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ORIGINAL PAPER

Bumble bee (*Bombus*) distribution and diversity in Vermont, USA: a century of change

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Abstract

Bumble bees (*Bombus*) play key roles as pollinators in temperate ecosystems. Some North American species have declined due to factors that include habitat loss, parasites, pesticides, and climate change. In many regions conservation is hampered by lack of quantitative data on historical abundance and distribution, making status assessments difficult. From 2012 to 2014, with help from 53 citizen scientists, we conducted surveys to determine the status of bumble bees throughout Vermont, USA. For historical comparison, we identified and digitized bumble bee specimens from 13 public and private collections. Our dataset contained 12,319 records, which we separated into historic (1915–1999; n = 1669) and modern (2000–2014; n = 10,650) periods, with our survey contributing 94% of modern data. Of 17 species, four were not detected and four showed significant declines. Rarefaction indicated that both modern and historic datasets slightly underestimated known species richness, diversity, and abundance, but confirmed a strong decline for all three parameters. Declining species broadly accorded with those reported elsewhere in eastern North America, and included those in subgenera *Bombus, Fervidobombus*, and *Psithyrus*. Four species in the subgenus *Pyrobombus* (*B. bimaculatus, B. impatiens, B. ternarius*, and *B. vagans*) greatly increased in relative abundance in the modern period. Landscape factors such as road density, elevation, and land use strongly predicted distribution of some species. Species diversity was correlated positively with grasslands, and negatively with deciduous and mixed forest cover, while abundance was correlated positively with evergreen forest cover, yet negatively with deciduous forest.

Keywords Land use · Conservation · Citizen science · Pollinator declines · Vermont

Introduction

Nearly 90% of flowering plant species, including 75% of agricultural crops, benefit from animal pollination (Klein et al. 2007; Ollerton et al. 2011). Bees are intimately tied to flowers by their use of pollen as a protein source, making them the most important pollinator taxon in many terrestrial ecosystems. Ongoing threats to managed non-native Western honey bees (*Apis mellifera* Linneaus, 1758) have raised public awareness of the importance of bees to human well-being, and there is concern that some of the ~20,000 bee species globally are also declining. We currently lack sufficient data to assess the status of most species, but there is evidence of bumble bee (*Bombus* spp.) declines worldwide, including in China, Europe, and North and South America (Williams and Osborne 2009; Williams et al. 2009; Cameron et al. 2011; Colla et al. 2012; Nieto et al. 2014; Schmid-Hempel et al. 2014; Goulson et al. 2015).

Several studies have documented declines of North American *Bombus* species (Grixti et al. 2009; Cameron et al. 2011; Colla et al. 2012; Bartomeus et al. 2013), and a recent assessment by the International Union for the Conservation of Nature found that 26% are vulnerable or endangered, with an additional 20% found to be 'data deficient' (IUCN 2017). Members

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of the subgenera *Bombus sensu stricto* and *Psithyrus* are particularly threatened, with endangered status protection for some in the U.S. and Canada (Colla 2016; Inouye et al. 2017; Arbetman et al. 2017). Some species assessed as rare in one part of their range remain stable in other areas (e.g., *Bombus occidentalis* Greene 1858 and *B. vosnesenskii* Radoszkowski 1882), complicating efforts to understand their conservation needs (Sheffield et al. 2016; Thomson 2016).

The decline of native bumble bee species could have effects on ecosystems, given the group's importance in pollinating many native plant species (Heinrich 2004). Moreover, such wild bees are integral to agriculture, often providing the majority of pollination service to crops, regardless of whether honey bees are deployed for that purpose (Garibaldi et al. 2013). For example, before its decline and listing as endangered by the U.S. Fish and Wildlife Service, the rusty-patched bumble bee (*B. affinis*) was documented as an important pollinator of cranberry and other crops, underscoring the value of these wild animals to the human food supply (Mackenzie and Averill 1995; Kleijn et al. 2015).

Assessment of bumble bee populations has been hampered by lack of baseline data. While few historic surveys of bumble bee abundance and diversity were conducted in a manner that allows resurvey, those that do reveal alarming losses of both abundance and diversity (Colla and Packer 2008; Dupont et al. 2011; Bommarco et al. 2012; Banaszak and Ratyńska 2014). In the absence of such historic surveys, researchers have analyzed collections of digitized museum specimen label data to characterize changes in bumble bee occurrences (Colla and Packer 2008; Colla et al. 2012; Bartomeus et al. 2013), but statistical inference permitted by these datasets is limited by lack of standardized collecting. With the help of citizen science volunteers (Dickinson et al. 2010), the goal of this study was to characterize the present and past distribution and abundance of bumble bee species in Vermont, USA. Previous studies have used citizen scientists to assess distribution and diversity of native bees, including bumble bees (Lye et al. 2011; Féon et al. 2016; Hatfield et al. 2017). We assembled a database of 12,319 determined bumble bee records spanning nearly a century (1915–2014) to characterize current and past diversity and distribution. Specifically, we examined the degree to which bumble bee species diversity, distribution, and relative abundance may have changed between historic (<2000) and modern (2000–2014) collecting periods, as a means to better inform conservation assessment and action.

Methods

Study site

Vermont is a small (24,901 km^2) New England state that straddles the Northeastern Highlands and Eastern Great Lakes and Hudson Lowlands level III Ecoregions (Omernik and Griffith 2014). A variety of ecological and climate conditions are created by mountainous terrain, as well as the state's history of land clearing, agriculture, afforestation, and increase in human development (Klyza and Trombulak 1999). The state's bumble bee fauna was poorly described before 2000, with the largest repository of specimens taken during a 150-year history of collection held at the state's land grant institution, the University of Vermont.

Collections and surveys

From 2012 to 2014, with the help of trained citizen scientists, we conducted a statewide survey (Vermont Bumble Bee Survey; VBBS) to inventory the distribution and status of the state's bumble bees. We recruited 53 participants through advertisement, direct contact, and solicitation from previous citizen science wildlife atlasing efforts. Project volunteers attended trainings and were provided with a detailed project manual (McFarland 2018), survey maps, guides for preliminary identification, and other instructions for reference during the season. Project staff and volunteers maintained engagement with volunteers through use of an online project space. Additionally, the authors and three experienced field biologists collected data in the field. Observers made one of three types of records: (1) photographs of live, free-foraging bumble bees; (2) pinned specimens collected opportunistically by net; or (3) pinned specimens of bumble bees collected according to a standardized roadside survey protocol designed to be repeatable and complement similar surveys in other states. Roadside surveys were conducted on stretches of town roads in 'priority survey blocks', 1/8th of an USGS topographic quadrangle randomly selected for previous Vermont citizen science inventories (Renfrew 2013), where traffic was generally light and floral resources were often available. We refer to road stretches driven in each of these physical areas as *routes*, and to stops along routes as *sites*. Priority blocks were surveyed 18 May to 3 October on days when weather was conducive to bee foraging, and many were resampled within or between years. Observers chose a road stretch to survey, stopping at sites separated by ≥ 1-km (10.44 ± 0.36 SE stations per route; range 3–20) to collect bumble bees from roadside vegetation. At each site, observers recorded coordinates, weather, plant species in flower, duration of collecting interval (usually 10 min), and number of individuals collected. During the collecting interval, observers captured all bumble bees that were detected on roadside vegetation, placing each in a collection jar. Specimens were later pinned and labeled. After observers submitted pinned specimens and field data, we digitized all information and determined vouchers.

Historic collections

To provide comparative information for our survey results, we obtained bumble bee specimen data from 13 public and private collections (Table S1), either accepting existing datasets from well-curated collections or completing specimen determination and digitization ourselves. Some records were assembled by LR for a previous publication (Williams et al. 2014).

Determinations

Initial identifications of VBBS specimens were made by volunteers and SZ and SH, with final determination by LR. Photographs were vouchered on secure servers at Vermont Center for Ecostudies and pinned specimens were deposited in the Zadock Thompson Zoological Collection at the University of Vermont. LR made determinations of > 99% of all specimens, and we accepted additional records from research collections where experts had made determinations (e.g., American Museum of Natural History and Yale Peabody Museum). We consulted a range of taxonomic treatments for identification (Mitchell 1960, 1962; Laverty and Harder 1988; Williams et al. 2014; Droege et al. 2018), and follow taxonomic concepts described in Table S2.

Data preparation

We obtained 12,723 Vermont bumble bee records, and after removing those with errors or without species determinations (n = 404), and lacking sufficient replication to consider collection year as a continuous variable in our analysis, we partitioned the remaining 12,319 records into 'historic' (n = 1669; 1915–1999) and 'modern' (n = 10,650; 2000–2014) time periods. The lower boundary for the 15-year modern period marks the onset of widespread concern over North American bumble bee species declines (Colla et al. 2012; Bartomeus et al. 2013), as well as the onset of intensive bumble bee sampling in the state. We performed several tests to determine whether our data violated assumptions of random sampling, a potential challenge of comparing standardized, modern collections with museum specimen data contributed by many collectors with varying sampling methodologies (Bartomeus et al. 2013). This is a realistic concern with our data, as undergraduate entomology student specimen records are common in the University of Vermont collection, and such collecting events may be more haphazard than those typical of the VBBS effort. First, to test whether varying sampling methodologies would skew our results, we filtered each dataset so that it contained only one individual of each species-caste combination per 'sampling event', which we defined as unique combinations of date, location, and collectors' names. Because we found that this filtering had negligible impact on estimates of relative abundance and other statistics, we present results drawn from the full rather than filtered data. Second, we tested for spatial bias in collection localities between the datasets. Finding that historic and modern collection localities differed significantly in spatial distribution and environmental characteristics (Fig. 1; Table S3), for comparative purposes we created a subsample of the modern data that included only those collections made within 5 km of a historic locality (N = 5299 records).

Diversity and relative abundance

We used two approaches to compare bumble bee abundance and diversity between historic and modern time periods. We computed relative abundance for each dataset as the number of specimens of one species divided by the total for all species, and made statistical comparisons of these measures in each pair of datasets (historic vs. modern, historic vs. subsample, modern vs. subsample) with Wilcoxon signed rank tests using the R library 'coin' (Zeileis et al. 2008; R Core Team 2018), specifying pairing of samples and exact distributions.

Second, we constructed rarefaction curves of extrapolated species richness, and Shannon and Simpson diversity indices using R statistical computing software (R Core Team 2018) and the R library 'iNEXT' (Chao et al. 2014; Hsieh et al. 2016; R Core Team 2018). We treated bee collections as individual-based sample data, and compared historic collections to the subsampled and full modern collections, using a 15,000-sample endpoint partitioned in 500 knots (i.e., n = 30 bees per simulated sampling event) and estimating species richness and diversity as the mean of 500 bootstrap replications with 95% CI.

Spatial analysis

We used elevation, precipitation, road, and land cover data to analyze how landscape characteristics and land use influenced bumble bee occurrence. We extracted elevation of each collection locality from the Vermont HydroDEM digital elevation model (VCGI 2017a) and mean summer (Apr.–Sept.) and winter (Oct.–Mar.) precipitation from GIS products of the Prism Climate Group (Daly et al. 1994). To estimate road density, we obtained and merged transportation spatial data from Vermont (VCGI 2017b) and adjacent states and provinces (MassGIS 2014; MRNF Québec 2014; NH DOT 2015; Winters 2017), and used the ArcGIS Spatial Analyst Line Density tool to calculate density of all road segments per unit area (km per km^2) around each collection locality. Because most bumble bee foraging is affected by habitat quality within 1-km of the nest (Greenleaf et al. 2007; Osborne et al. 2008; Geib et al. 2015), we used the

Fig. 1 Locations of Vermont, USA bumble bee specimen collections in historic (**a** 1915–1999) and modern (**b** 2000–2014) time periods. A total of 1669 historic records were assembled, and modern records totaled 10,650. Inset map depicts the state's location (star) in eastern North America

supplemental ArcGIS Spatial Analyst tool 'Tabulate area 2' to extract proportions of each cover type within 0.5-km and 1-km of each georeferenced specimen (circles of 0.78 km^2 and 3.14 km^2, respectively). To do this, we merged the 2011 National Land Cover Database (NLCD) for the US (Homer et al. 2015) and the Earth Observation for Sustainable Development of Forests land cover map for adjacent areas of Québec (Wulder et al. 2008). Finding that hay fields in southern Québec were commonly misidentified as barren land, and that inspection of aerial photos revealed very few pixels of actual barren land, we converted all 'barren land' in the that layer to 'hay' when combining with the NLCD dataset. This adjustment affected the 1-km buffers of just 18 of the specimens (0.15%) in our study. During our analysis we also made frequent comparisons of NLCD cover types to our own assessments of land use and cover from georeferenced aerial photos and our ground-truthing during field work. While misclassification of pixels is an ongoing challenge for such spatial models, the 2011 NLCD product features reduced error rates relative to previous versions (Homer et al. 2015), and we were generally satisfied with its accuracy in our study. In analyses, we simplified NLCD cover classes to nine categories that we consider to be biologically relevant to bumble bee distribution: grasslands (= grasslands/herbaceous and pasture/ hay), cultivated crops, deciduous forest, mixed forest, evergreen forest, shrubs, wetlands (= woody wetlands and emergent herbaceous wetlands), water, and areas of human development (= all developed classes combined). In Vermont, corn accounts for more than 90% of all area classed in NLCD as cultivated crops (USDA NASS 2017). For analyses that follow, we excluded areas covered by open water as they do not constitute bumble bee habitat.

To improve normality, we removed outliers from the analyses of some variables, including elevation, precipitation, and road density. We used linear models (base R function 'lm()') to assess the effects of elevation and precipitation (considered together with their interaction, due to better model fit (comparing AIC) than individual models) on bumble bee species richness, diversity, and abundance, and generalized linear models (Bates et al. 2016) to assess probability of each species' occurrence

in roadside survey collections as a function of elevation and precipitation. We used linear regression to ask how road density in 0.5-km and 1-km radii around collection localities affected richness, diversity, and abundance, and used one-way ANOVA and Tukey–Kramer post-hoc tests to ask whether road density around collection sites varied among species.

Because proportional land cover variables may violate the assumption of variable independence of other multivariate analytical tools, we used hierarchical partitioning (the 'hier.part' library in R) to assess the independent and conjoint contribution of each variable to patterns of diversity, abundance, and individual species occurrence (Mac Nally and Walsh 2004). Independent contributions are variable effects without influence of other variables, while conjoint contributions are a variable's overall effect on others. We used the function 'hier.part', specifying Gaussian (for species richness, Shannon's H', and abundance) or binomial (species presence vs. absence) distributions and a Goodness-of-Fit log-link function, and calculated statistical significance of independent contributions with the 'rand.hp' test, with a randomization routine of 500 iterations. We used separate linear and generalized linear (Bates et al. 2016) models to assess the sign (negative vs. positive) of the effect of proportion of each land cover type on the above variables.

Results

We obtained 12,319 determined, valid Vermont bumble bee observations, and separated these into 1669 historic (1915–1999) and 10,650 modern (2000–2014) records (Table 1; Fig. 1). The VBBS contributed 94% (10,017) of modern records, including 765 photographs for which we could make species determinations (68% of all photo vouchers submitted). Bumble bees were collected in 2012–2014 during the VBBS in all of Vermont's counties and biophysical regions, and in 81% of the state's 255 municipalities (Fig. 1).

Diversity

Sixteen species of bumble bees were collected in Vermont during the historic period, yet only 13 of these were collected during the modern period (Table 1; Fig. 2). Historically present species not collected in the modern period included *B. affinis* (historic n = 205), *B. ashtoni* (historic n = 14), and *B. fernaldae* (historic n = 1). Comparing historical and subsetted modern data, five species exhibited > 50% decline in relative abundance: *B. citrinus* (-65%), *B. fervidus* (-89%), *B. pensylvanicus* (-99.6%), *B. sandersoni* (-53%), and *B. terricola* (-79%) (Table 1). One of these (*B. pensylvanicus*) may have been extirpated locally, having not been detected in Vermont since a single collection in 2000. Our

Table 1 Numbers and relative abundance of specimens of bumble bees in historic (1915–1999) and modern (2000–2014) time periods, as well as a subsample of modern collections made within 5 km of historic records

Bombus species	No. collections			Relative abundance			RA change	RA change (subsample)
	Historic	Modern	5 km sample	Historic	Modern	5 km sample		
affinis	205	0	0	0.123	0.000	0.000	−0.123	−0.123
ashtoni	14	0	0	0.008	0.000	0.000	−0.008	−0.008
auricomus	0	1	1	0.000	0.000	0.000	0.000	0.000
bimaculatus	23	969	495	0.014	0.091	0.093	0.077	0.080
borealis	15	465	211	0.009	0.044	0.040	0.035	0.031
citrinus	65	115	73	0.039	0.011	0.014	−0.028	−0.025
fernaldae	1	0	0	0.001	0.000	0.000	−0.001	−0.001
fervidus	244	126	87	0.146	0.012	0.016	−0.134	−0.130
griseocollis	34	334	219	0.020	0.031	0.041	0.011	0.021
impatiens	447	2642	1612	0.268	0.248	0.304	−0.020	0.036
pensylvanicus	71	1	1	0.043	0.000	0.0002	−0.042	−0.042
perplexus	26	179	77	0.016	0.017	0.015	0.001	−0.001
rufocinctus	12	98	68	0.007	0.009	0.013	0.002	0.006
sandersoni	10	43	15	0.006	0.004	0.003	−0.002	−0.003
ternarius	141	1688	730	0.084	0.158	0.138	0.074	0.053
terricola	172	281	116	0.103	0.026	0.022	−0.077	−0.081
vagans	189	3708	1594	0.113	0.348	0.301	0.235	0.188
Totals	1669	10,650	5299					

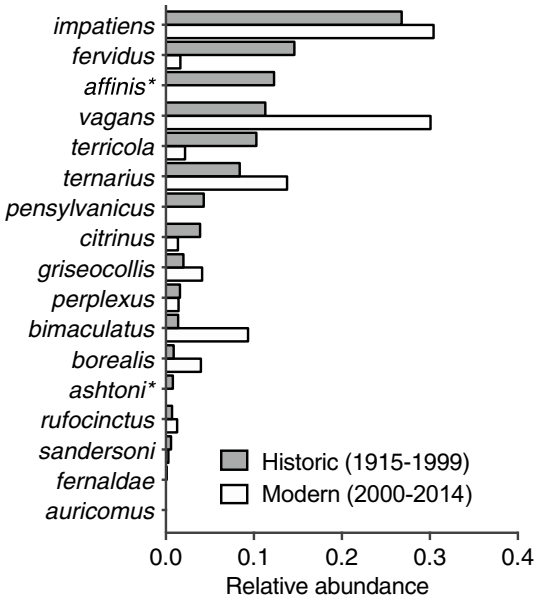

Fig. 2 Relative abundance of bumble bee species collected in historic and modern time periods, with the modern dataset subsampled to collections made ≤ 5 km from historic collection localities. Asterisks indicate species collected during the historic period that have not been detected in the modern period. See Fig. S1 for relative abundance comparison without the full modern dataset

comparison of historic vs. subsampled modern data reveals that *B. bimaculatus* (678%), *B. impatiens* (114%), *B. ternarius* (163%), and *B. vagans* (266%) have greatly increased in relative abundance in Vermont (Fig. 2). Although much less common, *B. borealis* (443%) and *B. griseocollis* (203%) also increased. One species not present in the historic data, *B. auricomus*, was collected a single time during the modern period. We found significant changes in species relative abundance, whether considering the full (Wilcoxon signed rank test; $Z = 4.75$, $P < 0.0001$) or subsampled modern data ($Z = 4.55$, $P < 0.0001$; Table 1; Fig. 2; Fig. S1). Subsampled and full modern datasets differed significantly in patterns of species relative abundance ($Z = 4.45$, $P < 0.0001$). In general, we found that among species that increased in relative abundance, the full modern dataset over-represented these increases for species associated with more natural land cover types, and under-represented increases for species more often associated with human development. In the most extreme example, our comparison showed a modest decrease in relative abundance of *B. impatiens* (-7%) when considering the full modern dataset, yet showed a strong increase when only subsampled modern data were considered (Table 1; Fig. 2; Fig. S1).

Rarefaction estimates of species richness and diversity were higher for historic than for modern collections, with all three curves approaching an asymptote, suggesting sampling effort was adequate (Table 2; Fig. 3). Extrapolated species richness in the historic period was not different from that observed ($n = 16$). In both modern samples, extrapolation estimated true species richness to be higher by one species than observed (i.e., 15 rather than 14 species).

Spatial analysis

We conducted a total of 124 roadside surveys comprising 1299 10-min counts in 64 priority blocks. Survey routes were completed an average 2.14 ± 0.19 SE (range 1–8) times. We collected an average of 4.74 ± 0.14 SE bumble bees at each site (range 0–35). At 17.6% of sites ($n = 228$) we collected no bees. We found 1.76 ± 0.04 SE (range 0–35) bumble bee species per site (Shannon's H': 0.53 ± 0.01 SE (range 0–1.80)), with the most commonly collected species, *B. vagans*, present in > 60% of sites (Fig. S2). Collections were strongly influenced by date, with per-event species richness and diversity peaking ~ 27 July, and abundance peaking ~ 1 August. Most common forage plants for these collections included non-native species such as clovers (*Trifolium* and *Melilotus* spp.) and vetches (*Vicia* spp.), and natives such as jewel weed (*Impatiens capensis* and *I. pallida*) and Joe-pye weed (*Eutrochium maculatum*).

Bumble bee abundance in site collections was positively correlated with total annual precipitation ($t = 3.03$,

Table 2 Observed and asymptotic estimates of species richness, Shannon diversity, and Simpson diversity from rarefaction analysis of Vermont bumble bee species collections in historic, modern, and subsampled modern datasets (Fig. 3)

Dataset	Diversity measure	Observed	Extrapolated	SE	Lower CI	Upper CI
Historic	Richness	16.00	16.00	0.48	16.00	17.34
	Shannon	9.01	9.05	0.18	9.01	9.41
	Simpson	6.98	7.01	0.19	6.98	7.38
Modern	Richness	14.00	15.00	2.29	14.07	28.17
	Shannon	6.06	6.06	0.06	6.06	6.17
	Simpson	4.54	4.54	0.05	4.54	4.63
Modern (subsample)	Richness	14.00	15.00	2.29	14.07	28.17
	Shannon	6.20	6.21	0.09	6.20	6.38
	Simpson	4.64	4.65	0.07	4.64	4.78

SE standard error of the extrapolations, *CI* 95% confidence intervals for Hill numbers

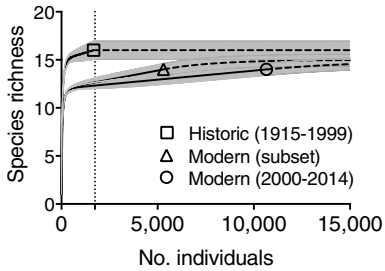

Fig. 3 Rarefaction of species numbers (±95% CI) in historic, modern, and subsampled modern bumble bee collections data. Solid lines represent interpolation from data, and dashed lines are extrapolations to an arbitrary 15,000-specimen limit. Symbols represent actual diversity and abundance of the three samples, and the vertical dashed line indicates sample size of the smallest dataset (i.e., historic). See Table 2 for summary statistics on species richness, and Shannon and Simpson diversity indices of collections

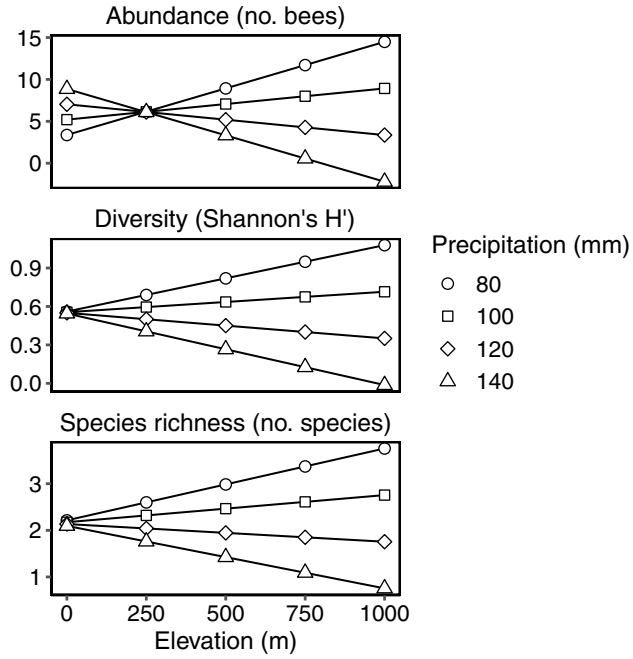

Fig. 4 Vermont bumble bee species richness, diversity, and abundance are predicted by a significant negative interaction between site annual precipitation and elevation, with highest means for each variable found at upper elevation sites with relatively low precipitation regimes. See Tables S4, S5

P = 0.003), but species richness and diversity were not associated with precipitation (t < |2.72|, P > 0.79; Table S4). All three response variables were positively correlated with site elevation (t > 1.93, P < 0.05). There was a significant negative interaction between annual precipitation and elevation for each variable, such that on axes of relatively low–high elevation and dry-wet precipitation regime, site species richness and diversity means were ordered as: high + dry > low + dry > low + wet > high + wet. Site mean abundances were ranked as: high + dry > low + wet > low + dry > high,+wet (t > |2.01|, P < 0.05; Fig. 4; Table S4). For *B. ternarius* and *B. terricola*, elevation was a significant positive predictor of their occurrence in roadside collections. Annual precipitation was significantly negatively correlated with probability of some species' occurrence (*B. borealis, B. fervidus, B. rufocinctus*), yet a positive predictor of occurrence of others (*B. impatiens, B. ternarius*). For *B. ternarius* and *B. terricola*, we observed an interaction between both variables, such that probability of occurrence was highest at driest upper elevations (Table S5). Splitting annual precipitation into seasonal phases, we discovered that the positive association between bumble bee abundance and precipitation was driven by deposition in winter (t = 4.22, P < 0.0001) but not summer (t = 0.77, P = 0.44). Considering only summer or winter precipitation, the negative interaction between precipitation and elevation was important to explaining bumble bee abundance (t > |3.35|, P < 0.0008), but not richness and diversity (t < |1.88|, P > 0.06; Table S4).

Bumble bee species richness was negatively associated with road density in both 0.5-km ($F_{1, 1224} = 4.30$, P = 0.04) and 1-km radii ($F_{1, 1224} = 4.61$, P = 0.03) around collection sites. Shannon H' diversity was negatively correlated with road density at 0.5-km radius ($F_{1, 1006} = 4.39$, P = 0.04); other effects on diversity and abundance were not significant (F < 1.68, P > 0.20). Average road density around collection localities varied significantly by bumble bee species at both 0.5-km ($F_{11, 10636} = 28.71$, P < 0.0001) and 1-km ($F_{11, 10636} = 48.92$, P < 0.0001; Fig. 5; Table S6). Species ranking was similar between the two distances. Species more strongly associated with roads included some that have increased most in relative abundance (e.g.; *B. bimaculatus* and *B. impatiens*); however, other increasing species (e.g., *B. ternarius, B. vagans*) were strongly negatively associated

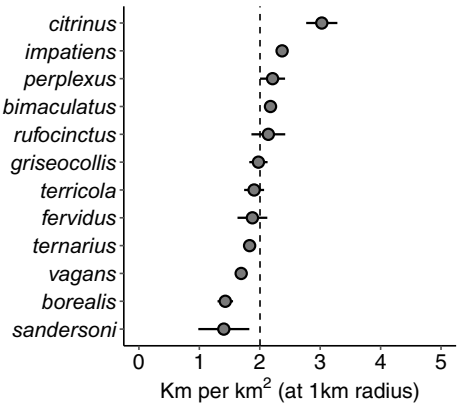

Fig. 5 Mean ± standard error road density within 1-km circles around bee collection localities (linear km per km^2). Dashed line indicates overall mean (2.0 km per km^2). Species were ranked similarly for mean road density within 0.5-km of collections (see Table S6)

with roads. One declining species, *B. citrinus*, was strongly associated with roads (Fig. 5; Table S6).

We discovered both negative and positive effects for individual land cover variables on per-site bumble bee species richness, diversity, and abundance (Table 3; Fig. 6). At both spatial scales, we found statistically significant negative effects of deciduous forest for all three variables, and mixed forest for species richness. At both scales, we found positive effects of evergreen forest for bumble bee abundance, and grasslands for species richness and diversity. Proportion cultivated crops and shrublands had positive effects on diversity at the 1-km scale; other effects were not statistically significant (Table 3; Fig. 6).

Table 3 Hierarchical partitioning analysis demonstrating importance of each land cover variable in explaining *Bombus* species richness, diversity (Shannon's H'), and abundance in 10-min roadside surveys

Radius	Land cover	Richness		Diversity (H')		Abundance	
		Coeff.	Z	Coeff.	Z	Coeff.	Z
0.5-km	Crops	0.44	−0.09	0.88	0.44	0.66	0.18
	Grass	**5.27**	**7.84**	**6.6**	**8.83**	1.19	1.05
	Deciduous	(**3.3**)	**3.61**	(**2.87**)	**3.29**	(**2.57**)	**2.9**
	Evergreen	0.35	−0.2	1.11	0.92	**5.35**	**7.47**
	Mixed	(**3.21**)	**4.09**	1.59	1.38	0.89	0.65
	Shrub	0.22	−0.42	1.49	1.34	0.21	−0.43
	Wetlands	0.56	0.05	0.29	−0.35	0.94	0.44
	Developed	0.35	−0.22	0.72	0.36	0.44	−0.05
1-km	Crops	1.01	0.64	**1.9**	**1.82**	0.76	0.43
	Grass	**3.11**	**3.28**	**4.99**	**6.26**	0.55	0.07
	Deciduous	(**3.25**)	**3.87**	(**3.05**)	**3.1**	(**3.48**)	**4.01**
	Evergreen	0.85	0.53	0.49	−0.09	**10.32**	**13.69**
	Mixed	(**2.09**)	1.9	0.91	0.69	0.87	0.66
	Shrub	0.21	−0.39	**2.13**	**2.11**	0.11	−0.53
	Wetlands	0.94	0.64	0.42	−0.15	1.62	1.43
	Developed	0.57	0.12	1.62	1.58	0.82	0.47

Test statistics in bold indicate statistically significant effects on these measures ($P < 0.05$; brackets = negative effects). See Fig. 6 for percent contributions of each variable

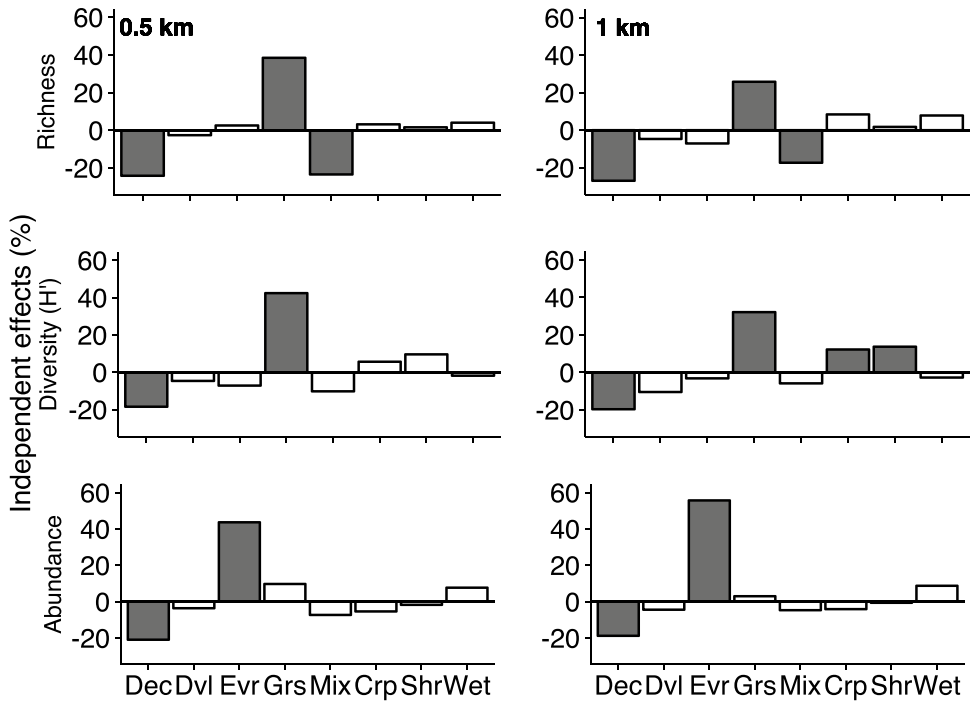

Fig. 6 Hierarchical partitioning analysis independent effects (%) of land cover classes on patterns of bumble bee species richness, diversity (Shannon's H'), and abundance in 10-min standardized collections, measured as proportional area within circles of 0.5-km and 1-km radii around sites. *Filled bars* statistically significant effects, *empty bars* non-significant effects. Land cover classes: *Dec* deciduous forest, *Dvl* developed areas, *Evr* Evergreen forest, *Grs* grasslands, *Mix* mixed forest, *Crp* cultivated crops, *Shr* shrubs, *Wet* wetlands

We collected 12 species during roadside surveys, and probability of each species' occurrence in these collections (mean = 0.147; range 0.009–0.614; Figure S2) varied with land cover (Table 4; S7). Many species were positively associated with grasslands at both 0.5-km (n = 6) and 1-km (n = 7) scales, including both common species (e.g., *B. bimaculatus* and *B. impatiens*) and those in decline (e.g., *B. citrinus* and *B. fervidus*); others were negatively associated with grasslands at one or both spatial scales, including *B. perplexus, B. ternarius, B. terricola*, and *B. vagans*. When forest cover types predicted species occurrence, their effect was negative for most species; exceptions were *B. ternarius, B. terricola*, and *B. vagans*. Developed lands were negative predictors of occurrence at both scales for some species (e.g., *B. borealis, B. citrinus*, and *B. fervidus*); however, they were positive predictors for *B. bimaculatus* and *B. impatiens*. Shrubs and wetlands had lower predictive power than other land cover variables; positive associations at one or both scales included *B. borealis, B. perplexus*, and *B. terricola*; those negatively associated were *B. fervidus* and *B. impatiens*. Overall, land cover variables were better predictors of species occurrence at 1-km than at 0.5-km radii. In only one case did the sign and significance for a land cover variable's effect on species occurrence differ between smaller and larger spatial scales: proportion cultivated crop was a negative predictor of *B. impatiens* occurrence at 0.5-km, yet positive at 1-km.

Discussion

We found significant declines in bumble bee diversity and abundance in Vermont. Seventeen bumble bee species were documented as native to the state and we documented the probable extirpation of three species and significant declines among four others. Our rarefaction analysis of both the historic and modern datasets slightly underestimated observed total species richness, but confirmed a strong decline in richness as well as diversity and abundance. Several additional bumble bee species have occasionally been observed in

Table 4 Effects of land cover on probability of individual species occurrence in 10-min standardized collections, measured as proportional of total area within circles of 0.5-km and 1-km radii around collection sites

		Crops	Grass	Deciduous	Evergreen	Mixed	Shrubs	Wetlands	Developed
0.5 km	*bimaculatus*		+	-	-	-			+
	borealis	+	+	-			+		-
	citrinus		+		-	-			-
	fervidus	+	+	-	-	-		-	-
	griseocollis		+						
	impatiens	-	+	-	+	-	-		+
	perplexus							+	
	rufocinctus	+	+		-	-			
	sandersoni								
	ternarius		-		+	+			
	terricola		-				+		
	vagans	-			+				
1 km	*bimaculatus*	+	+	-	-	-			+
	borealis	+	+	-		+	+	+	-
	citrinus		+		-	-			-
	fervidus	+	+	-	-	-		-	-
	griseocollis		+						
	impatiens	+	+	-	+	-			+
	perplexus		-					+	-
	rufocinctus	+	+	-	-	-			
	sandersoni								
	ternarius		-		+	+			
	terricola		-			+	+	+	
	vagans		-	+	+				

Light- and dark-shaded cells indicate negative and positive effects on species occurrence, respectively; unshaded = non-significant effects. Results are from hierarchical partitioning analyses. See Table S7 for statistical summaries

states and the province adjacent to Vermont (e.g., *B. frigidus, B. insularis, B. suckleyi*, and *B. variabilis*), suggesting that additional surveys could increase the number of native species found in the state. Our findings generally agree with recent studies documenting declines in diversity in other areas of North America (Cameron et al. 2011; Colla et al. 2012; Bartomeus et al. 2013).

Three bumble bees (*B. affinis*, B. *ashtoni*, and *B. fernaldae*) present in historical collections were not relocated in the modern period described by this study, including during our intensive citizen science inventory. Approximately one in eight bumble bees collected in Vermont during the historic period were *B. affinis*, which has not been observed in the state since 1999. Along with other species of the subgenus *Bombus*, this bee exhibited a precipitous decline throughout its range in the 1990s (Giles and Ascher 2006) and is now protected by federal endangered species statutes in both Canada and the U.S. Definitive explanation of this species' decline remains elusive and may involve a variety of factors. The most plausible has been that of 'pathogen spillover', the idea that bumble bee diseases native to Old World species may have been accidentally introduced to North America via widespread movement of colonies as commercial bumble bee pollination became possible in the 1990s (Colla et al. 2006; Szabo et al. 2012). While there is strong evidence of pathogen spillover as a cause of bumble bee population declines in other bumble bee faunas (e.g. South America) (Arbetman et al. 2012; Schmid-Hempel et al. 2014), recent research has demonstrated that *B. affinis* and other declining species had elevated loads of one common bumble bee pathogen during their population crashes, but that these were native rather than introduced pathogens (Cameron et al. 2016). It is important to note that pathogen spillover from species other than bumble bees, in particular non-native honey bees, could have played a role in declines of *B. affinis* and other bumble bee species (Graystock et al. 2016). Other leading hypotheses to explain the rapid decline of *B. affinis* and close relatives include habitat loss, pesticide exposure, and climate change (McFarland and Richardson 2014a); the true cause of these declines may be a synergistic combination of two or more factors.

B. ashtoni and *B. fernaldae* are part of a clade of socially parasitic 'cuckoo' bumble bees (subgenus *Psithyrus*) whose members demonstrate a pattern of decline globally (Arbetman et al. 2017). *B. ashtoni* exclusively parasitizes the nests of a few species in the subgenus *Bombus* (McFarland and Richardson 2014b; Williams et al. 2014), and we show here that both host species native to Vermont (*B. affinis* and *B. terricola*) have strongly declined. Given its rarity in historical collections, the fact that we did not relocate *B. fernaldae* is not surprising. However, *B. fernaldae* parasitizes a broad range of hosts (Williams et al. 2014), including subgenus *Pyrobombus* species, many of which have increased in relative abundance in Vermont (e.g. *B. bimaculatus* and *B. impatiens*). There are recent records of *B. fernaldae* from adjacent states and provinces (New York, Québec, and Maine; L. Richardson, *unpublished*), and it is not considered threatened across its broader North American range, although low sample size has prevented definitive assessment (Bartomeus et al. 2013; IUCN 2017). There are also modern records of *B. fernaldae* from warmer areas of its range (e.g., Pennsylvania and North Carolina; L. Richardson, *unpublished*) suggesting that its absence in this inventory is not related to thermal niche or other edge-of-range phenomena that can limit bumble bee distributions (Williams et al. 2007). Unexpectedly, in 2018 during revision of this manuscript we recorded the presence of a single *B. fernaldae* female in northwestern Vermont (Richardson 2018), confirming the persistence of this species in the state. We found that one other cuckoo bumble bee, *B. citrinus*, has also declined in relative abundance in Vermont. *Bombus citrinus* has been described as stable across its overall range (Colla et al. 2012; Bartomeus et al. 2013; Hatfield et al. 2014), however more recent anecdotal evidence from multiple regions of the eastern US indicate this species could be declining (Sam Droege, personal communication). Given that its primary hosts, *B. bimaculatus* and *B. impatiens*, are extremely common, such a decline would be due to causes other than host availability. Overall, our study additionally highlights the need for a comprehensive status assessment of North American *Psithyrus* species.

We found strong declines for three additional species, *B. fervidus, B. pensylvanicus*, and *B. terricola*. Previous studies have reported range-wide declines for each of these (Colla et al. 2012; Bartomeus et al. 2013). For *B. fervidus* and *B. pensylvanicus*, declines may be related to changes in agricultural practices. In the early twentieth century, Franklin (1912) described both species as associated with hayfields. *Bombus fervidus* was one of the most common species in northern New England at the time, while *B. pensylvanicus* was rare outside of agricultural areas in Vermont. As with certain birds associated with managed grasslands in Vermont (Perlut et al. 2006), these species' populations were likely increased by the field management practices prevalent in the state before the mid-twentieth century. *Bombus terricola* is of particular concern, having declined across its entire North American range by over 90% (IUCN 2017), and is currently undergoing a status review for listing as a Federally Threatened and Endangered species by the U.S. Fish and Wildlife Service. It is designated a species of Special Concern in Canada (Colla and Richardson 2015), and data from our study supported its 2015 listing as Endangered in Vermont (McFarland and Richardson 2014c). Despite strong evidence for decline of *B. terricola*, recent observations in Maine, Vermont, and areas of eastern Canada (L. Richardson, *unpublished*) suggest some populations may be

recovering, at least in restricted habitats such as those at high elevation (Tucker and Rehan 2017; Table S5).

We found that the five species that increased the most belonged to the dominant subgenus in North America, *Pyrobombus*, which is relatively stable or increasing globally (Arbetman et al. 2017). Our results for *B. bimaculatus, B. impatiens*, and *B. ternarius* accord with those reported elsewhere in North America (Colla and Packer 2008; Colla et al. 2012), and *B. impatiens* appears to be expanding its range, possibly in part due to transport of managed colonies for pollination of crops (Ratti and Colla 2010). Our observations for *B. vagans*, however, conflict with those of other studies that found varying degrees of decline (Colla and Packer 2008; Grixti et al. 2009; Bartomeus et al. 2013; Tucker and Rehan 2016). As a species associated in Vermont with natural land cover types, yet less common than other bumble bees as an agricultural pollinator (Nicholson et al. 2017), *B. vagans* is likely to be an important pollinator of wild plants, and as such a species that warrants additional study and monitoring throughout its range.

Declines in bumble bee abundance, diversity, and range extent have been attributed to numerous factors, in particular (1) parasite exposure, especially following contact with managed bees; (2) pesticides; (3) habitat loss; and (4) climate change. Honey bees, introduced to North America by the eighteenth century (Kalm 1770), may spread RNA viruses and other pathogens to wild bees through shared use of flowers (Graystock et al. 2015) and this is a documented mechanism of disease acquisition for *B. bimaculatus* and *B. vagans* in Vermont (Alger 2018). *Bombus impatiens* and other North American bumble bees have been managed for crop pollination since the 1990s, and are thought to have been infected with pathogens and parasites of Old World congeners when moved between European rearing facilities and North American farms, after which these diseases could have escaped to wild bumble bee populations that lack evolved resistance to them (Murray et al. 2013; Graystock et al. 2013; Schmid-Hempel et al. 2014). Some declining *Bombus* species have higher prevalence of a pathogen, *Nosema bombi*, than their non-declining congeners, but the pathogen appears to be a strain native to North American bumble bees rather than one accidentally introduced from Europe (Cameron et al. 2016). *N. bombi* is common in Vermont bumble bees (A. Burnham, *unpublished*). In addition, honey bees compete with wild bumble bees for floral resources, which may contribute to species declines (Goulson 2003; Thomson 2016). Second, there is strong evidence at multiple scales of analysis that pesticide use negatively impacts bumble bee populations. For example, routine agricultural use of neonicotinoid insecticides diminishes bumble bee colony fitness and the pollination service they deliver to crops (Whitehorn et al. 2012; Stanley et al. 2015), landscape-level organophosphate pesticide application to control forest pests reduces bumble bee abundance and diversity (Kevan 1975), and continent-scale patterns of fungicide use are correlated with disease prevalence in declining bumble bee species, including *B. affinis, B. pensylvanicus*, and *B. terricola* (McArt et al. 2017). There is current concern over the widespread prophylactic use of neonicotinoid insecticides as seed treatments on crops because the compounds are systemic, entering plants and rendering nectar and pollen toxic, with documented lethal and sublethal effects on bumble bees (Blacquière et al. 2012; Whitehorn et al. 2012; Douglas and Tooker 2015). Moreover, insecticides are commonly mixed with adjuvants and other plant protection products before application, which can cause synergistic increases in toxicity to bees (Sgolastra et al. 2016; David et al. 2016). In particular, recent evidence suggests that fungicides widely used in agriculture have strongly negative synergistic effects on bumble bees when combined with neonicotinoids and other classes of insecticides (McArt et al. 2017; Raimets et al. 2018). Vermont dairy farmers grow more than 40,000 ha of corn, and corn accounts for 90.2% of all cropped areas in the state (USDA NASS 2017). Nearly all of Vermont corn is grown from conventional seed coated with neonicotinoid insecticides and fungicides, making this crop the source of > 99% of all neonicotinoid application in the state (L. Richardson, *unpublished*), and suggesting that bees we observed in landscapes with high percent 'cultivated crop' land cover may be at increased risk of pesticide exposure. Third, increasing suburban and urban development, agricultural intensification, and habitat fragmentation may have negative effects on bumble bees (Williams 1986; Winfree et al. 2009; Carper et al. 2014; Ollerton et al. 2014; Schochet et al. 2016); Vermont has seen extensive conversion of natural land cover types and farmland to suburban development since the mid-twentieth century, as well as intensified management of hayfields and other agricultural lands (Perlut et al. 2006). Finally, warming, drought, and other effects of climate change are impacting bumble bees in both North America and Europe by causing both latitudinal and elevation changes in species distributions, with the majority of species experiencing consequent range contractions (Kerr et al. 2015). Bees and plants may have different responses to temperature cues resulting in phenological mismatch that could affect nectar and pollen availability (Kudo and Ida 2013), and climate change-associated shifts in precipitation regimes further affect bumble bee abundance by altering floral phenology (Ogilvie et al. 2017). While there is little doubt bumble bees face threats to their persistence, additional research is needed to clarify the nature and variability of these threats and the degree to which they interact to endanger bee populations in Vermont and elsewhere. We note also that the nature of some species' declines argues against particular causal factors; as one example, *B. affinis* has apparently been extirpated from our study area

but persists in the US Midwest, where threats associated with intensive agriculture and human development are much higher than those present in Vermont.

We found that Vermont's varied topography and seasonal precipitation structured patterns of bumble bee species richness, diversity, and abundance. Bee abundance was positively associated with precipitation, and all three variables were positively associated with elevation. In montane areas of western North America, bumble bee colony reproductive output and species diversity may be limited by floral resource availability (Bowers 1985), and precipitation exerts an indirect effect on bumble bee abundance, in which the availability of the floral resources upon which bees depend is positively correlated with moisture availability (Ogilvie et al. 2017). The effect of moisture on plant vigor may be beneficial to bumble bees found in Vermont's higher terrain, however, the lower temperatures and shorter growing season that characterize these sites could have opposing negative effects on bumble bee populations. Our analysis identifies potential trade-offs in this respect: species richness, diversity, and abundance were highest at higher elevation sites with relatively lower annual precipitation, and lowest at upper elevations with highest annual precipitation. Emergence of overwintered queens and colony initiation in spring is a function of snowmelt phenology, itself a product of both winter snow accumulation and spring temperature (Alford 1969; Ogilvie et al. 2017). One explanation for the patterns we describe here is that bumble bee populations at the driest Vermont sites (often those at low elevation) may be limited by floral resource availability and other negative impacts of drought (Rasmont and Iserbyt 2012), while those at the wettest sites may be limited by a late-melting snowpack or reduced foraging opportunities during rainy summer months. Our results suggest a potential mechanism to explain the significant increase in mean elevation of *B. terricola* occurrence we report here, a pattern also reported in the literature (Tucker and Rehan 2017) and present in an independent dataset of > 16,000 records of this species representing more than a century of collecting across the species' range (L. Richardson, *unpublished*). The interactive effects of elevation and abiotic factors we describe here clarify reports of climate-associated range shifts (Kerr et al. 2015) and should allow us to better forecast changes in the distribution of bumble bees, the ecological interactions in which they participate, and ecosystem services they provide.

We found that diversity and abundance of bumble bee assemblages in Vermont were strongly influenced by land use and land cover around collection localities. Previous research in Vermont (Nicholson et al. 2017) and beyond (MacFarlane 1974; Williams et al. 2011; Jha and Kremen 2013; Cusser et al. 2016), has shown positive effects of natural land cover on bees similar to the positive association we found between evergreen forest cover and bumble bee abundance. Forests dominated by conifers in our study area have a relatively low diversity of flowering plants, so this result could reflect effects of other factors correlated with such forests, for example the presence of nest sites and forage plants in wetlands and edges associated with Vermont spruce, fir, and hemlock forests. In contrast to the general conclusions of these studies, we also found that Vermont bumble bees were negatively associated with one of the most widely distributed natural cover types in the state, deciduous forest. One similar study in New England reported positive associations between forest cover and bumble bee abundance at smaller spatial scales, yet negative associations at larger scales (Scully 2010). Flowering canopy trees and spring ephemeral wildflowers in such forests can provide important forage for colony foundress queens, but they often harbor little forage in summer and fall. In Vermont, this pattern may be exaggerated by the fact that most deciduous forests are managed for timber and game wildlife species production, which can reduce diversity of understory flowering plants important to bees (Wyatt and Silman 2010).

Grassland cover was one of the strongest drivers of species diversity and predictors of individual species occurrence, a pattern described in previous research (Williams 2005; Morandin et al. 2007; Williams and Osborne 2009). Such habitats feature many native and invasive plant species that are important floral resources for bumble bees, and some species associated with this cover type, including *B. fervidus, B. griseocollis*, and *B. rufocinctus*, frequently nest aboveground in such habitats (Williams et al. 2014). Given this concentration of nesting and forage resources for bumble bees, it is perplexing that we did not find that bee abundance was positively associated with grassland cover. One potential explanation is that despite their value to bees, in Vermont most grassland cover is located in agricultural landscapes, where pesticide application is more frequent, and is maintained by periodic mowing, which can destroy bee nests and forage. The association of bumble bees with hayfields and other grasslands is cause for concern, because the state lost nearly 2% of its grassland cover between 1996 and 2010, an average of 368 Ha annually (NOAA 2013) (L. Richardson, *unpublished*). Land cover change may interact with other drivers of species loss, such as climate change, to drive bumble bee declines (Marshall et al. 2017), which could reduce the value of bumble bee crop pollination as an ecosystem service (Connelly et al. 2015; Nicholson et al. 2017).

Our analysis confirmed previous reports (Williams et al. 2014) that some bumble bees (e.g., *B. borealis, B. ternarius*, and *B. vagans*) are negatively associated with human development, including areas classed as developed land and those with high road density. By contrast, our results comport with earlier work (Matteson et al. 2008; Larson et al. 2014) demonstrating positive associations with such

anthropogenic habitats for *B. bimaculatus* and *B. impatiens*. Curiously, we found that *B. citrinus* was strongly positively associated with road density, similar to two of its primary hosts (*B. bimaculatus* and *B. impatiens*), yet negatively associated with developed lands, where those hosts are also common and road density is highest. Given its apparent decline in the state and the strong increase in abundance of its hosts, additional study of the bionomics of *B. citrinus* is warranted. Taken together, the patterns of bumble bee association with land cover and anthropogenic disturbance in our data permit predictions about how bumble bee distribution and diversity could shift in response to multiple complex drivers of global change. Although beyond the scope of this study, it is important to consider that bumble bee distributions may be structured by other complex interactions between land cover and abiotic factors such as elevation and precipitation.

Citizen science volunteers have been used effectively to assess status of bumble bees in other regions (Lye et al. 2011; Montalva et al. 2017; Suzuki-Ohno et al. 2017). Our study adds to the growing body of evidence that citizen science can help provide large datasets from a wide geographic area in a short time period that otherwise would not be possible. A longstanding concern with citizen science has been that science, policy, and conservation actions may be based on data that are unreliable (Cohn 2008; Dickinson et al. 2010, 2012). While we encouraged our citizen scientists to attempt species identifications, we made final determinations of all vouchers (Vantieghem et al. 2017).

While specimens were preferred as vouchers, some citizen scientists had disdain for collecting bumble bees. There has been some concern that over-collecting during inventories could cause harm to populations of monitored organisms (Minteer et al. 2014), however, available evidence suggests that bees, including bumble bees, are resilient to collecting intensity higher than was employed during this study (Gezon et al. 2015). Digital photographs submitted by users were an effective means of allowing them to collect data without collecting specimens. We were cautious in assigning determinations to bees vouchered only by photographs, which have been shown to be difficult to identify correctly, even for those considered to be experts in bumble bee identification (Austen et al. 2016). Our determination rate of 68% was far lower than a study in Japan which reported 95% of images were identified to species (Suzuki-Ohno et al. 2017). It is likely that identification success depends on the regional fauna (number of similar species) and the level of training for the citizen scientists who take photographs. While we provided some photo-voucher guidance for our volunteers, future studies could improve photo-vouchers with detailed, hands-on training and simple field tools such as temporary restraining devices to aid with photo-vouchers (Thomson and Zung 2015).

Other biases likely exist in our dataset. For example, detection of bumble bees may have varied by observer, habitat type, time of day, and other environmental conditions. However, detectability of large and ubiquitous species such as bumble bees that are readily visible on flowers is likely high for trained volunteers. Some citizen scientists collected bumble bee mimics (e.g., Robber Fly (*Laphria* species)) or eastern carpenter bees (*Xylocopa virginica*), indicating their strong ability to detect bumble bee forms on surveys. Additionally, many of the historic collections were from undergraduate students fulfilling beginning entomology class requirements and who were likely naive collectors, perhaps more so than our trained citizen scientists, visually searching areas for insects like bumble bees for their collections.

We highlight three caveats for interpretation of our data. First, our analysis relies on comparison of many independent bumble bee collecting events, most with no record of survey effort or methods. Museum data are indispensable for the study of bee species distributions and declines (Bartomeus et al. 2013; Kerr et al. 2015) and interactions with plants and pathogens (Miller-Struttmann et al. 2015; Cameron et al. 2016), but this data must be used with caution (Campbell Grant 2015). Specimens held by museums are not necessarily random samples with equal collecting effort and adequate spatio-temporal distribution, and it is unclear whether combining multiple datasets addresses this issue. Errors may be introduced to such datasets in a variety of ways, including transcription, determination, digitization, and data management (Lukyanenko et al. 2016). Here we sought to avoid such pitfalls (e.g., through examination of effects of species redundancy within collecting events and spatial subsampling) and we designed our survey so that it may be used by future researchers using more sophisticated statistical tools, but we suggest there is a need for additional research on how this important historical data can be best managed in studies like ours. It is important to note that our study includes some Vermont specimen data used in previous research on the status of North American bumble bees (Colla et al. 2012; Bartomeus et al. 2013). However, our analysis considers only collections made in Vermont, the majority of which (> 90% of our historic dataset) come from local institutions whose material was not available to the research community before we digitized it as part of this project.

Second, while relative abundance comparisons are widely used to analyze this type of data, their treatment of historical collections as random samples can lead to erroneous conclusions. For example, the commonness of any one species in the environment is not necessarily relative to that of any other in such a dataset, as assumed by the method. An additional weakness of relative abundance methods that has received less scrutiny is that they incorporate bias related to species detection probability that may not be related to

abundance. Different bumble bee species colony durations in Vermont vary by more than 2 months, meaning that phenology could influence their occurrence in collections donated to museums, and thus our conclusions about their commonness.

Third, our study should be interpreted in light of the fact that we asked volunteers to collect along roads rather than in less disturbed habitats. While many of our survey routes were on dirt roads through rural landscapes where traffic is light, roads are known to impact bumble bee movement patterns and forage resources (Bhattacharya et al. 2003; Andersson et al. 2017). Moreover, we show here that bumble bee species have different responses to road density in Vermont, suggesting that our survey method had species-specific effects on detection probability. This observation notwithstanding, occurrence of the most commonly collected species in roadside surveys, *B. vagans*, was negatively correlated with road density. We designed the study around roadside collection points in order to facilitate resurvey efforts, and we suggest that such future surveys take into account the biases inherent in roadside collections.

In conclusion, we compared a comprehensive survey of bumble bees with historical occurrence data to show that the fauna has undergone sweeping changes in Vermont over the last century. We demonstrate that current patterns of bumble bee occurrence are related to the state's topography, environment, and land cover, and predict that future demographic changes in this group will be responsive to ongoing changes in land use and other environmental factors. Our study represents a rigorous baseline dataset that may be used to characterize such changes in the future, and it underscores the value of citizen science volunteers as partners in such research. While the loss or decline of a substantial fraction of the state's bumble bee fauna could have important implications for ecosystem functioning and pollination in Vermont's thriving agricultural sector, we note that this study concerns less than 10% of Vermont's overall native bee species diversity. Several other native bee species found in the region that are rare due to specialized host plant interactions or other factors (Sheffield et al. 2004; Fowler 2016) may be present in the state, and additional inventory for these species is urgently needed. Both the results of this study and its limited taxonomic scope support a growing consensus that native bee inventory is a research and conservation priority; among the most important means of addressing this issue in Vermont and beyond are commitment of public resources to a national bee monitoring program (Lebuhn et al. 2013; Inouye et al. 2017), and the training of additional taxonomists, who are needed to interpret such collections (Kim and Byrne 2006).

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Table S1.Collections contributing bumble bee specimen records used in this analysis. The American Museum of Natural History dataset includes digitized records from a variety of secondary sources. Bold collection names indicate specimen determinations completed by the authors.

Collection	Records
Vermont Center for Ecostudies	10,017
University of Vermont Zadock Thompson Museum	1,386
Leif Richardson Research Collection	631
Yale University Peabody Museum	93
University of Vermont (Dr. Taylor Ricketts)	60
American Museum of Natural History	52
Castleton State College	24
Lyndon State College	20
Vermont Department of Forests and Parks	10
Ohio State University	9
Michael Veit Research Collection	7
University of California Berkeley Essig Museum	7
McGill University	3
	12,319

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Table S2.Taxonomic concepts used for each bumble bee (Hymenoptera: Apidae) species.

Scientific Name	**Common Name**	Authority	Alternative Concept
subgenus *Bombus*			
Bombus affinis	Rusty-patched bumble bee	Cresson, 1863	
Bombus terricola	Yellow-banded bumble bee	Kirby, 1837	
subgenus *Bombius*			
Bombus auricomus	Black and gold bumble bee	Robertson, 1903	
subgenus *Cullumanobombus*			
Bombus rufocinctus	Red-belted bumble bee	Cresson, 1863	
subgenus*Fervidobombus*			
Bombus fervidus	Yellow bumble bee	Fabricius, 1798	
Bombus pensylvanicus	American bumble bee	De Geer, 1773	
subgenus *Psithyrus*			
Bombus ashtoni	Ashton cuckoo bumble bee	Cresson, 1864	= *B. bohemicus* Seidl, 1838 sec.(Cameron et al. 2007)
Bombus citrinus	Lemon cuckoo bumble bee	Smith, 1854	
Bombus fernaldae	Fernald cuckoo bumble bee	Franklin, 1911	= *B. flavidus* Eversmann, 1852 sec. (Cameron et al. 2007)
Bombus insularis	Indiscriminate bumble bee	Smith, 1861	
subgenus*Pyrobombus*			
Bombus bimaculatus	Two-spotted bumble bee	Cresson, 1863	
Bombus impatiens	Common eastern bumble bee	Cresson, 1863	
Bombus perplexus	Confusing bumble bee	Cresson, 1863	
Bombus sandersoni	Sanderson bumble bee	Franklin, 1913	
Bombus ternarius	Tri-colored bumble bee	Say, 1837	
Bombus vagans	Half-black bumble bee	Smith, 1854	
subgenus*Separatobombus*			
Bombus griseocollis	Brown-belted bumble bee	De Geer, 1773	
subgenus*Subterraneobombus*			
Bombus borealis	Northern amber bumble bee	Kirby, 1837	

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Table S3.Mean ± SE values for environmental variables and spatial coordinates for collections in the historic and modern periods.

	Historic	Modern	F	P
Elevation (m)	141.84 ± 3.46	248.56 ± 1.43	756.7	<0.0001
Precipitation (cm)	99.83 ± 0.32	108.30 ± 0.13	575.7	<0.0001
Latitude	44.33 ± 0.01	44.02 ± 0.01	458.7	<0.0001
Longitude	-73.05 ± 0.01	-72.66 ± 0.01	10,308.0	<0.0001

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Table S4.Effects of elevation, precipitation, and their interaction on species richness, diversity (Shannon's H'), and abundance in roadside survey collections. Statistically significant effects (P < 0.05) and indicated in bold.

Dataset	Response	Term	Est. ± SE	t	P
Annual	Species richness	Intercept	2.37 ± 0.75	3.18	**0.002**
		Elevation	0.01 ± 0.00	2.05	**0.04**
		Precipitation	0.00 ± 0.01	-0.27	0.79
		Elevation*precipitation	0.00 ± 0.00	-2.07	**0.04**
	Shannon's H'	Intercept	0.58 ± 0.29	2.02	**0.04**
		Elevation	0.00 ± 0.00	1.93	**0.05**
		Precipitation	0.00 ± 0.00	-0.09	0.93
		Elevation*precipitation	0.00 ± 0.00	-2.01	**0.05**
	Abundance	Intercept	-3.95 ± 3.11	-1.27	0.20
		Elevation	0.04 ± 0.01	3.72	**0.0002**
		Precipitation	0.09 ± 0.03	3.03	**0.003**
		Elevation*precipitation	0.00 ± 0.00	-3.82	**0.0001**
Summer only	Species richness	Intercept	2.81 ± 0.93	3.02	**0.003**
		Elevation	0.01 ± 0.00	1.83	0.07
		Precipitation	-0.01 ± 0.02	-0.71	0.48
		Elevation*precipitation	0.00 ± 0.00	-1.79	0.07
	Shannon's H'	Intercept	0.68 ± 0.36	1.89	0.06
		Elevation	0.00 ± 0.00	1.85	0.06
		Precipitation	0.00 ± 0.01	-0.37	0.71
		Elevation*precipitation	0.00 ± 0.00	-1.88	0.06
	Abundance	Intercept	1.97 ± 3.88	0.51	0.61
		Elevation	0.04 ± 0.01	3.55	**0.0004**
		Precipitation	0.05 ± 0.07	0.77	0.44
		Elevation*precipitation	0.00 ± 0.00	-3.35	**0.0008**
Winter only	Species richness	Intercept	2.07 ± 0.55	3.77	**0.0002**
		Elevation	0.00 ± 0.00	1.69	0.09
		Precipitation	0.00 ± 0.01	0.30	0.76
		Elevation*precipitation	0.00 ± 0.00	-1.86	0.06
	Shannon's H'	Intercept	0.51 ± 0.21	2.42	**0.02**
		Elevation	0.00 ± 0.00	1.49	0.14
		Precipitation	0.00 ± 0.00	0.32	0.75
		Elevation*precipitation	0.00 ± 0.00	-1.71	0.09
	Abundance	Intercept	-3.70 ± 2.28	-1.62	0.11
		Elevation	0.03 ± 0.01	3.28	**0.001**
		Precipitation	0.21 ± 0.05	4.22	**< 0.0001**
		Elevation*precipitation	0.00 ± 0.00	-3.60	**0.0003**

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Table S5.Effects of elevation, precipitation, and their interaction on presence of individual bumble bee species in timed collections. Mean elevation (m) and precipitation (cm) of species occurrences are presented. Statistically significant effects (P < 0.05) and indicated in bold.

Species	Term	Mean ± SE	Estimate	SE	Z	P
B. bimaculatus	Intercept		0.256	1.607	0.160	0.873
	Elevation	183.24 ± 3.63	-0.007	0.007	-1.007	0.314
	Precipitation	103.17 ± 0.34	-0.005	0.016	-0.288	0.773
	Elevation*precipitation		0.000	0.000	0.250	0.802
B. borealis	Intercept		6.994	2.041	3.426	**0.001**
	Elevation	276.55 ± 6.88	0.004	0.006	0.637	0.524
	Precipitation	106.91 ± 0.54	-0.097	0.021	-4.655	**<0.0001**
	Elevation*precipitation		0.000	0.000	0.432	0.666
B. citrinus	Intercept		3.696	7.162	0.516	0.606
	Elevation	173.59 ± 12.24	0.001	0.041	0.020	0.984
	Precipitation	102.25 ± 1.30	-0.069	0.075	-0.922	0.357
	Elevation*precipitation		0.000	0.000	-0.143	0.886
B. fervidus	Intercept		18.573	7.751	2.396	**0.017**
	Elevation	104.17 ± 7.92	-0.034	0.042	-0.812	0.417
	Precipitation	94.96 ± 0.69	-0.212	0.085	-2.501	**0.012**
	Elevation*precipitation		0.000	0.000	0.615	0.539
B. griseocollis	Intercept		3.116	2.762	1.128	0.259
	Elevation	163.36 ± 7.18	-0.008	0.011	-0.696	0.486
	Precipitation	100.27 ± 0.66	-0.054	0.028	-1.922	0.055
	Elevation*precipitation		0.000	0.000	0.602	0.547
B. impatiens	Intercept		-1.834	1.376	-1.333	0.182
	Elevation	196.94 ± 2.28	-0.005	0.005	-1.037	0.300
	Precipitation	106.31 ± 0.23	0.031	0.013	2.277	**0.023**
	Elevation*precipitation		0.000	0.000	-0.213	0.832
B. perplexus	Intercept		-11.670	4.603	-2.535	**0.011**
	Elevation	288.45 ± 10.74	0.030	0.014	2.122	0.034
	Precipitation	110.14 ± 0.98	0.069	0.042	1.646	0.100
	Elevation*precipitation		0.000	0.000	-1.907	0.057
B. rufocinctus	Intercept		13.235	5.343	2.477	**0.013**
	Elevation	116.19 ± 9.35	-0.024	0.022	-1.080	0.280
	Precipitation	93.25 ± 0.68	-0.162	0.058	-2.801	**0.005**
	Elevation*precipitation		0.000	0.000	0.984	0.325
B. sandersoni	Intercept		-2.738	4.946	-0.554	0.580

	Elevation	320.07 ± 25.95	0.008	0.016	0.532	0.595
	Precipitation	114.00 ± 2.38	-0.017	0.048	-0.360	0.719
	Elevation*precipitation		0.000	0.000	-0.348	0.728
B. ternarius	Intercept		-14.916	1.925	-7.749	**<0.0001**
	Elevation	309.46 ± 2.87	0.057	0.007	8.719	**<0.0001**
	Precipitation	111.53 ± 0.24	0.122	0.018	6.884	**<0.0001**
	Elevation*precipitation		0.000	0.000	-8.230	**<0.0001**
B. terricola	Intercept		-13.983	5.818	-2.403	**0.016**
	Elevation	324.79 ± 9.67	0.054	0.018	2.988	**0.003**
	Precipitation	112.92 ± 0.90	0.084	0.054	1.574	0.115
	Elevation*precipitation		0.000	0.000	-2.684	**0.007**
B. vagans	Intercept		-0.954	1.405	-0.679	0.497
	Elevation	280.89 ± 2.66	0.008	0.005	1.420	0.156
	Precipitation	111.03 ± 0.26	0.013	0.014	0.934	0.350
	Elevation*precipitation		0.000	0.000	-0.969	0.332

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Table S6. Mean ± standard error density of roads (linear km per km^2) in 0.5-km and 1-km circles around bumble bees by species. HSD = Tukey Honest Significant Differences among species means, where those sharing letters are not different.

Species	0.5-km			1-km		
	Mean	SE	HSD	Mean	SE	HSD
B. bimaculatus	2.71	0.06	b	2.18	0.05	c
B. borealis	1.93	0.08	e	1.43	0.07	e
B. citrinus	3.91	0.17	a	3.03	0.13	a
B. fervidus	2.30	0.16	c,d,e	1.88	0.13	c,d,e
B. griseocollis	2.25	0.10	c,d,e	1.98	0.08	c,d
B. impatiens	2.75	0.04	b	2.37	0.03	b
B. perplexus	3.01	0.14	b	2.21	0.11	b,c
B. rufocinctus	2.30	0.18	c,d,e	2.14	0.14	c,d
B. sandersoni	1.91	0.28	e	1.40	0.22	e
B. ternarius	2.35	0.04	c,d	1.83	0.03	d,e
B. terricola	2.56	0.11	b,c	1.91	0.08	c,d
B. vagans	2.18	0.03	d,e	1.69	0.02	d,e

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Table S7. Hierarchical partitioning analysis of effects of land cover variables on species presence vs. absence at collecting sites. Data are coefficients, Z-scores, and the sign of the effect. Bold values are statistically significant.

Radius	Land cover	*B. bimaculatus*	*B. borealis*	*B. citrinus*	*B. fervidus*	*B. griseocollis*	*B. impatiens*
0.5 km	Cultivated crops	1.28, 1.02 (+)	**2.06, 2.04 (+)**	0.46, -0.04 (+)	**8.37, 9.83 (+)**	1.37, 1.37 (+)	**1.81, 1.95 (-)**
	Deciduous forest	**6.03, 7.39 (-)**	**6.88, 8.68 (-)**	0.52, 0.04 (-)	**4.04, 5.62 (-)**	1.31, 1.10 (-)	**3.44, 4.54 (-)**
	Developed	**3.77, 5.09 (+)**	**10.32, 13.92 (-)**	**1.87, 1.89 (-)**	**1.68, 1.67 (-)**	0.22, -0.35 (-)	**6.83, 10.04 (+)**
	Evergreen Forest	**6.10, 7.79 (-)**	0.75, 0.39 (-)	**2.02, 1.97 (-)**	**13.32, 15.82 (-)**	0.42, -0.10 (-)	**2.35, 2.49 (+)**
	Grasslands	**6.14, 8.55 (+)**	**4.22, 5.21 (+)**	**4.62, 5.88 (+)**	**13.17, 17.76 (+)**	**3.79, 4.71 (+)**	**7.76, 11.70 (+)**
	Mixed forest	**6.10, 8.26 (-)**	0.87, 0.44 (-)	**2.36, 2.56 (-)**	**9.04, 11.69 (-)**	1.53, 1.54 (-)	**25.21, 35.17 (-)**
	Shrubs	0.31, -0.28 (+)	**2.58, 3.20 (+)**	0.05, -0.69 (+)	0.21, -0.46 (-)	0.23, -0.42 (+)	**1.96, 2.03 (-)**
	Wetlands	1.06, 0.65 (+)	1.08, 0.61 (+)	1.33, 1.04 (-)	**4.07, 4.78 (-)**	0.33, -0.22 (-)	0.88, 0.53 (-)
1 km	Cultivated crops	**1.86, 2.02 (+)**	**3.25, 3.64 (+)**	1.22, 0.98 (+)	**8.22, 10.43 (+)**	0.41, -0.13 (+)	**2.24, 2.73 (+)**
	Deciduous forest	**6.13, 8.17 (-)**	**7.39, 9.78 (-)**	0.92, 0.60 (-)	**3.20, 3.99 (-)**	1.41, 1.27 (-)	**4.66, 5.89 (-)**
	Developed	**3.45, 3.74 (+)**	**20.11, 28.15 (-)**	**2.64, 2.85 (-)**	**2.34, 2.42 (-)**	0.26, -0.40 (+)	**10.56, 14.19 (+)**
	Evergreen Forest	**5.52, 7.66 (-)**	1.14, 0.84 (-)	**1.84, 2.17 (-)**	**8.86, 12.40 (-)**	0.30, -0.21 (-)	**5.06, 6.68 (+)**
	Grasslands	**8.14, 10.24 (+)**	**4.18, 5.96 (+)**	**5.43, 7.54 (+)**	**13.44, 21.06 (+)**	**3.64, 4.83 (+)**	**8.66, 10.44 (+)**
	Mixed forest	**5.89, 8.82 (-)**	**2.40, 2.78 (+)**	**3.30, 4.43 (-)**	**12.84, 18.17 (-)**	1.09, 0.83 (-)	**28.25, 30.61 (-)**
	Shrubs	0.47, -0.01 (+)	**3.66, 4.98 (+)**	0.19, -0.45 (+)	1.40, 1.35 (-)	0.05, -0.63 (+)	1.69, 1.53 (-)
	Wetlands	1.04, 0.70 (+)	**2.54, 3.09 (+)**	1.05, 0.90 (-)	**1.96, 2.06 (-)**	0.17, -0.55 (+)	1.04, 0.86 (-)
		B. perplexus	*B. rufocinctus*	*B. sandersoni*	*B. ternarius*	*B. terricola*	*B. vagans*
0.5 km	Cultivated crops	0.44, -0.07 (-)	**3.58, 4.06 (+)**	0.56, 0.08 (+)	0.57, 0.06 (-)	0.66, 0.29 (-)	**2.03, 2.05 (-)**
	Deciduous forest	0.96, 0.73 (+)	1.60, 1.64 (-)	0.08, -0.55 (-)	0.64, 0.13 (+)	0.43, -0.05 (-)	0.78, 0.39 (+)
	Developed	1.56, 1.41 (-)	1.33, 1.01 (-)	0.14, -0.54 (-)	0.67, 0.27 (-)	0.23, -0.39 (-)	1.08, 0.84 (-)

	Evergreen Forest	1.06, 0.64 (-)	**12.48, 16.59 (-)**	0.23, -0.36 (-)	**3.01, 3.66 (+)**	1.76, 1.59 (+)	**2.50, 2.71 (+)**
	Grasslands	1.06, 0.79 (-)	**12.00, 15.09 (+)**	0.08, -0.70 (-)	**3.78, 4.66 (-)**	**2.08, 1.94 (-)**	1.10, 0.94 (-)
	Mixed forest	0.58, 0.09 (+)	**6.65, 7.94 (-)**	0.06, -0.64 (-)	**5.83, 7.81 (+)**	1.40, 1.42 (+)	0.54, 0.04 (+)
	Shrubs	1.36, 1.32 (+)	0.20, -0.42 (-)	1.35, 1.31 (+)	0.50, 0.01 (-)	**2.27, 2.64 (+)**	0.98, 0.68 (+)
	Wetlands	**4.93, 6.51 (+)**	1.26, 0.86 (-)	0.18, -0.46 (+)	0.58, 0.10 (-)	0.37, -0.13 (+)	0.67, 0.24 (+)
1 km	Cultivated crops	0.30, -0.30 (-)	**4.24, 4.47 (+)**	0.56, 0.07 (+)	1.39, 1.35 (-)	0.35, -0.17 (-)	1.59, 1.56 (-)
	Deciduous forest	1.37, 1.29 (+)	**1.87, 2.27 (-)**	0.12, -0.52 (-)	1.32, 1.18 (+)	0.56, 0.11 (-)	**1.89, 2.07 (+)**
	Developed	**2.81, 3.01 (-)**	1.59, 1.62 (-)	0.29, -0.33 (-)	1.48, 1.42 (-)	0.92, 0.57 (-)	1.41, 1.41 (-)
	Evergreen Forest	1.18, 0.89 (-)	**7.93, 10.69 (-)**	0.34, -0.24 (-)	**6.94, 10.31 (+)**	0.93, 0.63 (+)	**3.05, 3.47 (+)**
	Grasslands	**2.08, 2.12 (-)**	**13.86, 22.00 (+)**	0.20, -0.41 (-)	**10.22, 13.25 (-)**	**3.75, 4.66 (-)**	**3.14, 3.89 (-)**
	Mixed forest	0.48, -0.07 (+)	**6.09, 7.95 (-)**	0.30, -0.28 (+)	**12.06, 15.73 (+)**	**2.32, 2.34 (+)**	0.56, 0.17 (+)
	Shrubs	0.05, -0.69 (-)	0.35, -0.31 (+)	0.72, 0.36 (+)	0.34, -0.27 (-)	**2.45, 2.89 (+)**	0.30, -0.23 (+)
	Wetlands	**5.10, 7.09 (+)**	0.51, -0.06 (-)	0.09, -0.52 (+)	1.45, 1.21 (-)	**2.06, 2.17 (+)**	1.30, 1.11 (+)

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Figure S1.Relative abundance of bumble bee species collected in two time periods, with all modern dataset included (compare with Fig. 2, depicting only modern collections made within 5 km of historic localities). Asterisks indicate species collected during the historic period that were not relocated in the modern period.

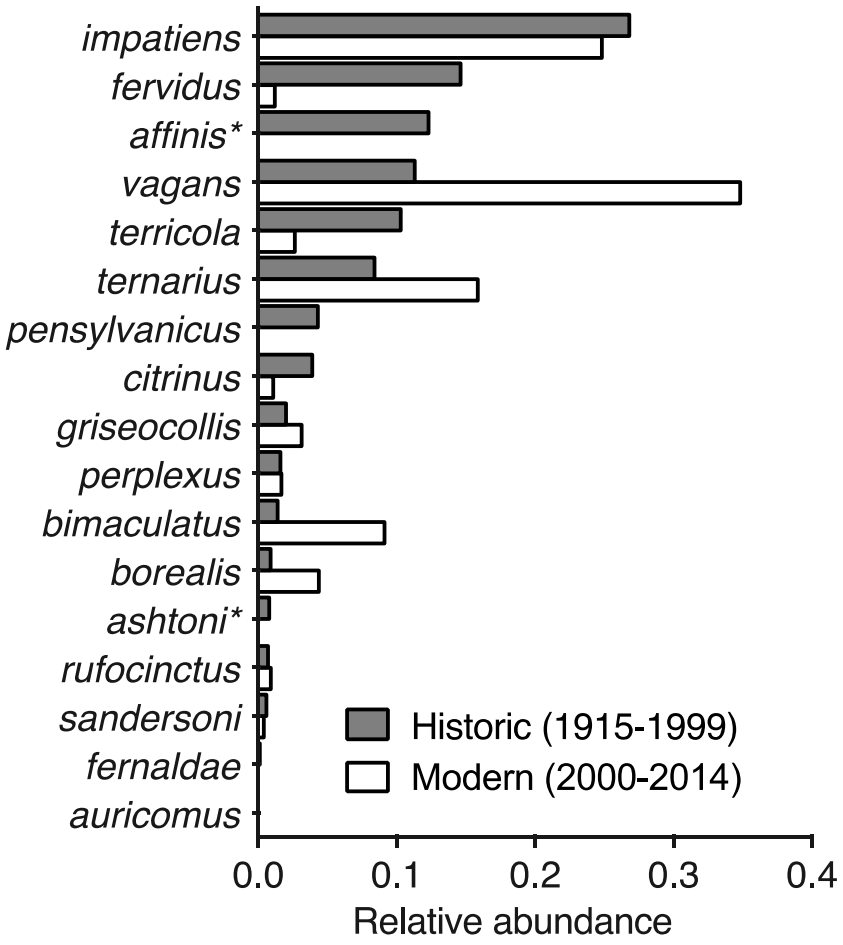

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Figure S2.Probability of bumble bee species occurrence during 1,299 roadside collection events (mean = 0.147; range = 0.009-0.614).