 2006; Goulson et al. 2015) corroborating comparisons between the selected time bins. Henceforth, records from 1897 to 1926 are referred to as “historical” and from 1987 to 2016 as “recent”.

## Morphological trait measurements

For each *Bombus* species, female specimens within the worker caste were selected to conduct a suite of morphological measurements using a Nikon SMZ800 stereomicroscope with an ocular micrometer to an accuracy of ~0.01 mm. Based on previous studies, five body size measures for bees were selected: (i) head width, measured in full frontal view at the maximum width including the outer margin of both compound eyes (Rust 1991); (ii) inter-orbital distance, measured as the shortest horizontal distance between the compound eyes (Moure 1965); (iii) inter-tegular distance (ITD), measured as the distance between tegulae in a straight line across the bee’s thorax (Cane 1987); (iv) marginal cell of the right fore wing, measured as the length of the cell from proximal to distal end (Owen 1988); (v) costal vein, measured in a straight line from the basal margin at the tegula to the distal end of the radial cell (Harder 1982).

## Geographical distribution

To map the distributions of the two declining and two increasing *Bombus* species throughout NH in historic and current time periods, we used the geospatial software QGIS 2.18.3. Maps were constructed with three background layers: a natural earth of the United States (100-m resolution) obtained from the USGS, and state and county boundaries (each 1:1,000,000-scale) of the United States from The National Map (TNM).

## Data analyses

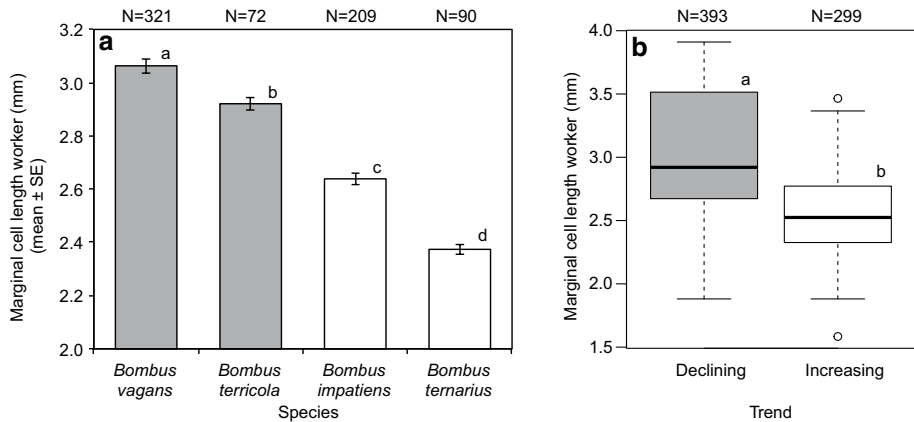
Statistical analyses were performed using the statistical software *R* (R Development CoreTeam 2017). As our aim was to use these morphological trait measures for specimen comparisons between historic and current time periods, we determined co-linearity between morphological measures by calculating Pearson's *r*. We used an ANOVA followed by Tukey posthoc comparisons for significant effects to compare body size (i) among the four *Bombus* species and ii) between increasing and declining species. UNHC bee specimen location data—longitude, latitude and elevation—were obtained from the record labels (metadata accessible at: <https://unhcollection.unh.edu/database/>). Their co-linearity was calculated using Pearson's *r*. In NH, land rises in elevation when proceeding from the coast inland or west- or northwards (<https://www.usgs.gov>); therefore, elevation was used as a geographical parameter to compare historic vs. current time periods in the statistical analyses. Generalized linear models (GLMs) with a Gaussian distribution were used to analyze associations of body size with time and elevation for all species, except for *B. vagans* where a GLM with gamma distribution was used (Zuur et al. 2009). We also analyzed changes in bee body size over time using year as a continuous variable. To differentiate between effects of time and elevation, the dataset was separated into high (> 90 m a.s.l.) and low (< 90 m a.s.l.) elevation, based on the elevational mean (= 89.94 m) of the bees in this study. Body size was then compared (1) between historic vs. current time for high and low elevation bees, and (2) across elevations for historic and current time specimens separately. Lastly, we investigated whether specimen records from historic and current time differed in elevation, using an ANOVA with log-transformed values for elevation.

## Results

For all four *Bombus* species, measures of head width, inter-orbital distance, inter-tegular distance and costal vein were all correlated with marginal cell length ( $r=0.93\text{--}0.99$ ). Therefore, we selected one measure—marginal cell length—for the analyses, and referred to hence forth as 'body size'. We used marginal cell because it is commonly used in the genus *Bombus* (Foster and Cartar 2011; Gerloff et al. 2003; Owen 1988) and ITD cannot be reliably measured in bees with many thoracic hairs. Longitude and latitude records for the four species were significantly correlated with elevation ( $r=0.74\text{--}0.96$ ), thus elevation was used as a geographical parameter in the analyses.

### Body size differences among bumble bee species

A total of  $n=692$  *Bombus* specimens were measured, of the species *B. impatiens* ( $n=209$ ), *B. ternarius* ( $n=90$ ), *B. terricola* ( $n=72$ ) and *B. vagans* ( $n=321$ ). Overall, the four *Bombus* species differed significantly in body size measured as marginal cell length ( $F_{3,688}=96.79$ ;  $P<0.001$ ), with *B. vagans* being largest (mean  $\pm$  SE mm,  $3.063 \pm 0.028$ ), followed by *B. terricola* ( $2.921 \pm 0.024$ ), then by *B. impatiens* ( $2.639 \pm 0.022$ ) and *B. ternarius* ( $2.374 \pm 0.019$ ) (Fig. 1a); all species-pair comparisons were significant ( $P<0.05$ ). Species with declining population sizes and geographic distributions (*B. vagans* and *B.*



**Fig. 1** **a** Mean ( $\pm$ SE) marginal cell length of *Bombus* workers from four species. **b** Box and whisker plot of species with declining (*B. vagans* and *B. terricola*) and increasing (*B. impatiens* and *B. ternarius*) trend, showing median and upper and lower quartile, whiskers extend to 10th and 90th percentile. Small letters indicate statistical significance

*terricola*) were overall significantly larger, by an average of 19%, than increasing ones ( $F_{2,690} = 241.6$ ;  $P < 0.001$ ) (Fig. 1b).

### Intra-specific body size trends in bumble bees

Body size of the four tested *Bombus* species was significantly associated with time, elevation and their interaction (Table 1a). Overall, specimens collected in current time were significantly, by an average of 15%, smaller ( $2.603 \pm 0.020$ ) than in the historic time period ( $2.988 \pm 0.024$ ;  $P < 0.0001$ ). Increasing species were significantly smaller with time and elevation (*B. impatiens*) or only elevation (*B. ternarius*), whereas both declining species (*B. vagans* and *B. terricola*) were significantly smaller with time and the interaction of current time with elevation (Fig. 2; Table 1b). *B. impatiens* was significantly smaller (by an average of 11%) in current time ( $2.538 \pm 0.025$ ) and in high elevations than in the historic time period ( $2.811 \pm 0.035$ ;  $P < 0.0001$ ; Fig. 2a; Table 1b). Body size of the smallest bee in this study (*B. ternarius*) was significantly 5% smaller in higher elevations ( $P = 0.003$ ; Fig. 2c; Table 1b); current time specimens ( $2.301 \pm 0.031$ ) being smaller than those collected in the historic time period ( $2.412 \pm 0.021$ ). *B. terricola* specimens were also significantly 5% smaller in current time ( $2.837 \pm 0.029$ ) than in the historic time period ( $2.981 \pm 0.032$ ;  $P = 0.002$ ; Fig. 2e; Table 1b). There was a significant interaction between current time and elevation, resulting from species range shifts both to higher latitudes and elevations (Fig. 2f). Likewise, the largest bee (*B. vagans*) was significantly 17% smaller in current time ( $2.724 \pm 0.039$ ) at higher elevations and the interaction thereof, as compared to the historic time period ( $3.196 \pm 0.031$ ;  $P < 0.0001$ ; Fig. 2g; Table 1b).

Similar associations between bumble bee body size, time and elevation were obtained when analyzing time as a continuous variable. *B. impatiens* significantly decreased in size over time ( $Wald \chi^2 = 29.4134$ ,  $P < 0.0001$ ;  $df = 208.2$ ) (Fig. 3a) but not with elevation ( $Wald \chi^2 = 3.807$ ,  $P = 0.06$ ) (Fig. 3b). Body size of *B. ternarius*, however, was significantly negatively related to elevation ( $Wald \chi^2 = 9.835$ ,  $P = 0.002$ ;  $df = 89.2$ ; Fig. 3d), but not to time ( $Wald \chi^2 = 2.438$ ,  $P = 0.118$ ;  $df = 89.2$ ; Fig. 3c). Both declining species significantly

**Table 1** Summary of generalized linear model (GLM) for marginal cell length of (a) four *Bombus* species combined, (b) single species and associated variables

	Parameter	Estimate	SE	t-Value	Pr(>  t )	<sup>a</sup> Pseudo-R <sup>2</sup>
(a)						
All (spp.)	Intercept	3.10158	0.02459	126.115	<0.0001	0.24
	Time-bin	-0.50654	0.03957	-12.801	<0.0001	<i>0.17</i>
	Elevation	-0.00230	0.00029	-8.046	<0.0001	<i>0.05</i>
	Time:Elev	0.00235	0.00031	7.491	<0.0001	<i>0.06</i>
(b)						
<i>B. impatiens</i>	Intercept	2.88072	0.04574	62.982	<0.0001	0.19
	Time-bin	-0.31215	0.05584	-5.590	<0.0001	<i>0.17</i>
	Elevation	-0.00228	0.00102	-2.225	0.0272	<i>0.02</i>
	Time:Elev	0.00192	0.00105	1.823	0.0697	<i>0.07</i>
<i>B. ternarius</i>	Intercept	2.46083	0.02630	93.568	<0.0001	0.17
	Time-bin	-0.06269	0.03903	-1.606	0.1120	<i>0.09</i>
	Elevation	-0.00036	0.00012	-3.063	0.0029	<i>0.15</i>
	Time:Elev	-0.00017	0.00024	-0.693	0.4901	
<i>B. terricola</i>	Intercept	2.99275	0.02995	99.911	<0.0001	0.21
	Time-bin	-0.33135	0.08048	-4.117	0.0001	<i>0.12</i>
	Elevation	-0.000138	0.00012	-1.141	0.2579	<i>0.02</i>
	Time:Elev	0.00061	0.00022	2.816	0.0064	<i>0.02</i>
<i>B. vagans</i>	Intercept	3.040e-01	4.257e-03	71.394	<0.0001	0.21
	Time-bin	6.410e-02	7.780e-03	8.239	0.0001	<i>0.18</i>
	Elevation	2.816e-04	9.909e-05	2.842	0.0045	<i>0.03</i>
	Time:Elev	-2.885e-04	1.025e-04	-2.813	0.0052	<i>0.03</i>

± SE mean, *Estimate* model coefficient, *SE* standard error, *Pr(> |t|)* t- value, partial P, (*R*<sup>2</sup>) F-Statistic and Pseudo-R<sup>2</sup>

<sup>a</sup>Note: Partial pseudo-R<sup>2</sup> are shown in italics

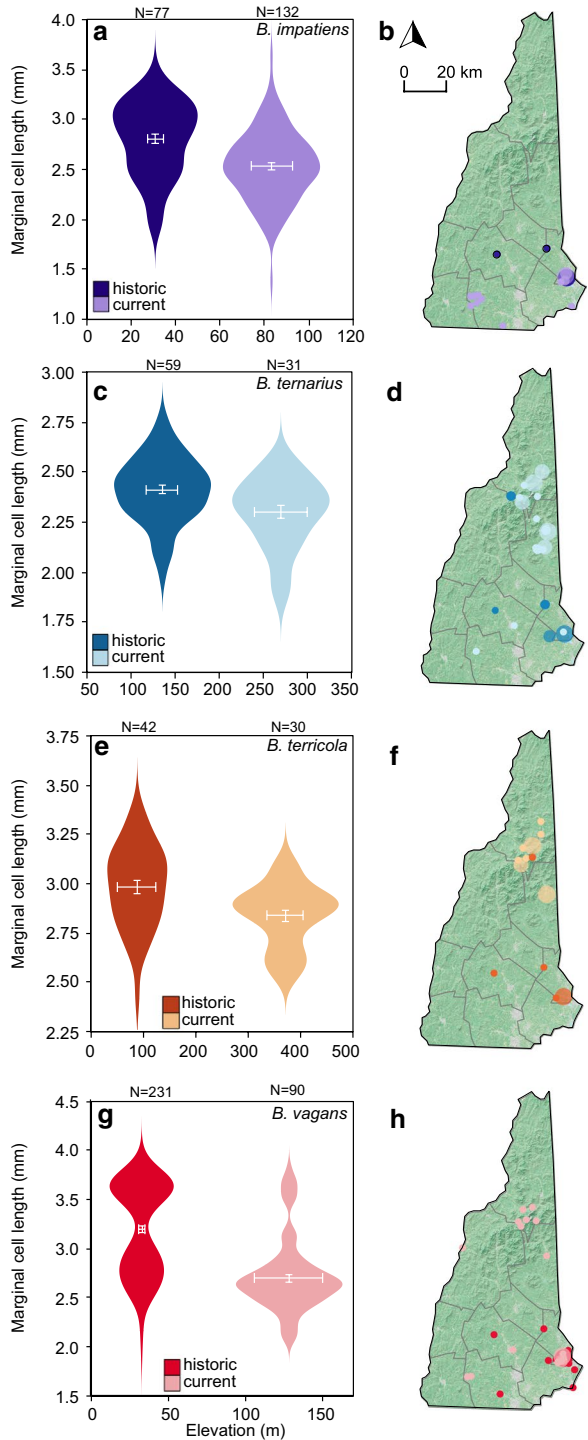
decreased in size over time, with higher elevations and the interaction thereof: *B. terricola* ( $Wald\chi^2 = 13.0523$ ,  $P = 0.0003$ ;  $df = 70.2$ ; Fig. 3e, f), *B. vagans* ( $Wald\chi^2 = 70.828$ ,  $P < 0.0001$ ;  $df = 365.2$ ; Fig. 3g, h).

Bees collected from low elevation sites were significantly by (17%) smaller in current time as compared to the historic period ( $Wald\chi^2 = 110.038$ ,  $P < 0.0001$ ;  $df = 524.1$ ; Fig. 4a), whereas bees from high elevations showed no such trend ( $Wald\chi^2 = 0.1504$ ,  $P = 0.698$ ;  $df = 164.1$ ; Fig. 4b). High elevation bees from the historic time period were significantly negatively associated with elevation ( $Wald\chi^2 = 5.6795$ ,  $P = 0.02$ ;  $df = 59.1$ ; Fig. 4c), but not specimens from the current time period ( $Wald\chi^2 = 2.5146$ ,  $P = 0.113$ ;  $df = 104.1$ ; Fig. 4d).

### Geographical shifts in bumble bee distribution

Overall, there was a significant shift to higher elevation between historically and currently collected *Bombus* specimens for all four species ( $P < 0.0001$ ; Table 2; Fig. 2, left panel). Specimen locations are mapped based on geographical information on specimen labels (Fig. 2, right panel). All *B. impatiens* specimens in historic and current time period were collected from the southern part of NH (Fig. 2b), but there was a significant

**Fig. 2** Maps of New Hampshire (NH) (right panel) showing historical and current specimen records and violin plots (left panel) showing kernel probability density plots of marginal cell length of historic and current specimens from four *Bombus* species: **a, b** *B. impatiens*, **c, d** *B. ternarius*, **e, f** *B. terricola*, **g, h** *B. vagans*. Circle sizes on maps indicate relative abundance (tiny < 10%; small < 25%, medium < 50% and large > 50%). White bars in violin plots show mean  $\pm$  SE for marginal cell length on y-axis and elevation on x-axis





difference in elevation ( $P < 0.0001$ ). Current specimens were collected from locations on average 53 m higher than historic ones (Table 2; Fig. 2a). The majority (90%) of the historic *B. ternarius* individuals came from the southern part of NH, and few (10%) from northern latitudes, this trend is reversed for the current time period (Fig. 2d). Individuals from the current time period were collected from significantly higher elevations on average 134 m higher than historic ones ( $P < 0.0001$ ; Table 2; Fig. 2c). All (100%) current time specimens of *B. terricola*, a declining species, came from the northern part of NH, about 100 km higher latitude than historically collected individuals (Fig. 2f). None were collected from the southern part of NH where they have been found in the past. This species experienced a significant elevational shift by an average of 283 m in recent times ( $P < 0.0001$ ; Table 2; Fig. 2e). All historically collected *B. vagans* specimens were from the southern part of the state, while 20% of the recently collected ones came from the northern part of NH (Fig. 2h). This species also shows a significant elevational shift by an average of 95 m in the current time period as compared to the historic time ( $P < 0.0001$ ; Table 2; Fig. 2g).

## Discussion

This study assessed intra-specific body size variation of four *Bombus* species over the last century. We further compared body sizes among species with declining and increasing status assessments and investigated shifts in geographical distribution. All four investigated species were smaller in current time than a century ago, suggesting floral resource limitation in the present time. Declining species were about 20% larger than increasing species, suggesting greater vulnerability of larger bee species to nutritional deprivation and regional extirpation. All four species experienced an upward shift in elevation indicating range shifts consistent with land use and climate change over the last century.

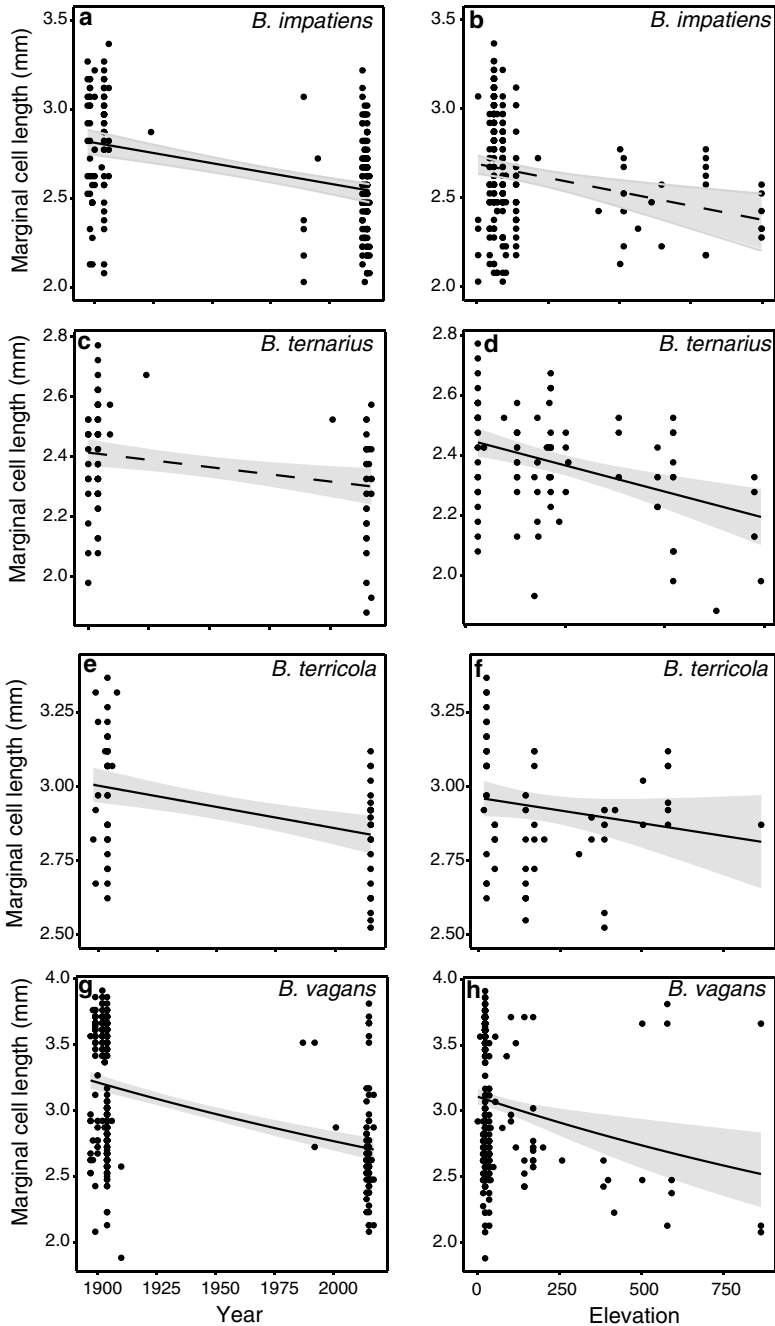
### Declining bumble bees are larger

We found that species currently experiencing range contractions and numerical declines throughout North America were larger than increasing ones. The two declining species *B. vagans* and *B. terricola* were 19% larger than the two increasing species, *B. impatiens* and *B. ternarius*. Our results support previous long-term assessments of bee specimens using museums records in the Netherlands, showing declines of large bodied bee species over the last century (Scheper et al. 2014), and in the northern United States, where declines in relative abundance over the last 140 years were associated with large body size (Bartomeus et al. 2013). Land use change may have more marked effects on larger bodied bee species than smaller ones, due to their greater nutritional requirements (Müller et al. 2006). The recurrent observation of larger bodied species decline is most likely due to large-scale land use modifications over the last half-century, such as increasing urbanization and agricultural intensification (Burkle et al. 2013; Kleijn and Raemakers 2008; Scheper et al. 2014). Our results, however, differ from another study in Europe where wingspan, did not differ between five declining and stable bumble bee species over the last 129 years (Kleijn and Raemakers 2008). Contradictory findings might be due to using wingspan as a proxy for body size; if measurements have been carried out from distal wing margins, wing wear could have confounded this measurement

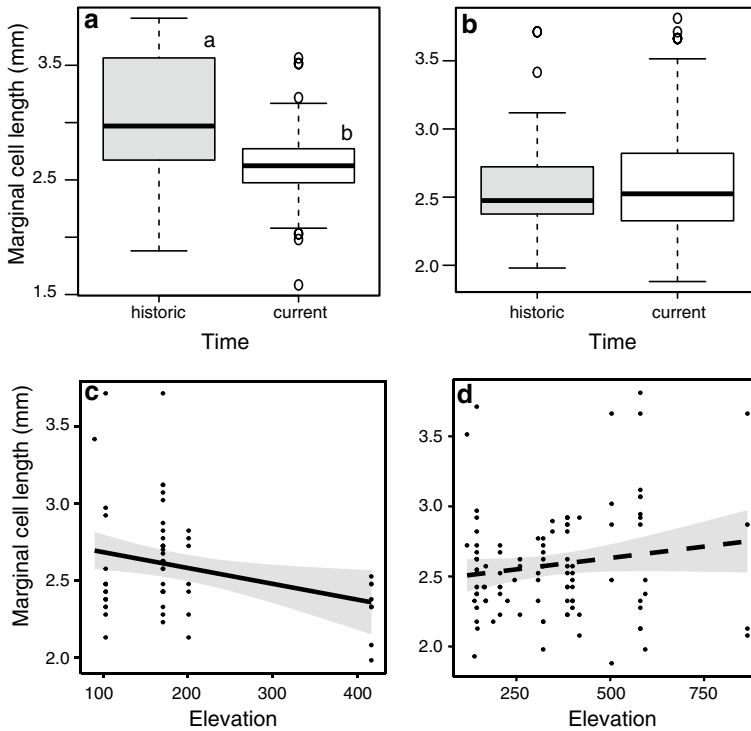
(Mueller and Wolf-Mueller 1993; O'Neill et al. 2015; Rehan and Richards 2010). Here we measured five morphometric characters across four *Bombus* species and confirm standard practices from former studies. These data suggest that marginal cell length is a robust proxy for body size in bumble bees and encourage the use of this metric in future studies.

### Intra-specific body size reduction in bumble bees

We found an intra-specific reduction in body size over the last century for all four bumble bee species. Bees from low elevation sites were by 17% smaller in current time than historically, while bees from high elevations showed no such trend. Bees from high elevations decreased with increasing elevation in historic times but not currently. This indicates, that the observed body size reduction are mainly driven by bees at low elevation sites, where the predominant land use types across NH are mainly forests and some agriculture (Foster 1992; Gerhardt and Foster 2002). The largest species *B. vagans* reduced the most, by an average of 17% and the smallest, *B. ternarius*, the least by 5%. This is in line with findings from museum records in Netherlands where large-bodied female bees reduced in size significantly more so over the last 129 years than small-bodied ones (Oliveira et al. 2016). Drivers of intra-specific body size decrease in bees include climate warming (CaraDonna et al. 2018), landscape simplification (Persson and Smith 2011), and declines in floral resources (Scheper et al. 2014). Furthermore, changes in species interactions, such as increased competition with managed honey bees are known to reduce body size in bumble bees (Goulson and Sparrow 2009), as is an increased use of agrochemicals, which negatively effects bumble bee development (Barbosa et al. 2015; Bernauer et al. 2015; Fauser-Misslin et al. 2014). Parasitism might also play a role, as larger bodied bumble bees are susceptible to infestations with different parasites than smaller ones (Colla et al. 2006). Whether some of the above-mentioned factors are driving the observed intra-specific reduction in body size remains unknown in this study, as ecological variables including floral availability, parasite and pathogen loads, regional agricultural practices and land use data do not exist for museum specimens over such a large time frame. Regardless the nature of the underlying drivers, certain advantages are associated with smaller body size. These include protection against starvation, as smaller sized bumble bee workers live longer when food is scarce (Couvillon and Dornhaus 2010), and reproduction efficiency, as smaller sized bees reproduce more readily as their offspring require less pollen (Müller et al. 2006). However, as large bees appear to be more vulnerable to diminishing habitat quality and quantity, reduced body size might be a first adaptation to changing environmental conditions (Bartomeus et al. 2013; CaraDonna et al. 2018; Oliveira et al. 2016; Scheper et al. 2014), but might not prevent population declines. A disadvantage of smaller body size in bumble bees is reduced colony growth, as colony performance increases with mean bumble bee size and smaller bumble bee workers return with lighter foraging loads (Goulson et al. 2002; Herrmann et al. 2018). Body size reduction might have contributed to the long-term population declines apparent for many bumble bee species in North America and across the globe (Colla et al. 2012; Colla and Packer 2008; Goulson et al. 2015).



**Fig. 3** Relationships between bumble bee marginal cell length, over time and elevation for four species: **a, b** *B. impatiens*, **c, d** *B. ternarius*, **e, f** *B. terricola*, **g, h** *B. vagans*. Solid black lines show significant relationships between traits and variables (at  $P < 0.05$ ), dashed black lines show non-significant ones, grey shaded area shows 95% confidence interval



**Fig. 4** Relationships between bumble bee marginal cell length and time **a** at low elevation, **b** high elevation and across elevation for **c** historic and **d** current bees. Upper panel boxplots showing median and upper and lower quartile, whiskers extend to 10th and 90th percentile, small letters indicate statistical significance). Lower panel plots: solid black lines show significant relationships between traits and variables (at  $P < 0.05$ ), dashed black lines show non-significant ones, grey shaded area shows 95% confidence interval

**Table 2** Summary of ANOVA for elevational differences of specimen records between current and historic time for (a) four *Bombus* species combined, (b) single species

	F	dF	P	Elevation historic	Elevation current	Dif.
4 Species	104.9	1.689	< 0.0001	52 ± 5	148 ± 11	95
<i>B. impatiens</i>	16.89	1.207	< 0.0001	30 ± 4	88 ± 9	30
<i>B. ternarius</i>	23.39	1.88	< 0.0001	135 ± 17	270 ± 30	134
<i>B. terricola</i>	172.64	1.69	< 0.0001	88 ± 36	371 ± 34	283
<i>B. vagans</i>	60.277	1.319	< 0.0001	33 ± 2	128 ± 22	95

(F) F-Statistic, (dF) degrees of freedom, (P) P value, ( $\pm SE$ ) including average elevation (*Elevation historic*) historic, (*Elevation current*) current time in m a.s.l., (*Dif.*) average differences thereof

### Bumble bees indicate regional range shifts

We found that current time specimens of all four bumble bee species were collected from higher elevations than historic specimens. Average elevational shifts over the last century ranged from as little as 53 m (*B. impatiens*) to about 100 m (*B. vagans* and *B. ternarius*) and

were highest (283 m) for *B. terricola*. These elevational shifts could be associated with a warming climate, as the average temperature in northeast US has increased by  $\sim 1$  °C since the turn of the last century (Horton et al. 2014; Wuebbles et al. 2017). Our results support previous findings across Europe and America, where cold adapted bumble bees (Cameron et al. 2007; Ploquin et al. 2013) migrated upwards in elevation into cooler mountainous areas to stay within their preferred climate envelope (Kerr et al. 2015; Ploquin et al. 2013). However, while museum specimens are invaluable for long-term assessments of shifts in abundance, distribution and functional traits (Colla and Packer 2008; Bartomeus et al. 2018; Jacobson et al. 2018), museums-typical sampling biases are associated with such datasets, because standardized sampling protocols spanning a period of one hundred years do not exist. Thus, the here observed elevational shifts should be interpreted with caution, as it is possible that these are affected by inconsistent sampling over time.

Current specimen records for three of the four tested bumble bee species came from more northerly regions in NH than in the past—about 20% of the currently collected *B. vagans* specimens came from more northerly regions in NH than historically. The current data suggest that *B. ternarius* and *B. terricola* are more abundant in the northern part than *B. vagans*, which can occur with low numbers in surveys (Colla and Packer 2008; Hatfield et al. 2015b; Tucker and Rehan 2017a). It is possible that there were too few *B. vagans* in the past to be collected.

The increasing species *B. ternarius* and the declining *B. terricola* were predominantly collected from the northern part of NH in current times, while none were found in the historically occupied southern part of the state, despite thorough sampling efforts in recent years in this area (Tucker and Rehan 2016, 2017b, 2018). Besides climate, modifications in land use might be associated with the lack of species in the southern part of the state. In NH, large-scale changes in land use have occurred since European settlement: at the turn of the last century, large parts, more than 70% of the land cover, were cleared and used as pastures for life stock grazing, while extensive areas (>90%) are now covered by forests (Foster 1992; Gerhardt and Foster 2002). Such habitat changes in concurrence with loss of flower resources may have facilitated the observed shifts in bumble bee distribution.

These data suggest range contraction at the warmer end of these species' distribution and supports previous assessments, revealing overall population declines and loss of historically occupied areas throughout their ranges in northeast America for *B. terricola* and *B. vagans* (Bartomeus et al. 2013; Cameron et al. 2011; Colla et al. 2012; Grixti et al. 2009; Hatfield et al. 2015a; Jacobson et al. 2018). However, regional scale studies as presented here can reveal local population variation from range-wide studies. This is evidenced for *B. ternarius*, which is of little concern across its entire range (Colla et al. 2012; Hatfield et al. 2014), but has suffered local extinctions at the southern extent of its range (Grixti et al. 2009). Our results further indicate that bumble bees in NH may persist in cool mountainous areas, such as the White Mountains, where relatively high numbers of declining species have been collected during bee biodiversity surveys in the current time period (Tucker and Rehan 2017a). Such climatic refugia are vital for the mitigation of range losses for cold adapted species under accelerating climate warming (Kerr et al. 2015; Sirois-Delisle and Kerr 2018).

## Conclusion

Bumble bees contribute substantially to pollination services in natural and agricultural ecosystems. Their drastic declines during the last half-century necessitate effective conservation programs. Therefore, more detailed approaches incorporating performance related

traits are needed, to complement assessments of species declines based on richness and abundance data. This regional study shows that bumble bees suffer decreases in body size and experience range contractions in warmer habitats and might migrate to higher elevations into cool mountainous areas as climatic refugia. Our results indicate that major land use changes, coupled with loss of flower resources and climate warming may drive the observed changes in bumble bees. As intra-specific body size declines may be a first adaptation to stressful environmental conditions, morphometric data may be used as an additional tool for assessing species vulnerability statuses. We suggest a stronger incorporation of body size assessments into future studies experimentally investigating underlying factors of species declines across their range as well as the need for regionally specific studies.

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