

## Effects of climate change on phenologies and distributions of bumble bees and the plants they visit

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**Abstract.** Surveys of bumble bees and the plants they visit, carried out in 1974 near the Rocky Mountain Biological Laboratory in Colorado, were repeated in 2007, thus permitting the testing of hypotheses arising from observed climate change over the intervening 33-yr period. As expected, given an increase in average air temperature with climate warming and a declining temperature with increasing elevation, there have been significant shifts toward higher elevation for queens or workers or both, for most bumble bee species, for bumble bee queens when species are combined, and for two focal plant species, with no significant downward shifts. However, contrary to our hypotheses, we failed to observe significant altitudinal changes for some bumble bee species and most plant species, and observed changes in elevation were often less than the upward shift of 317 m required to maintain average temperature. As expected, community flowering phenology shifted toward earlier in the season throughout our study area, but bumble bee phenology generally did not change, resulting in decreased synchrony between bees and plants. However, we were unable to confirm the narrower expectation that phenologies of bumble bee workers and community flowering coincided in 1974 but not in 2007. As expected, because of reduced synchrony between bumble bees and community flowering, bumble bee abundance was reduced in 2007 compared with 1974. Hence, climate change in our study area has apparently resulted primarily in reduced abundance and upward shift in distribution for bumble bees and shift toward earlier seasonality for plant flowering. Quantitative disagreements between climate change expectations and our observations warrant further investigation.

**Key words:** altitudinal transect; asynchrony; *Bombus*; bumble bee; community ecology; elevation; flowering; pollination; reproduction; Rocky Mountain Biological Laboratory.

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## INTRODUCTION

Organisms are expected to respond to changing climate by shifting geographical ranges and phenology toward remaining in their compatible

climate zones (Forister et al. 2010, Bedford et al. 2012, Roth et al. 2014). Consistent with global warming (Parmesan 2006), for example, the distributions of a wide range of species have shifted toward higher latitudes (Nakamura et al. 2013,

Cavanaugh et al. 2014, McCain and King 2014, Paprocki et al. 2014) and higher elevations (Narins and Meenderink 2014, Pizzolotto et al. 2014, Urli et al. 2014), and there have been phenological shifts toward earlier spring events (Dunn and Moller 2014, Polgar et al. 2014).

Such changes may result in mismatches, either temporal or spatial, between interacting species (Tylianakis et al. 2008), especially when they are from different trophic levels such as plants and their pollinators (Visser and Both 2005, Both et al. 2009). Plants and animals generally respond differently to climatic variables (Visser and Both 2005, Doi et al. 2008, Forrest and Thomson 2011, Parsche et al. 2011, Rafferty and Ives 2011, Kudo and Ida 2013) and so formerly synchronous plants and pollinators are likely to become asynchronous through shifts in the phenology of one relative to the other (Rafferty and Ives 2011, 2012, Willmer 2012, Kudo and Ida 2013). Pollinators may become seasonally active later relative to the plants they visit (Doi et al. 2008, McKinney et al. 2012), although no dislocation between plants and animals was found in one study (Bartomeus et al. 2011). It has similarly been found that breeding by birds may have become disrupted through a climate-induced temporal mismatch with food supply (Burger et al. 2012). However, we are not aware of any community-level study that has considered possible mismatches, arising from asynchronous climate-induced shifts in altitude, latitude or other spatial variable, in plants relative to their pollinators or among interacting species in general.

The mutualistic relationship between plants and their pollinators, their long period of co-evolution, and the relatively little anthropogenic climate change that had occurred prior to about 40 yr ago, make it likely that synchrony between them should have been high up till then. More recent climate change, with associated global warming, has been much greater since then, with the period from 1983 to 2012 “likely the warmest 30-yr period of the last 1400 yr in the Northern Hemisphere” (IPCC 2013). There should therefore have been significant deterioration in plant-pollinator synchrony over about the last 40 yr.

Although synchrony between plants and their pollinators should have declined, with increasing temporal disconnect between the two groups, the expected direction and magnitude

of this temporal disconnect is unknown. We lack information concerning how animals and plants are responding to changing climate, and whether these two groups are responding synchronously (Miller-Rushing and Inouye 2009). Hence, while both groups are expected to have shifted toward being seasonally earlier, it is not possible to predict the relative magnitudes of these shifts, and so not possible to predict which group should have become seasonally earlier than the other, nor what the difference between the two groups should now be. However, other studies have so far mostly found that phenologies of the plants have shifted earlier by more than their animal pollinators, so that the animals are now late relative to the plants (Doi et al. 2008, Forrest and Thomson 2011, McKinney et al. 2012).

As temporal mismatches between phenologies of plants and their pollinators have developed or increased, pollinator reproduction will likely have been reduced, leading to a decline in pollinator abundance. Times would have increasingly arisen in which there were either too few pollinators to take advantage of abundant flowering or too many relative to available floral resources (Rafferty and Ives 2011), with reduced pollinator reproduction occurring in both circumstances. Subsequently, reduced reproduction over successive years would have compounded, resulting in a decrease in pollinator abundance.

Plant reproduction, and hence plant abundance, may also have declined as a result of decreased synchrony between plants and pollinators. If, for example, some plants are now flowering early relative to the timing of their pollinators, as has been reported in some cases (Doi et al. 2008, Forrest and Thomson 2011, McKinney et al. 2012), and their reproduction is limited by pollen receipt, then such plants could suffer reduced reproduction, resulting in their decreased abundance.

Evolution of plant and pollinator phenologies could counteract any effects arising from decreased synchrony, but it seems unlikely that this would have occurred in long-lived perennials that characterize our study area, over the 33 yr of this study. A temporal disconnect between plants and their pollinators should favor, through natural selection, more synchronous individuals, for both plants and pollinators. However, any consequent evolutionary change in overall

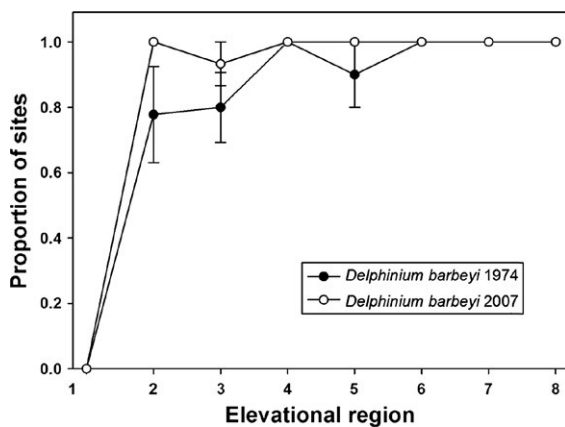


Fig. 1. Proportion of sites where *Delphinium barbeyi* was present vs. elevation region in 1974 and 2007.

synchrony between the two groups would require many generations.

Studies of mountain ecosystems should be particularly informative in terms of understanding effects of climate change. Organisms are more likely to shift distributions in terms of altitude than latitude, because of the shorter distances to track a particular climatic regime (Crimmins et al. 2009). Furthermore, mountain ecosystems are predicted to experience some of the earliest and strongest effects of climate change (Nogués-Bravo et al. 2007, Saunders et al. 2008), and extinction risks associated with climate warming are expected to be aggravated for species endemic to mountainous areas, especially those restricted to the highest elevations (Dirnböck et al. 2011). On the other hand, because of the relatively short distances between areas of different elevation in mountainous regions, short-term movements of organisms may mask or ameliorate effects of climate change. Despite this, evidence is accumulating for both plants and pollinators that latitudinal and altitudinal ranges are changing (Roth et al. 2014), and if they are not changing synchronously, there is the potential for altered interactions among them (Rafferty and Ives 2012).

We consider the possible effects of climate change on a plant-pollinator system in the mountainous area around the Rocky Mountain Biological Laboratory (RMBL) in Colorado, through surveys of bumble bees and the flowers they visit carried out initially in 1974 (Pyke 1982, Pyke et al. 2011, 2012) and repeated in 2007. Direct human-induced modification to the environment should

not have influenced our comparison, as most of our sites were within National Forest and there were no apparent changes to land-use between 1974 and 2007 at any of the sites.

We hypothesized that observed climate change in our study area during the 33-yr period between 1974 and 2007 would have affected bumble bees and plants as follows.

*Hypothesis 1: Species distributions have shifted upwards by about 317 m for both bumble bees and the plants on which they feed, matching the change in temperature with elevation.*

Consistent with increases in average temperature, a number of plant and animal species in our study area have shown evidence of the expected upward shifts (Perfors et al. 2003, Menke et al. 2014). However, none of these studies has tested whether the magnitudes of observed changes in elevation are quantitatively as expected under climate change.

Both bumble bees and plants in our study would have had to shift upwards in elevation by 317 m to maintain an unaltered average temperature. The observed lapse rate at which average daily temperature during summer decreases with increasing elevation in a nearby area of central Colorado is about 6.3°C/1000 m (Meyer 1992). The observed increase in average monthly spring/summer temperature in the study area of about 2°C is therefore equivalent to a decrease in elevation of 317 m (i.e.,  $1000 \times 2/6.3$  m).

*Hypothesis 2: Bumble bee and flowering plant phenologies have shifted toward earlier in the season, but not identically, resulting in lost temporal synchrony between them (It was not possible to predict the direction or magnitude of this temporal disconnect between bumble bees and plant flowering.).*

Consistent with warming temperatures in our study area, events associated with spring have been occurring earlier, and so the phenologies of bumble bees and the plants they visit should have shifted toward earlier in the season. Over the period between 1973 and 2006, the average monthly air temperature recorded at the nearby town of Crested Butte (fig. 1 in Pyke et al. 2012) during April-June has increased by an estimated 2.0°C (Miller-Rushing and Inouye 2009). Similar increases in average air temperature have presumably occurred throughout the

local area. Associated with such increased average temperatures, snowmelt in the area during spring/summer has tended to occur earlier (Miller-Rushing and Inouye 2009), and the activities of some plants and animals have shifted phenologically toward earlier in the season (Inouye et al. 2000, 2003, Miller-Rushing and Inouye 2009, Lambert et al. 2010). However, as discussed above, we currently have no basis for predicting changes in the phenology of one species relative to another.

*Hypothesis 3: Bumble bee abundance was lower in 2007 than in 1974.*

With increasing temporal disconnect between bumble bees and the plants they visit, we expected declines in bumble bee reproduction, and consequent declines in bumble bee abundance, as discussed above. Changes in abundance, consistent with climate change, have been observed in our study area for various species of plants (Harte and Shaw 1995, de Valpine and Harte 2001, Perfors et al. 2003, Saavedra et al. 2003, Harte et al. 2006, Miller-Rushing and Inouye 2009) and animals (Ozgul et al. 2010).

## METHODS

### *Study area and sites*

This study was carried out near the Rocky Mountain Biological Laboratory (RMBL) in Colorado, USA during 1974 and 2007. In this area elevations may vary by 1,000 m or more over only a few km of horizontal distance (fig. 1 in Pyke et al. 2012). The study area encompassed an elevation range of just over 1000 m from near the town of Crested Butte at 2693 m to mountain tops about 16 km to the north with maximum elevations of  $\approx 3760$  m (fig. 1 in Pyke et al. 2012). Within this area the woody vegetation was dominated by sagebrush at the lowest elevations, and by aspen and spruce-fir forest at higher elevations, with willows along streams. Our study focused on sites that were dominated by grasses and herbaceous plants, and occurred throughout the study area.

Study sites were established in 1974 to cover the elevation range present in our study area, while using available trails and roads that provided site access and replication for elevation (Pyke 1982, Pyke et al. 2012). Sites consisted of both

circular areas spaced along-side roads (i.e., circle sites) and roughly rectangular lengths along walking tracks or routes between the main road and highest nearby elevations (i.e., transect sites). Sites along roads consisted of areas within about 50 m from central points, while sites along walking routes consisted of the areas within about 25 m on either side of the route for particular segments of the route. These walking segments were either determined naturally by changes in topography and vegetation along the route, or defined by elevation intervals of 500 ft (e.g., 10 500 to 11 000 ft, i.e., 3182 to 3333 m). Further information regarding these sites may be found in earlier publications (Pyke 1982, Pyke et al. 2011, 2012) and location details for these sites and walking routes have been archived at RMBL.

This study considers 47 of the sites from 1974 that were re-surveyed in 2007. The identities and locations of all but one of these sites have been presented previously in Appendix Tables A2-1 and A2-2 in Pyke et al. (2012). The identities of those sites that were re-surveyed in 2007 are listed in the appendix to the current article, using previous location codes, along with details for one additional site that was surveyed in both years (see Appendix Section A1). The road-side circle sites traversed topography that was generally flatter and lower in elevation than the transect sites (Pyke et al. 2012; see Appendix Section A1 for details).

### *Bumble bee and flower surveys*

Both years we surveyed as much of the summer flowering season as possible, at intervals sufficiently short to capture seasonal changes. During 1974 most sites were visited about every 8 d during the period between 22 June and 8 September (Pyke 1982); during 2007 they were visited about every 6 d between 20 June and 8 August. The difference in survey period meant that some data collected toward the end of the 1974 season could not be used in comparisons between the 2 yr (see below).

Survey methods adopted in the 2 yr were essentially identical (Pyke 1982, Pyke et al. 2011, 2012). In both years, surveys were carried out at each site, generally between about 09:00 and 18:00. As a result of variation in daily start time, initial site, and sequence direction of surveyed sites along transects, each site was surveyed at different times of day over the course of each season.

During survey visits to a site, one to three people walked within the site and separately recorded the identities of any bumble bees observed (i.e., species and caste), along with the identity of any visited flower. In addition, the identities of plant species in flower were recorded for each survey visit to a site. We adopt the plant species names of Hartman and Nelson (2001) and parenthetically include older names used in Pyke (1982). Except for two species of cuckoo bumble bee (*B. insularis* and *B. suckleyi*), all bumble bee species could be distinguished in the field (Pyke 1982, Pyke et al. 2011, 2012). Surveys in the 2 yr were also essentially identical in terms of site coverage and duration (See Appendix Section A1).

#### *Spatial and temporal variables*

To facilitate analyses, spatial and temporal variables were assigned to discrete categories. For spatial analysis, sites were categorized, as previously (Pyke 1982), into eight equal elevation regions of 500 vertical ft or 152 m (i.e., region 1 = 8500–9000 ft = 2576–2727 m; region 2 = 9000–9500 ft = 2727–2879 m; etc.). Surveys were also categorized into three roughly equal time periods (i.e., before 12 noon, 12 noon to 3 pm, after 3 pm), resulting in reasonable sample sizes for each category. Seasonal analyses were based on date periods that were the first and second halves of each month (e.g., date period 1 was 16–30 June, date period 2 was 1–15 July, etc.). Finer subdivisions of time resulted in too few observations for some date periods and no surveys for some site-period combinations.

#### *Plant species*

Twelve plant species in our study, all perennial (Treshow 1975), have been identified as being of particular importance to bumble bees, by virtue either of accounting for high proportions of bumble bees recorded visiting their flowers or being preferred by particular bumble bee species over other plant species (Pyke 1982). For sites surveyed during both 1974 and 2007, these plant species accounted for 74.5% of recorded bumble bees in each year (Table 1). We focus below on these species.

#### *Bumble bee species*

We focused on eight bumble bee species (i.e., *B. appositus*, *B. balteatus* [*kirbyellus*], *B. bifarius*,

*B. flavifrons*, *B. frigidus*, *B. mixtus*, *B. occidentalis*, *B. sylvicola*) as these species accounted in most cases for over 97% of recorded bumble bees, excluding Region 1, for all castes (i.e., queens, workers, males) in both years (Appendix: Table A1-1).

#### *Measures of bumble bee and plant density*

We assume that the number of bumble bees recorded per person hour (i.e., recording rate) is proportional to bumble bee density (Pyke et al. 2011, 2012), and considered each caste separately because they exhibited distinctly different phenologies, with spring queens seasonally earliest, followed by workers, and then males and autumn queens together at the end of the season. It is then relatively straightforward to consider how these recording rates are affected by other variables, such as species, caste, time of day, date period and elevation range (Pyke et al. 2011, 2012), and how these patterns may differ between years (see below). Of course, bumble bee recording rate does not measure actual density of bumble bees.

As measures of plant density we took the proportions of sites, within each elevation region, at which particular plant species were recorded as present, as these proportions should be correlated with plant density and variation in them reflected known elevation distributions for the various plant species (e.g., Fig. 1). To compare the 2 yr, we therefore scored presence or absence (1 or 0) for each plant species at a particular site, calculated a presence change value by subtracting the presence score in 1974 from the score in 2007, and then used this presence change value as a dependent variable. In this case, for example, an average change in presence of  $-0.5$  would mean that there had been a net disappearance between years across half the sites. Unfortunately, it was not possible to carry out transect or plot-based counts of flowers or plants in either year.

#### *Phenologies*

As representations of bumble bee and flowering phenologies, we took the seasonal patterns of bumble bee recording rate and number of plant species in flower, each reaching a peak during the summer season, but with different shapes to their seasonal pattern. Graphs of bumble bee recording rate over time typically

Table 1. Twelve plant species considered particularly important to bumble bees are listed in order of decreasing numbers of recorded bumble bees in 1974. Also presented for each of these species are the results of fitting the model  $CP = A + B \cdot R + C \cdot R^2$ , where CP is change in presence between years, R is Elevational Region and A-C are unknown coefficients). Threshold for significance is  $P = 0.01$ .

| Plant Species                              | # Bumble bee records 1974 | # Bumble bee records 2007 | Directions and significance of coefficients, with probabilities and SE values |
|--------------------------------------------|---------------------------|---------------------------|-------------------------------------------------------------------------------|
| <i>Delphinium barbeyi</i>                  | 2922                      | 800                       | B & C negative. No significant coefficients ( $P$ 's > 0.3)                   |
| <i>Hymenoxys (Helenium) hoopesii</i>       | 1369                      | 100                       | B & C negative. No significant coefficients ( $P$ 's > 0.02)                  |
| <i>Helianthella quinquenervis</i>          | 1168                      | 449                       | B & C negative. No significant coefficients ( $P$ 's > 0.3)                   |
| <i>Mertensia ciliata</i>                   | 891                       | 67                        | B & C positive. $C = 0.012$ (SE = 0.004, $P = 0.003$ )                        |
| <i>Chamerion (Epilobium) angustifolium</i> | 853                       | 224                       | B & C positive. No significant coefficients ( $P$ 's > 0.5)                   |
| <i>Aconitum columbianum</i>                | 776                       | 154                       | B & C negative. No coefficients significant ( $P$ 's > 0.2)                   |
| <i>Senecio triangularis</i>                | 695                       | 17                        | B & C negative. No significant coefficients ( $P$ 's > 0.5)                   |
| <i>Senecio bigelovii</i>                   | 605                       | 107                       | B & C negative. No significant coefficients ( $P$ 's > 0.1)                   |
| <i>Senecio crassulus</i>                   | 582                       | 28                        | B & C positive. No significant coefficients ( $P$ 's > 0.05)                  |
| <i>Viguiera multiflora</i>                 | 499                       | 205                       | B & C negative. No significant coefficients ( $P$ 's > 0.4)                   |
| <i>Phacelia leucophylla</i>                | 359                       | 58                        | B & C negative. No significant coefficients ( $P$ 's > 0.04)                  |
| <i>Castilleja sulphurea</i>                | 161                       | 37                        | B & C positive. No significant coefficients ( $P$ 's > 0.04)                  |
| Total these species                        | 10880 (74.5%)             | 2246 (74.5%)              |                                                                               |
| Total all species                          | 14595                     | 3013                      |                                                                               |

appear bell-shaped, increasing roughly exponentially until reaching maximum levels before declining, rapidly at first, then more slowly (Figs. 2 and 3). On the other hand, phenology in terms of number of plant species in flower (hereafter referred to as community flowering phenology) is generally shaped like an upturned U (Figs. 2 and 3). For both bumble bees and flowering, the dates of the peaks then provide comparative measures of their phenologies across elevation region and year. In the case of bumble bees, we considered queens and workers separately, as they have quite different phenologies, but combined species because earlier analysis had indicated that there are no phenological differences between species in our study area (Pyke et al. 2011). Because our surveys in 2007 ended seasonally earlier than in 1974, we were unable to consider male bumble bees. We focused on plant species used as sources of floral resources by bumble bees.

We estimated dates of peak bumble bee recording rate and peak number of plant species in

flower by assuming that the seasonal patterns of these recording rates are Gaussian and Quadratic functions of date period respectively, where the date of the peak is an unknown parameter. Hence, our models were of the forms  $BRR = A \cdot \exp(-[P-C]^2/B)$  and  $NPF = A + B \cdot (P-C)^2$  respectively, where BRR is bumble bee recording rate, NPF is number of plant species in flower, P is date period, A-C are all unknown, and C is the date of the peak. We considered the possibilities that bumble bee recording rates and numbers of plant species in flower may have varied with Elevation Region (R) and Year, and their interaction, by allowing the unknowns to be functions of  $R^i, Y$  and  $R^i Y$  [ $i, j = 1, 2$ ], where Y equals Year/1000. The coefficients of these parameters, with associated standard errors, were estimated using nonlinear regression.

#### *Allowance for differences in bumble bee phenology between regions and years*

As bumble bee phenology varied with elevation region and year, comparisons of bumble

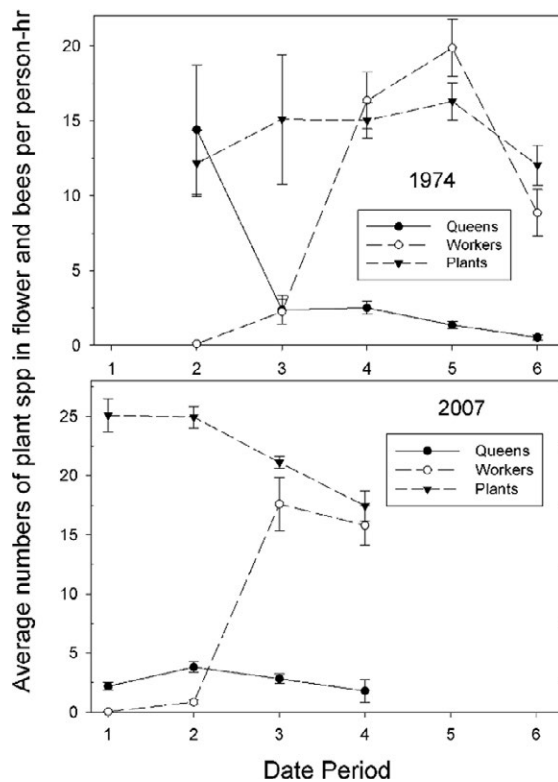


Fig. 2. Average numbers of plant species in flower and bumble bees recorded per person hour vs. time period for transect surveys carried out in 1974 and 2007.

bee abundance between elevation regions and years were based on the date periods for each region and year when maximum abundances were observed (Pyke et al. 2011). If, for example, a particular bumble bee species reached peak worker abundance at relatively low elevations during the second half of July, but did not reach peak worker abundance at higher elevations until later, then an analysis of the distribution of this bumble bee based on the second half of July would be biased toward the lower elevations. The same problem applies to comparing years if there are similar differences in phenology between years. It is therefore necessary to make phenological restrictions such that recording rates are maximal before comparing bumblebee recording rates across regions and years.

However, rather than making separate phenological restrictions for each combination of year

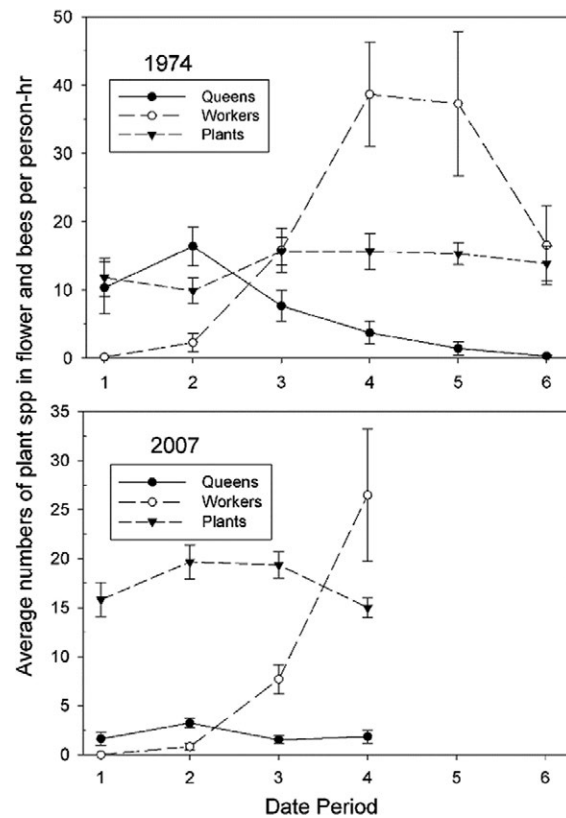


Fig. 3. Average numbers of plant species in flower and bumble bees recorded per person hour vs. time period for circle surveys within regions 4–5 and carried out in 1974 and 2007.

and elevation region, we simplified the process through adoption of a relatively small number of year/region/date period combinations (see Appendix Section A1 for explanation and Table A1-2 for results). In addition, we separately considered spring queens and workers, but combined all bumble bee species, excluding the cuckoo bumble bees (see Appendix: Section A2).

#### *Elevational distributions of bumble bees and plants*

We assumed that recording rates for bumble bee workers (after phenological adjustment as described above) varied with elevation region in a Gaussian manner, while allowing for observed elevations to cover only part of such a distribution. Hence, we included those bumble bee observations that satisfied the identified phenological constraints (see Appendix: Table A1-2) and modelled bumble bee recording

rate (BRR) as  $BRR = A \cdot \exp(-[R-C]^2/B)$  where  $R$  is elevation region,  $A$ - $C$  are all unknown but  $B$  is assumed to be positive, and  $C$  is the region of peak recording rate. We considered the possibility that bumble bee recording rates, and hence dates of peak recording rate, may have varied with Year, by allowing the unknowns to be functions of  $Y$ , where  $Y$  equals Year/1000. The coefficients of these parameters, with associated standard errors, were estimated using Non-linear Regression.

For queen bumble bees, we characterized elevational distributions on the basis of weighted averages of recorded elevations, because sample sizes were small and it was generally impossible to estimate the parameters in the above model. Assuming that bumble bee abundance is proportional to bumble bee recording rate and again applying appropriate phenological constraints (see Appendix Table A1-2), we calculated average elevations from distributions of survey elevations weighted by numbers of bees per person hour across the identified date periods for each elevation region. For completeness, we carried out the same analyses for workers.

We assumed that elevational distributions of plants could be described by observed relationships between elevation region and proportion of sites for which particular plant species were recorded as present (e.g., Fig. 1).

### Testing hypotheses

Testing hypotheses was then a relatively straightforward matter of comparing elevational and phenological patterns between years, comparing bumble bee and plant flowering phenologies for each year, and assessing possible differences in bumble bee abundance between years (see Appendix Section A2 for further details). We used the General Linear Model (GLM) approach whenever possible, incorporating non-linear effects through inclusion of quadratic and cubic terms as well as linear terms; when this was not possible we used nonlinear regression. We adopted a forward stepwise approach, assumed that survey visits to the same site could be considered independent of each other, and employed an adjusted threshold  $P$ -value of 0.01 for significance at each test (see Appendix Section A2). All analyses were carried out using the software package SYSTAT (Wilkinson 1990).

## RESULTS

### Testing Hypothesis 1a: Upward shifts in bumble bee distributions

For worker bumble bees, differences between 1974 and 2007 in elevation regions with peak recording rates were partially consistent with expected upward shifts of 317 m. For four bumble bee species (i.e., *B. bifarius*, *B. frigidus*, *B. mixtus*, and *B. occidentalis*), there were, as expected, significant upward shifts that were not significantly different from 317 m (i.e.,  $C_1$  significantly positive in assumed Gaussian distribution of recording rate with elevation region; estimates of elevational shift not significantly different from 317 m; Table 2; e.g., Fig. 4 for *B. bifarius*). Results were equivocal for two species (i.e., *B. balteatus*, *B. sylvicola*), in that differences between the 2 yr in elevation with peak recording rates were not significantly different from either zero or an upward shift of 317 m (Table 2). Two species (*B. appositus*, *B. flavifrons*), contrary to expectation, exhibited elevational shifts that were not significantly different from zero, but significantly different from upward shifts of 317 m (Table 2; e.g., Fig. 5 for *B. flavifrons*). As expected, no species declined significantly in elevation with peak recording rate and no species exhibited an upward shift in elevation greater than 317 m (Table 2).

For queen bumble bees, the only result was contrary to expectations and queens reached peak recording rate at a higher elevation than workers. For queens of *B. flavifrons*, the observed difference between years in elevation region with peak recording rate was not significantly different from zero but significantly different from an upward shift of 317 m (Table 2). For queens of the other bumble bee species, sample sizes were small and estimation of model parameters did not converge, and so these cases are omitted from Table 2. The elevation region where queens exhibited peak recording rate was significantly higher for queens than for workers (Table 2; difference = 0.75 regions = 114 m; SE = 33 m,  $t = 3.45$ ,  $P = 0.001$ ).

For queen bumble bees, considering each species separately, differences between 1974 and 2007 in weighted average elevations were partially consistent with expected upward shifts

Table 2. Testing for shifts in elevation and abundance for workers of common bumble bee species, assuming Gaussian distributions of bumble bee recording rate with elevation region. Model was  $BRR = A \cdot \exp(-[R-C]^2/B)$  where BRR is bumble bee recording rate, R is elevation region, and A-C are linear functions of Y (= Year/1000) with unknown coefficients (e.g.  $A = A_0 + A_1 \cdot Y$  where  $A_1$  are unknown). Estimates for  $A_0$  and  $B_0$  and are presented in all cases, as neither can be zero in the model;  $C_1$  is also always presented, as it is parameter of particular interest; other parameter values are presented only when significant. Important and significant results have \* and are in bold. *B. mixtus* was absent below region 3. Threshold P for significance is 0.01.

| Caste and<br>Bumble bee<br>species | Parameter                   | Estimate     | SE           | t            | P                 | Change in elevation |           | Comparison with upward<br>shift of 317 m |             |                   |
|------------------------------------|-----------------------------|--------------|--------------|--------------|-------------------|---------------------|-----------|------------------------------------------|-------------|-------------------|
|                                    |                             |              |              |              |                   | No.<br>regions      | m†        | Difference<br>(m)                        | t           | P                 |
| Workers                            |                             |              |              |              |                   |                     |           |                                          |             |                   |
| <i>B. bifarius</i>                 | A <sub>0</sub>              | 9.23         | 1.14         | 8.07         | <0.001‡           | +2.214              | 337 ± 85  | 20                                       | 0.24        | 0.4               |
|                                    | B <sub>0</sub>              | 4.41         | 1.50         | 2.94         | <0.001‡           |                     |           |                                          |             |                   |
|                                    | C <sub>0</sub>              | -130.9       | 33.7         | -3.88        | <0.001            |                     |           |                                          |             |                   |
|                                    | C <sub>1</sub>              | <b>67.1</b>  | <b>16.9</b>  | <b>3.96</b>  | <b>&lt;0.001*</b> |                     |           |                                          |             |                   |
| <i>B. frigidus</i>                 | A <sub>0</sub>              | 2.67         | 0.36         | 7.35         | <0.001‡           | +4.788              | 730 ± 260 | 413                                      | 1.59        | 0.06              |
|                                    | B <sub>0</sub>              | 13.04        | 7.94         | 1.64         | 0.05†             |                     |           |                                          |             |                   |
|                                    | C <sub>0</sub>              | -281.6       | 100.2        | -2.81        | 0.003             |                     |           |                                          |             |                   |
|                                    | C <sub>1</sub>              | <b>145.1</b> | <b>50.7</b>  | <b>2.86</b>  | <b>0.003</b>      |                     |           |                                          |             |                   |
| <i>B. mixtus</i><br>(R ≥ 3)        | A <sub>0</sub>              | 2.64         | 1.15         | 2.30         | 0.01‡             | +4.877              | 743 ± 280 | 426                                      | 1.52        | 0.07              |
|                                    | B <sub>0</sub>              | 21.7         | 32.2         | 0.68         | 0.25‡             |                     |           |                                          |             |                   |
|                                    | C <sub>0</sub>              | -294.8       | 113.9        | -2.59        | 0.01              |                     |           |                                          |             |                   |
|                                    | C <sub>1</sub>              | <b>147.8</b> | <b>55.7</b>  | <b>2.66</b>  | <b>0.01*</b>      |                     |           |                                          |             |                   |
| <i>B. occidentalis</i>             | A <sub>0</sub>              | 2.1          | 0.35         | 5.94         | <0.001            | +1.168              | 178 ± 62  | 139                                      | 2.24        | 0.02              |
|                                    | B <sub>0</sub>              | 1.19         | 0.68         | 1.76         | 0.25‡             |                     |           |                                          |             |                   |
|                                    | C <sub>0</sub>              | 67.61        | 24.4         | -2.77        | 0.007             |                     |           |                                          |             |                   |
|                                    | C <sub>1</sub>              | <b>35.39</b> | <b>12.28</b> | <b>2.88</b>  | <b>0.005*</b>     |                     |           |                                          |             |                   |
| <i>B. appositus</i>                | A <sub>0</sub>              | 8.31         | 1.74         | 4.79         | <0.001            | -0.053              | 8 ± 45    | <b>-325</b>                              | <b>7.22</b> | <b>&lt;0.001*</b> |
|                                    | B <sub>0</sub>              | 10.79        | 3.55         | 3.04         | 0.003             |                     |           |                                          |             |                   |
|                                    | C <sub>1</sub> (when added) | -1.60        | 9.01         | -0.18        | 0.86              |                     |           |                                          |             |                   |
| <i>B. balteatus</i>                | A <sub>0</sub>              | 5.06         | 0.96         | 5.27         | <0.001            | +2.947              | 448 ± 239 | 131                                      | 0.55        | 0.3               |
|                                    | B <sub>0</sub>              | 11.42        | 7.01         | 1.63         | 0.05‡             |                     |           |                                          |             |                   |
|                                    | C <sub>0</sub>              | 7.36         | 1.15         | 6.41         | <0.001            |                     |           |                                          |             |                   |
|                                    | C <sub>1</sub> (when added) | 89.31        | 47.62        | 1.88         | 0.06              |                     |           |                                          |             |                   |
| <i>B. flavifrons</i>               | A <sub>0</sub>              | 12.67        | 1.40         | 9.05         | <0.001            | +0.59               | 90 ± 66   | <b>227</b>                               | <b>3.44</b> | <b>0.001*</b>     |
|                                    | B <sub>0</sub>              | 4.16         | 1.16         | 3.57         | <0.001‡           |                     |           |                                          |             |                   |
|                                    | C <sub>0</sub>              | 4.01         | 0.15         | 26.0         | <0.001            |                     |           |                                          |             |                   |
|                                    | C <sub>1</sub> (when added) | 18.01        | 13.11        | 1.37         | 0.17              |                     |           |                                          |             |                   |
| <i>B. sylvicola</i>                | A <sub>0</sub>              | 3.66         | 0.68         | 5.37         | <0.001            | +1.20               | 182 ± 116 | 135                                      | 1.16        | 0.1               |
|                                    | B <sub>0</sub>              | 16.8         | 8.58         | 1.96         | 0.03              |                     |           |                                          |             |                   |
|                                    | C <sub>1</sub> (when added) | 36.31        | 22.96        | 1.58         | 0.12              |                     |           |                                          |             |                   |
| Queens                             |                             |              |              |              |                   |                     |           |                                          |             |                   |
| <i>B. flavifrons</i>               | A <sub>0</sub>              | 699.3        | 86.9         | 8.05         | <0.001            | +0.27               | 41 ± 121  | 276                                      | 2.28        | 0.02              |
|                                    | <b>A<sub>1</sub></b>        | <b>347.8</b> | <b>43.4</b>  | <b>-8.01</b> | <b>&lt;0.001*</b> |                     |           |                                          |             |                   |
|                                    | B <sub>0</sub>              | 1.79         | 0.50         | 3.61         | <0.001            |                     |           |                                          |             |                   |
|                                    | C <sub>0</sub>              | 4.91         | 0.16         | 30.83        | <0.001            |                     |           |                                          |             |                   |
|                                    | C <sub>1</sub> (when added) | 8.10         | 24.04        | 0.34         | 0.7               |                     |           |                                          |             |                   |

† Values are mean ± SE.

‡ One-tailed.

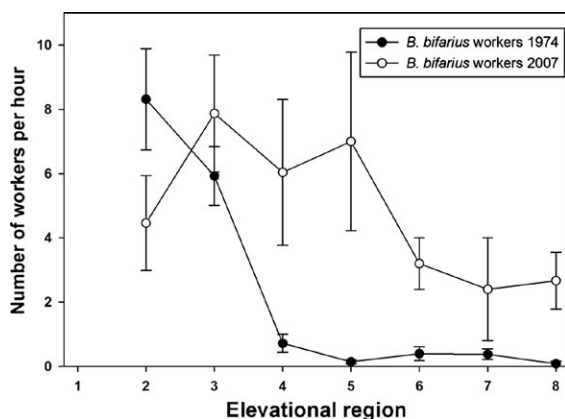


Fig. 4. Average recording rate for *B. bifarius* workers vs. Elevation region for 1974 and 2007.

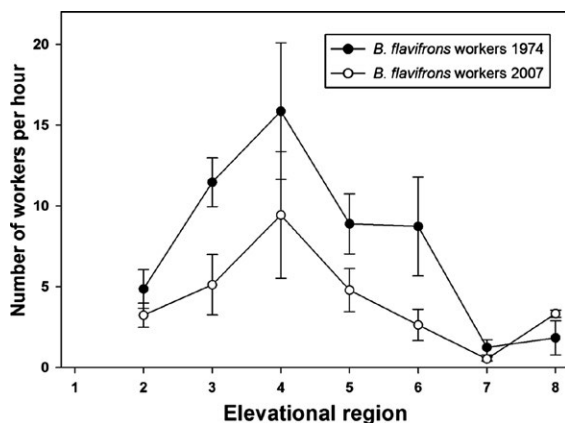


Fig. 5. Average recording rate for *B. flavifrons* workers vs. Elevation region for 1974 and 2007.

of 317 m. Four species (*B. balteatus*, *B. bifarius*, *B. frigidus*, *B. silvicola*) exhibited significant upward shifts in weighted average elevation that did not differ significantly from expected shift of 317 m (Table 3). One species (*B. appositus*) shifted upwards, but by significantly less than 317 m (Table 3). Results were equivocal for *B. occidentalis* as it exhibited a difference between years in weighted average elevation that did not differ significantly from either zero or 317 m (Table 3). Contrary to expectation, observed differences between years in weighted average elevation for two species (*B. flavifrons*, *B. mixtus*) were not significantly different from zero, and significantly less than 317 m (Table 3). As expected, no species

declined significantly in weighted average elevation and no species exhibited an upward shift in average elevation greater than 317 m (Table 3).

When bumble bees species were considered together, results were consistent with an upward shift of 317 m for queen bumble bees. Between 1974 and 2007, the weighted average elevation for queens of the eight most common bumble bees, when considered together for region 3 and above, shifted significantly upwards by a combined average of 244 m, which is significantly greater than zero and not significantly different from 317 m (Table 3). Across the species there was a consistent increase in average elevation (Table 3), a result that departs significantly from what would be expected if positive and negative changes in elevation were equally likely ( $P = 0.004$ , Binomial Test).

For worker bumble bees, differences between 1974 and 2007 in weighted average elevation were either equivocal or contrary to expectations. No species exhibited a significant difference in weighted average elevation between the 2 yr (Table 4) and there was no consistent pattern (Table 4; 5 upward differences, 3 downward,  $P = 0.73$ , Binomial test). For four species (*B. bifarius*, *B. frigidus*, *M. mixtus*, *B. silvicola*) the observed difference between years was not significantly different from either zero or 317 m, an equivocal result (Table 4). Contrary to expectation, the observed difference in weighted average elevation was significantly less than 317 m for the remaining four species (*B. appositus*, *B. flavifrons*, *B. balteatus*, *B. occidentalis*). Averaging across all species, there was an elevational increase of 65 m which, contrary to expectation, is not significantly different from zero, but significantly less than 317 m (Table 4).

#### Testing Hypothesis 1b: Upward shifts in plant distributions

*Delphinium barbeyi*, upon which bumble bees were most commonly recorded in both 1974 and 2007 (Table 1), showed no change in elevation distribution between the 2 yr. In both years, this plant species was not recorded within the lowest elevation region but was near ubiquitous at higher elevations (Fig. 1). There was no significant elevation shift (Fig. 1; coefficients of  $R$  and  $R^2$  [B, C in model] not significant; GLM,  $P$ 's > 0.3).

Table 3. Mean weighted elevations in each year, change in mean weighted elevation between years, for queens of each bumble bee species. Significant results are in bold and have \*. Threshold for significance is  $P = 0.01$ .

| Bumble bee species     | Mean elevation – 1974 (m)† | Mean elevation – 2007 (m)† | Change in elevation between 1974 and 2007 |             |                   | Comparison between elevation change and increase of 317 m |             |                   |
|------------------------|----------------------------|----------------------------|-------------------------------------------|-------------|-------------------|-----------------------------------------------------------|-------------|-------------------|
|                        |                            |                            | Change (m)†                               | t           | P                 | Difference (m)†                                           | t           | P                 |
| <i>B. appositus</i>    | 2966 ± 27                  | 3118 ± 42                  | <b>+152 ± 50</b>                          | <b>3.04</b> | <b>0.003*</b>     | <b>–165</b>                                               | <b>3.30</b> | <b>0.001*</b>     |
| <i>B. bifarius</i>     | 2970 ± 71                  | 3345 ± 69                  | <b>+375 ± 99</b>                          | <b>3.79</b> | <b>0.001*</b>     | 58                                                        | 0.59        | 0.6               |
| <i>B. flavifrons</i>   | 3121 ± 45                  | 3207 ± 27                  | +86 ± 52                                  | 1.65        | 0.1               | <b>–231</b>                                               | <b>4.44</b> | <b>0.001*</b>     |
| <i>B. frigidus</i>     | 3053 ± 39                  | 3483 ± 51                  | <b>+430 ± 83*</b>                         | <b>5.18</b> | <b>&lt;0.001*</b> | 113                                                       | 1.36        | 0.2               |
| <i>B. balteatus</i>    | 3179 ± 57                  | 3433 ± 42                  | <b>+254 ± 71*</b>                         | <b>3.58</b> | <b>0.001*</b>     | –63                                                       | 0.89        | 0.4               |
| <i>B. mixtus</i>       | 3156 ± 36                  | 3229 ± 58                  | +73 ± 68                                  | 1.07        | 0.3               | <b>–244</b>                                               | <b>3.59</b> | <b>&lt;0.001*</b> |
| <i>B. occidentalis</i> | 2924 ± 16                  | 3186 ± 171                 | +262 ± 172                                | 1.52        | 0.2               | –55                                                       | 0.32        | 0.7               |
| <i>B. sylvicola</i>    | 3165 ± 47                  | 3484 ± 32                  | <b>+319 ± 57</b>                          | <b>5.60</b> | <b>&lt;0.001*</b> | 2                                                         | 0.04        | 0.97              |
| Combined               |                            |                            | <b>+244 ± 32</b>                          | <b>7.63</b> | <b>&lt;0.001*</b> | –73                                                       | 2.28        | 0.03              |

† Values are mean ± SE.

Table 4. Mean weighted elevations in each year, change in mean weighted elevation between years, for workers of each bumble bee species. Significant results are in bold and have\*. Threshold for significance is  $P = 0.01$ .

| Bumble bee species     | Mean elevation – 1974 (m)† | Mean elevation – 2007 (m)† | Change in elevation between 1974 and 2007 |      |      | Comparison between elevation change and increase of 317 m |             |                   |
|------------------------|----------------------------|----------------------------|-------------------------------------------|------|------|-----------------------------------------------------------|-------------|-------------------|
|                        |                            |                            | Change (m)†                               | t    | P    | Difference (m)†                                           | t           | P                 |
| <i>B. appositus</i>    | 2980 ± 33                  | 2907 ± 58                  | –73 ± 67                                  | 1.09 | 0.3  | <b>–390</b>                                               | <b>5.82</b> | <b>&lt;0.001*</b> |
| <i>B. bifarius</i>     | 2917 ± 27                  | 2997 ± 97                  | +80 ± 101                                 | 1.26 | 0.2  | –237                                                      | 2.35        | 0.02              |
| <i>B. flavifrons</i>   | 3083 ± 56                  | 3022 ± 82                  | –61 ± 99                                  | 0.62 | 0.5  | <b>–378</b>                                               | <b>3.82</b> | <b>&lt;0.001*</b> |
| <i>B. frigidus</i>     | 3144 ± 45                  | 3419 ± 106                 | +275 ± 115                                | 2.39 | 0.02 | –42                                                       | 0.37        | 0.7               |
| <i>B. balteatus</i>    | 3342 ± 59                  | 3310 ± 107                 | –32 ± 122                                 | 0.26 | 0.8  | <b>–339</b>                                               | <b>2.78</b> | <b>0.006*</b>     |
| <i>B. mixtus</i>       | 2994 ± 48                  | 3134 ± 85                  | +140 ± 98                                 | 0.70 | 0.5  | –177                                                      | 1.81        | 0.07              |
| <i>B. occidentalis</i> | 2927 ± 28                  | 2946 ± 45                  | +19 ± 53                                  | 0.36 | 0.7  | <b>298</b>                                                | <b>5.62</b> | <b>&lt;0.001*</b> |
| <i>B. sylvicola</i>    | 3235 ± 48                  | 3410 ± 103                 | +175 ± 132                                | 1.33 | 0.2  | –142                                                      | 1.08        | 0.3               |
| Combined               |                            |                            | +65 ± 48                                  | 1.35 | 0.2  | –252                                                      | 5.25        | <0.001            |

† Values are mean ± SE.

For the other 11 focal plant species, just one showed significant upwards change in distribution between 1974 and 2007, and there was no indication of the expected general increase in elevation between the 2 yr. *Mertensia ciliata* shifted upwards in distribution between 1974 and 2007 (Table 1; coefficient of  $R^2$  [C in model] = 0.012 with SE = 0.004,  $P = 0.003$ ,  $n = 47$ ). No other plant species changed significantly in overall abundance or elevation distribution (Table 1; GLM,  $P$ 's > 0.01). Across the 12 plant species, the observed relationships between presence change and elevation region were positive in four cases and negative in the remaining eight, which does

not deviate significantly from an equal prevalence of both (Table 1;  $P = 0.39$ , Binomial Test).

#### Testing Hypothesis 2a: Bumble bee phenology shifted earlier

Phenological differences in bumble bees between 1974 and 2007 were partially consistent with expectations. Bumble bee workers, surveyed along transect sites, exhibited a significant forward shift in date of peak recording rate between 1974 and 2007, estimated at 17 d (Table 5, Fig. 2). However, differences in phenology between the 2 yr were not significant for workers surveyed across circle sites, nor

for queens across any of the sites (Table 5; Figs. 2 and 3).

Dates of peak recording rate varied with elevation and caste. Peak recording rates for bumble bee workers occurred about 2 weeks earlier in Regions 2–3 than in the higher regions (i.e., 16 d,  $P < 0.01$ ,  $t$ -test; Table 5). A similar trend was observed for queens, but it was not significant (i.e., 12 d,  $P > 0.01$ ,  $t$ -test; Table 5). Peak abundance of queen bumble bees generally occurred about 5–6 weeks before that of workers (Table 5).

#### ***Testing Hypothesis 2b: Flowering phenology shifted earlier***

Consistent with expectations, plant community flowering phenology, based on the number of plant species in flower, was significantly earlier in 2007 compared with 1974, for all but the lowest circle sites. The date of peak community flowering is estimated by  $C$  in the model  $NPF = A + B(P-C)^2$  and  $C$  was found to decrease significantly with increasing year for both the transect sites, which occur in regions 3–8, and circle sites in regions 3–5 (i.e., coefficient  $C_1$  significantly negative in expanded model for both sets of sites; Figs. 2 and 3; Table 6). Hence, for these sites, the estimated dates of peak community flowering were earlier for 2007 than for 1974. Interestingly, the peak number of plant species in flower per site per survey was significantly higher in 2007 than in 1974 (i.e., coefficient  $A_1$  in expanded model significantly positive for both sets of sites; Table 6). On the other hand, for circle sites in region 2, year had no significant effect on either the date when peak community flowering occurred or peak number of plant species in flower (i.e., none of coefficients of  $Y$  were significant in expanded model; Table 6).

#### ***Testing Hypothesis 2c: Lost synchrony between bumble bee and flowering phenologies***

For all but the lowest sites, we found the expected reduction in synchrony between bumble bee phenology and community flowering, with the community flowering phenology shifted earlier in 2007 *relative* to bumble bee phenology. For transect sites, both bumble bee and community flowering phenologies were

shifted earlier in 2007 as compared with 1974 (Tables 5 and 6), but the shift was significantly greater for flowering than for bumble bees (i.e., flowering: 47 d, SE = 10 d; bumble bees: 16 d, SE = 2 d;  $P = 0.003$ ; see Tables 5 and 6). For circle sites in regions 3–5, peak community flowering occurred significantly earlier in 2007 in comparison with 1974 (Table 6), while there was no significant difference in dates of peak recording rate of bumble bee workers (Table 5). For circle sites in region 2, there were no significant differences between the 2 yr for either bumble bee or community flowering phenology (Tables 5 and 6), and hence no significant reduction in synchrony.

However, our results provided no significant evidence in support of the narrower hypothesis that phenologies of community flowering and bumble bees coincided seasonally in 1974, but not in 2007. Except for circle sites in regions 4–5, there were no significant differences in phenology within each year between community flowering and bumble bees (Table 7). Contrary to expectations, peak community flowering occurred significantly earlier than peak bumble bee recording rate in 1974 for circle sites in regions 4–5 (Table 7).

#### ***Testing hypothesis 3: Lower bumble bee abundance in 2007 compared with 1974***

Bumble bee abundance was generally lower in 2007 than in 1974, especially at relatively low elevation. After allowing for possible differences in phenology between years, the average recording rates for queens were significantly lower in 2007, compared with 1974, for both transect and circle surveys, and across all regions (Table 5). For workers, recording rates were significantly lower in 2007 for the circle surveys within regions 2–3, but otherwise observed differences between the 2 yr were not significant (Table 5).

However, such differences between years in abundance of bumble bees were not generally apparent when species were considered separately. For workers, when recording rates were modelled as Gaussian functions of region for each species, there were no significant effects of year (Table 2). For queens, it was possible to apply this approach to just one species, *B. flavifrons*, and it exhibited the expected lower abundance in

Table 5. Bumble bee phenology in 2007 versus 1974 (Model:  $BRR = A \cdot \exp(-[P-C]^2/B)$  where BRR is bumblebee recording rate in bees per person hour, P is date period and A-C are unknown functions of the form  $A_0 + A_1Y + A_2R^i + A_3R^jY$  [i, j = 1,2] where Y = Year/1000, R = Elevational Region and coefficients are all unknown parameters). Unknowns in model were estimated using nonlinear regression. Threshold for significance is  $P = 0.01$ . "Est" is estimate.

| Survey type,<br>elev. regions,<br>caste | Parameter      | Est   | SE   | P      | n   | 1974 vs.<br>2007  | Peak                          |                 |                 | Shift<br>– days† |
|-----------------------------------------|----------------|-------|------|--------|-----|-------------------|-------------------------------|-----------------|-----------------|------------------|
|                                         |                |       |      |        |     |                   | Years<br>combined<br>P, date† | 1974<br>P, date | 2007<br>P, date |                  |
| Transect                                |                |       |      |        |     |                   |                               |                 |                 |                  |
| 3–8                                     |                |       |      |        |     |                   |                               |                 |                 |                  |
| Workers                                 | A <sub>0</sub> | 21.6  | 1.4  | <0.001 | 284 |                   |                               | 4.71<br>19 Aug  | 3.64<br>2 Aug   | –17 ± 2          |
|                                         | B <sub>0</sub> | 1.53  | 0.30 | <0.001 |     |                   |                               |                 |                 |                  |
|                                         | C <sub>0</sub> | 68.4  | 8.7  | <0.001 |     |                   |                               |                 |                 |                  |
|                                         | C <sub>1</sub> | –32.3 | 4.4  | <0.001 |     |                   |                               |                 |                 |                  |
| Queens                                  | A <sub>0</sub> | 545   | 91   | <0.001 | 284 | Higher in<br>1974 | 1.59<br>2 Jul ± 5             |                 |                 |                  |
|                                         | A <sub>1</sub> | –270  | 45   | <0.001 |     |                   |                               |                 |                 |                  |
|                                         | B <sub>0</sub> | 3.37  | 0.87 | <0.001 |     |                   |                               |                 |                 |                  |
|                                         | C <sub>0</sub> | 1.59  | 0.31 | <0.001 |     |                   |                               |                 |                 |                  |
| Circles                                 |                |       |      |        |     |                   |                               |                 |                 |                  |
| 4–5                                     |                |       |      |        |     |                   |                               |                 |                 |                  |
| Workers                                 | A <sub>0</sub> | 40    | 3.57 | <0.001 | 114 |                   | 4.62<br>18 Aug ± 2            |                 |                 |                  |
|                                         | B <sub>0</sub> | 2.14  | 0.40 | <0.001 |     |                   |                               |                 |                 |                  |
|                                         | C <sub>0</sub> | 4.62  | 0.11 | <0.001 |     |                   |                               |                 |                 |                  |
| Queens                                  | A <sub>0</sub> | 800   | 114  | <0.001 | 114 | Higher in<br>1974 | 1.87<br>4 Jul ± 3             |                 |                 |                  |
|                                         | A <sub>1</sub> | –397  | 57   | <0.001 |     |                   |                               |                 |                 |                  |
|                                         | B <sub>0</sub> | 1.92  | 0.65 | <0.01  |     |                   |                               |                 |                 |                  |
|                                         | C <sub>0</sub> | 1.87  | 0.18 | <0.001 |     |                   |                               |                 |                 |                  |
| 2–3                                     |                |       |      |        |     |                   |                               |                 |                 |                  |
| Workers                                 | A <sub>0</sub> | 1132  | 160  | <0.001 | 247 | Higher in<br>1974 | 3.58<br>2 Aug ± 1             |                 |                 |                  |
|                                         | A <sub>1</sub> | –557  | 80   | <0.001 |     |                   |                               |                 |                 |                  |
|                                         | B <sub>0</sub> | 2.53  | 0.43 | <0.001 |     |                   |                               |                 |                 |                  |
|                                         | C <sub>0</sub> | –3.58 | 0.09 | <0.001 |     |                   |                               |                 |                 |                  |
| Queens                                  | A <sub>0</sub> | 427   | 51   | <0.001 | 247 | Higher in<br>1974 | 0.96<br>22 Jun ± 5            |                 |                 |                  |
|                                         | A <sub>1</sub> | –211  | 26   | <0.001 |     |                   |                               |                 |                 |                  |
|                                         | B <sub>0</sub> | 3.34  | 1.22 | <0.01  |     |                   |                               |                 |                 |                  |
|                                         | C <sub>0</sub> | 0.96  | 0.35 | <0.01  |     |                   |                               |                 |                 |                  |

† Values are mean ± SE (days).

2007 compared with 1974 (Table 2;  $A_1$  significantly negative in model).

## DISCUSSION

### *Climate change vs. variability in weather*

Although we have only 2 yr of observations, there is good reason to believe that observed changes are more likely caused by climatic change than by short-term variability in weather.

In our study area, based on essentially continuous weather records, there is significant climatic variation among years in winter snowfall, spring air temperature, snowmelt, summer air temperature, and summer precipitation, and this variation significantly affects plant and animal phenologies (Inouye 2008, Miller-Rushing and Inouye 2009, Lambert et al. 2010). However, the spatial distributions of plants, which provide significant floral resources to

Table 6. Flowering phenology in 2007 vs. 1974 (Model:  $NPF = A + B*(P-C)^2$  where NPF is # plant species in flower, P is date period, and A–C are unknown functions of the form  $A_0 + A_1Y + A_{2i}R^i + A_{3j}R^jY$  [ $i, j = 1, 2$ ] where  $Y = \text{Year}/1000$ ,  $R = \text{Elevational Region}$  and coefficients are all unknown parameters). Unknowns in model were estimated using nonlinear regression. Threshold for significance is  $P = 0.01$ .

| Survey type | Elev. regions | Parameters of interest, if significant |          |      |        | Other parameters, if significant |          |      |        |
|-------------|---------------|----------------------------------------|----------|------|--------|----------------------------------|----------|------|--------|
|             |               | Parameter                              | Estimate | SE   | P      | Parameter                        | Estimate | SE   | P      |
| Transect    | 3–8           | $A_1$                                  | 287      | 47   | <0.001 | $A_0$                            | –550     | 93   | <0.001 |
|             |               | $C_1$                                  | –95.4    | 20.3 | <0.001 | $B_0$                            | –0.94    | 0.35 | 0.007  |
|             |               |                                        |          |      |        | $C_0$                            | 192      | 40   | <0.001 |
| Circles     | 3–5           | $A_1$                                  | 107      | 27   | <0.001 | $A_0$                            | –195     | 54   | <0.001 |
|             |               | $C_1$                                  | –41      | 12   | <0.001 | $B_0$                            | –1.03    | 0.22 | <0.001 |
|             |               |                                        |          |      |        | $C_0$                            | 86       | 23   | <0.001 |
| Circles     | 2             |                                        |          |      |        | $A_0$                            | 17       | 0.7  | <0.001 |
|             |               |                                        |          |      |        | $B_0$                            | –1.16    | 0.26 | <0.001 |
|             |               |                                        |          |      |        | $C_0$                            | 2.90     | 0.17 | <0.001 |

Table 7. Comparisons of bumble bee and flowering phenologies (in bold and with \*Significant; threshold for significance is  $P = 0.01$ ). B74 and F74 are dates of peak bumble bee recording rate and peak community flowering for 1974; B07 and F07 are same for 2007.

| Survey type and elev. regions | Bumble bee peak 1974 | Flower peak 1974   | B74-F74                           | Bumble bee peak 2007 | Flower peak 2007    | B07-F07            | B07-B74            | F07-F74                                |
|-------------------------------|----------------------|--------------------|-----------------------------------|----------------------|---------------------|--------------------|--------------------|----------------------------------------|
|                               | Date†                | Date†              | Days‡                             | Date†                | Date†               | Days‡              | Days‡              | Days‡                                  |
| Transect                      |                      |                    |                                   |                      |                     |                    |                    |                                        |
| 3–8                           | 19Aug ± 1.5<br>169   | 10Aug ± 5.1<br>173 | –9 ± 5.3<br>0.09                  | 27Jul ± 26.4<br>112  | 24Jun ± 11.5<br>124 | –34 ± 28.8<br>0.24 | –22 ± 26.4<br>0.41 | <b>–47 ± 12.6</b><br><b>&lt;0.001*</b> |
| Circle                        |                      |                    |                                   |                      |                     |                    |                    |                                        |
| 4–5                           | 16Aug ± 2.1<br>62    | 4Aug ± 3.2<br>164  | <b>–12 ± 3.8</b><br><b>0.002*</b> | 19Aug ± 35.4<br>49   | 14Jul ± 2.1<br>110  | –36 ± 35.5<br>0.31 | +3 ± 35.5<br>0.93  | <b>–21 ± 3.8</b><br><b>&lt;0.001*</b>  |
| 3                             | 2Aug ± 1.4<br>146    | 4Aug ± 3.2<br>164  | +2 ± 3.5<br>0.57                  | 19Aug ± 60.8<br>98   | 14Jul ± 2.1<br>110  | –36 ± 60.8<br>0.55 | +17 ± 60.8<br>0.78 |                                        |
| 2                             | 2Aug ± 1.4<br>146    | 24Jul ± 3.8<br>44  | –9 ± 4.1<br>0.03                  | 19Aug ± 60.8<br>98   | 18Jul ± 3.6<br>42   | –31 ± 60.8<br>0.61 |                    | –6 ± 5.3<br>0.26                       |

† Mean ± SE, with df below.

‡ Mean ± SE, with P below.

bumble bees, vary negligibly from 1 yr to the next, as they are all long-lived perennial species (see below). Furthermore, a survey that was carried out in part of our study area in 1975 indicated that the altitudinal distributions of bumble bee species were no different between 1974 and 1975 (Inouye 1976), although these 2 yr were climatically different (e.g., snowmelt was about 3 weeks later in 1975). Hence, differences in distribution for plants or bumble bees between widely separated survey years should indicate climate change rather than climatic variation. Finally, it would be expected that plants and bumble bees would have evolved

responses to background climatic variation such that their phenologies would correspond each year despite variation between years in their respective phenologies, so any temporal disconnect between plant and bumble bee phenologies is an expected consequence of climate change, but not of background climatic variation.

#### Shifts in elevation (Hypothesis 1)

Consistent with our hypothesis #1 and similar to what has been reported in many other studies (e.g., Roth et al. 2014), we found significant shifts between 1974 and 2007 toward higher

elevation for bumble bees. Queen bumble bees shifted toward higher elevations when all species are considered together, as did workers of most bumble bee species, and two plant species. No significant downward shifts were observed. Most bumble bee species exhibited a significant increase in elevation between 1974 and 2007 for queens, for queens or workers or both, manifest as an increase in either the elevation with peak recording rate (Table 2) or the weighted average elevation (Table 3). When bumble bee species were combined, an increase in elevation was evident for queens (Table 3). One of our focal plant species (i.e., *Mertensia ciliata*) exhibited an upwards shift in distribution (Table 1). There were no significant downward shifts in elevation by either bumble bees or plants.

Quantitatively, however, our results were mixed, as has been found in other similar studies (Hart et al. 2014). In some cases, our observed changes in elevation for bumble bees were consistent with an upward shift of 317 m, which is expected on the basis of the likely lapse rate for average temperature with elevation and observed temperature increase in our study area; in others, they were inconsistent with this expectation (Tables 2–4). For some bumble bee species in our study, there was apparently little to no change in elevation (e.g., *B. flavifrons*; Fig. 5, Tables 2–4).

#### *Shifts in phenology of bumble bees and community flowering (Hypotheses 2a and 2b)*

In our study, all significant changes in phenology between the 2 yr were toward earlier in the season, as predicted and in agreement with other studies (Inouye and Wielgolaski 2003), but while observed community flowering phenology generally shifted in this direction (Hypothesis 2b), bumble bee phenology generally showed no significant difference between the 2 yr (Hypothesis 2a). Plant community flowering phenology was significantly earlier in 2007 compared with 1974 for all surveys and regions except for circle surveys within region 2, the lowest region surveyed fully in both years, where there was no significant difference in community flowering phenology between years (Table 6). Although, we did not detect it, there was probably also a similar shift

in community flowering for this region, as observations in the flower plots, near the top of region 2, indicate that flowering phenologies advanced within this region for all wildflowers between 1974 and 2007 (Miller-Rushing and Inouye 2009, Lambert et al. 2010, Thomson 2010). A large number of studies now document the ongoing changes in phenology of plants, with almost all plant species at high altitudes demonstrating earlier flowering (Inouye and Wielgolaski 2003). Worker abundance peaked earlier in the 2007 season within the transect surveys, but there were otherwise no significant differences between years for both workers and queens (Table 5). There were no significant shifts toward later in the season.

#### *Bumble bee – Plant synchrony (Hypothesis 2c)*

Our results generally supported the expectation that synchrony between bumble bees and community flowering was reduced in 2007 compared with 1974, with a shift in community flowering toward being earlier *relative* to bumble bees, but we were not able to confirm the narrower hypothesis that bumble bee and community flowering phenologies coincided seasonally in 1974, but not in 2007 (Table 7). In retrospect, the latter result seems unsurprising as our 2007 surveys ended before recording rates for bumble bee workers had exhibited much decline, making it difficult to estimate accurately dates for peak recording rates (see Table 7).

That community flowering phenology peaked earlier than recording rate for bumble bee workers across circle sites in regions 4–5 suggests that further research is warranted in terms of bumble bee population dynamics and how, in particular, bumble bee biomass compares with available floral resources. Maximum bumble bee biomass may not coincide with maximum numbers of foraging workers, as bumble bee colonies will generally also contain developing larvae and nonforaging workers. Seasonal variation in bumble bee biomass is thus unclear.

#### *Effects of reduced seasonal synchrony on reproduction and abundance (Hypothesis 3)*

The generally lower recording rates for bumble bees in 2007 compared with 1974 are consistent with reduced seasonal synchrony

between bumble bees and community flowering leading to reduced bumble bee reproduction, and consequently to reduced bumble bee abundance. We observed both reduced seasonal synchrony between bumble bees and flowering and reduced bumble bee abundance. Reduced reproduction by bumble bees seems a likely intermediary step toward reduced abundance.

Phenological mismatch between plants and their pollinators can adversely impact plants as well as animals through its effects on pollinator visitation and consequent seed production. In our case, some early-flowering plant species could be suffering reduced seed set, as a result of climate change, because pollinator numbers are low then, and evidence suggests this may be occurring for one such plant species (*Erythronium grandiflorum*) near our study area (Thomson 2010). Similar results have been obtained in Japan, where a warm spring generated early flowering and a significant decline in pollination of an early-flowering plant (Kudo et al. 2004).

#### Future research

Our study suggests that future surveys of plants and their pollinators, whatever their motivation, should include estimates of density for both kinds of organism. Having to rely on presence/absence to determine elevation distributions of plant species, rather than having estimates of flower or plant density, would have made it relatively difficult to detect changes in their distributions. Recording rates of bumble bees during surveys apparently provided adequate measures of densities of foraging bumble bees, but similar observations along line transects of specified width and length might have been better, and capture/recapture methods better still. Of course, it is easy to have such clear hindsight, and the baseline studies in 1974 were carried out without thought about climate change (Pyke 1982). However, researchers at some future time may seek to understand further changes, and so it is important to facilitate such future research.

Our results and the fact that we were unable to confirm all of our hypothesized effects of climate change also indicate the importance, for possible future studies along similar lines, of ensuring that surveys cover the full range of available sites

over essentially the entire season. The lowest elevation region, where any effects of climate change might be most apparent, was little surveyed in 2007 and so could not be included in most analyses. Ending of surveys in 2007 before there had been much decline in recording rates for workers resulted in relatively large errors associated with their patterns. It also meant that males could not be included in the analyses, which was unfortunate as male production should provide a good measure of bumble bee reproductive success at the end of the summer season.

Our study has agreed qualitatively with expectations from observed climatic change, but suggests further research focusing on potential changes in altitudinal distribution for early-flowering plant species and male bumble bees toward the end of the season, and on the reasons why plant and animal phenologies have responded differently to climate change. Mismatch between phenologies of plants and bumble bees, with bumble bee abundance peaking later than flower abundance, should have greatest effects on plants at the beginning and on bumble bees at the end of the season. Understanding of effects of climate change would also be enhanced through investigation of factors that determine phenologies of plants and pollinators, apparently in different ways (Petanidou et al. 2014).

Quantitative disagreements between observed and expected results suggest the need to repeat our surveys and to consider other factors besides climate change. It is possible, for example, that changes to bumble bees and their plants are occurring as predicted, but with time lags. It is also possible that distributions of plants and bumble bees are determined by substrate and drainage, in addition to or instead of climatic factors.

#### CONCLUSIONS

Our results, comparing 2007 with 1974, were qualitatively consistent with expected effects of climate change on bumble bees and their plants in terms upward shifts in elevation, shifts in seasonal phenologies toward earlier in the season, especially for flowering, decreased seasonal synchrony between bumble bees and community flowering, and decreased bumble bee abundance. Queens and workers of most bumble bee species, and queens of all species combined,

showed evidence of upward shifts in elevation between the 2 yr. Upward shifts in elevation were evident for two plant species. There were no significant downward shifts. Within our study area, peak community flowering generally occurred earlier in 2007 compared with 1974, while peak bumble bee recording rate either occurred earlier or showed no significant difference. Seasonal synchrony between bumble bees and flowering was generally lower in 2007 compared with 1974, with bumble bee phenology advanced relative to that of flowering. Bumble bees were generally less abundant in 2007, as indicated by differences in recording rates. There were no significant differences between the 2 yr that conflicted qualitatively with expectations based on observed climate change.

Quantitatively, however, our results were mixed. Combining bumble bee species, queens increased in average elevation between the 2 yr by an estimated 244 m, which is not significantly different from the increase of 317 m required to maintain constant average air temperature in the face of observed climate change. For workers or queens of several individual species, there were also increases in elevation consistent with the expected 317 m. However, in a number of cases the observed change in elevation was significantly less than the expected upward shift of 317 m. Similarly mixed results, in quantitative terms, have been found in other studies (Hart et al. 2014).

Not surprisingly, given such a mixed outcome, we recommend further research. Our study needs to be repeated, to detect trends and time lags, and expanded in terms of season coverage and potentially important factors additional to climate change.

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