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LETTER

Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology

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Abstract

Climate change can influence consumer populations both directly, by affecting survival and reproduction, and indirectly, by altering resources. However, little is known about the relative importance of direct and indirect effects, particularly for species important to ecosystem functioning, like pollinators. We used structural equation modelling to test the importance of direct and indirect (via floral resources) climate effects on the interannual abundance of three subalpine bumble bee species. In addition, we used long-term data to examine how climate and floral resources have changed over time. Over 8 years, bee abundances were driven primarily by the indirect effects of climate on the temporal distribution of floral resources. Over 43 years, aspects of floral phenology changed in ways that indicate species-specific effects on bees. Our study suggests that climate-driven alterations in floral resource phenology can play a critical role in governing bee population responses to global change.

Keywords

Bumble bee, *Bombus*, climate change, floral resources, phenology, pollinator, precipitation, snowmelt, structural equation model.

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INTRODUCTION

Climate change is affecting the abundance and distribution of organisms worldwide (Parmesan 2006; Van der Putten *et al*. 2010). Continuing changes in temperature, precipitation and the incidence of extreme weather events (IPCC 2013) can affect population sizes directly, by affecting survival and reproduction (Bale *et al*. 2002; Roland & Matter 2016), and indirectly, by altering resource availability and species interactions (Boggs & Inouye 2012; Høye *et al*. 2013; Kudo & Ida 2013). Because few studies examine both direct and indirect effects in a single analytical framework, we know little about the relative importance of these climate effects. It is critical to understand how the combined direct and indirect effects of climate affect populations to make better predictions of population responses to climate change, especially for species key to ecosystem functioning.

Bumble bees (*Bombus* spp.) are functionally important organisms because they are abundant and effective pollinators in both natural and agricultural systems (e.g. Hegland & Totland 2008; Garratt *et al*. 2014). Many bumble bee species are experiencing dramatic declines (Williams *et al*. 2009; Cameron *et al*. 2011). Although many factors are implicated – including habitat loss, agrochemicals and novel parasites – climate change is a likely driver of current and potential future declines (Goulson *et al*. 2015; Kerr *et al*. 2015). Understanding the effects of climate on high-elevation bumble bees is especially urgent because montane regions are expected to experience the most extreme changes in climate (Nogués-Bravo *et al*. 2007), and bumble bees are some of the primary pollinators in these areas (Bergman *et al*. 1996; Bingham & Orthner 1998). The available evidence suggests that bumble bee populations are responding to climate change: some species have undergone recent latitudinal and elevational range shifts (Ploquin *et al*. 2013; Kerr *et al*. 2015; Pyke *et al*. 2016), others morphological changes likely in response to changing floral resources (Miller-Struttmann *et al*. 2015), and some are active earlier in the season than in the past (Bartomeus *et al*. 2011). However, the relative importance of direct and indirect climate effects on bumble bee populations is poorly understood, which limits our ability to explain how climate change may affect these important pollinators.

Bumble bees are eusocial insects whose population sizes rely on continuous floral resource availability (abundance of flowers used by bees) for successive life stages during the flight season: overwintered queens start colonies in the spring, overlapping worker cohorts forage during mid-season, and reproductive males and queens are produced late in the season (Goulson 2010). Though research is limited, climate may have negative direct effects on bumble bees if extreme temperatures or precipitation cause high mortality in overwintered queens or colonies (e.g. Vesterlund & Sorvari 2014; Oyen *et al*. 2016)

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or reduce critical foraging activity (e.g. Bergman *et al.* 1996). However, warmer temperatures may also have positive effects by increasing rearing temperatures and brood production (Holland & Bourke 2015), or foraging activity and provisioning, as in mason bees (Forrest & Chisholm 2017). Climate may also have indirect effects by altering the abundance and phenology of vital floral resources (Thomson 2016). Bumble bee populations often increase with floral abundance (e.g. Inari *et al.* 2012; Crone & Williams 2016), and colony growth may be impeded by aspects of floral phenology, such as gaps in floral availability (Williams *et al.* 2012; Kudo 2014) and season length (Elliott 2009a). Flowering is strongly responsive to climate, and there are widespread reports of shifting phenologies and floral abundance declines over time or with climate extremes (e.g. Høye *et al.* 2013; Iler *et al.* 2013; Miller-Struttmann *et al.* 2015; Thomson 2016). In other pollinator groups, such as flower-feeding butterflies, there is strong evidence for direct climate effects on populations (Roland & Matter 2016), as well as both direct and indirect climate effects via floral resource abundance (Boggs & Inouye 2012). However, the relative importance of direct and indirect climate effects on bee populations remains unresolved.

We examined the direct and indirect effects of climate on the abundance of three subalpine bumble bee species in the Rocky Mountains of Colorado, USA (Fig. S1). At our study site over the last four decades, there has been documented earlier spring snowmelt, warmer spring and summer temperatures, and more frequent damaging spring frosts (Inouye 2008; Iler *et al.* 2013). Simultaneously, the flowering season is shifting earlier and extending (CaraDonna *et al.* 2014), and a mid-season floral decline is expanding (Aldridge *et al.* 2011). Given these complex changes that could influence bee populations, we used long-term data on climate, flowers and bee abundance to ask: (1) whether the direct or indirect effects (via floral resources) of climate variation were more closely linked to changes in bee abundance over 8 recent years, and (2) whether these climate and floral resource variables – potentially important for bee abundance – have changed directionally over the last 43 years, suggesting future flower and bee responses to continued climate change. We used piecewise structural equation modelling (SEM; Lefcheck 2015) to disentangle the direct and indirect effects of climate on bee abundance (Fig. 1). We show that climate variation affects the abundance of three bumble bee species indirectly by altering the temporal distribution of floral resources. Our study suggests that climate-driven alterations in floral resource phenology can play a critical role in governing bee population responses to global change.

METHODS

Study system and approach

We used three long-term datasets collected near the Rocky Mountain Biological Laboratory (RMBL; 38°57.5 N, 106°59.3 W, 2900 m) in Colorado, USA. We combined bee, flower and climate datasets over 2009–2016 (8 years) to examine the direct and indirect effects of climate on interannual bumble bee abundance, and flower and climate data over

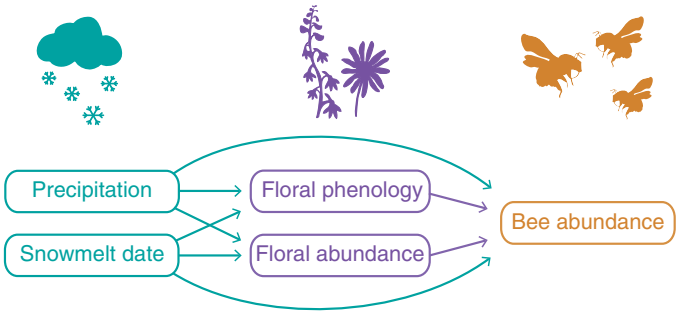

Figure 1 Path diagram showing all hypothesized direct and indirect links among climate variables, flower variables and bumble bee abundance. Floral phenology and abundance may directly affect bee abundance (purple arrows), while climate variables could affect bee abundance both directly (green arrow to bee abundance) and indirectly through their effects on floral phenology and abundance (green arrows to floral variables).

1974–2016 (43 years) to examine the long-term trends in variables potentially important for bumble bee populations. Bee data were collected from sites between 0.4 and 1.8 km from the central site where flowers and climate were measured, although the sites shared dominant habitats and plant species. The area has flower-rich subalpine meadows (*c.* 120 non-graminoid plant species occur in our floral plots), and up to 16 bumble bee species including two parasitic species. We focused on three common and distinguishable species, *B. bifarius, B. flavifrons* and *B. appositus* (Fig. S1; Williams *et al.* 2014). They have short, medium and long tongues, respectively, which match differences in relative body size and the plant species they frequently visit (Inouye 1980; Pyke 1982). Flowering season timing and length is governed by climate: it begins when the winter snowpack melts (April 23 to June 19 over 1975–2016) and ends with the onset of frequent freezing temperatures (September–October).

Bee dataset

The bumble bee abundance data are from an ongoing project described elsewhere (Gezon *et al.* 2015). Briefly, during the flowering season from 2009 to 2016, typically June through August, bumble bees were sampled at 2-week intervals at each of three sites (4–9 sampling periods totalling 20–54 observation hours, mean 35 h, in each site and year). Each site was composed of three habitats representative of the meadows visited by bees in the area (dry meadow, *Salix* spp.-dominated wet meadow and *Veratrum tenuipetalum*-dominated wet meadow). The three sites – A, B and D – were at 2980, 2930 and 3070 m elevation, respectively, and the area sampled at each site was *c.* 4500 m^2. All three bee species were common at each site. On each sampling day, bumble bees were hand-netted from flowers for *c.* 1 h in each of the three habitat types in both the morning and afternoon (6 h per sampling period, although poor weather sometimes shortened sampling). Bee species were identified in the field based on distinctive pile colour patterns (Williams *et al.* 2014) and were marked with paint to avoid recounting individuals within days. We combined counts of the uncommon *B. sylvicola* and abundant *B. bifarius* to form a species complex, because they

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are difficult to differentiate in the field and both have similar flight phenologies, short tongues and visit similar plant species (Pyke 1982). On each sampling date at each bee site, we also recorded the plant species in bloom and the species of flower each bee was netted from, both of which informed our choice of floral resource variables.

Our response variable for each of the three bumble bee species was annual peak abundance (worker and male bees combined), which is an estimate of population size that was comparable across years. We could not use summed bee abundances across a season because the number of seasonal sampling periods varied across years. Peak abundances were unimodal and marked, which is the typical seasonal abundance curve of bumble bees (e.g., Pyke *et al.* 2011). Although peak abundances could be sensitive to weather conditions on a sampling day, we only sampled during suitable weather conditions. We pooled bees within sites because habitats were too close to be independent. For each site and species, peak abundance was the maximum number of bees caught/hour in a year. In the few site-years in which peak abundance occurred on the last sampling date, we are confident that we captured the peak due to a predictable seasonal decline in bumble bees that coincides with cooler overnight temperatures and floral abundance declines. Because peak bumble bee abundances occur late in the summer (Pyke *et al.* 2011), our analyses emphasize colony growth over a season. Moreover, in similar Colorado habitats, foraging worker numbers were highly correlated with the number of colonies (Geib *et al.* 2015). The previous year's peak bee abundance had no relationship with the current year's peak (Fig. S2), so we did not include the previous year's abundance in our analyses.

Flower dataset

To measure bumble bee floral resources, we used a detailed flower community dataset collected from 1974 to 2016 at the RMBL (Inouye 2008; CaraDonna *et al.* 2014), a site central to the bee sampling sites. These data are housed at the Open Science Framework (https://doi.org/10.17605/osf.io/jt4n5). Within permanent 2 × 2 m plots, we counted all open flowers approximately every second day throughout the growing season. Individual flowers were the unit counted, except for plants in the Asteraceae for which we counted capitula. Over 2009–2016, data are from 30 plots (7 in dry meadow, 21 in wet meadow including that dominated by *Salix* spp. and *Veratrum tenuipetalum* and 2 in aspen forest), while over 1974–2016, data are from 23 plots (7 in dry meadow, 14 in wet meadow and 2 in aspen forest). From this dataset, we compiled a separate plant list for each bee site that matched the plant species recorded at that site. From each site-specific list, we made separate lists of plant species heavily visited by each of the three bee species (pooling plant species visited by *B. bifarius* and *B. sylvicola* for the *B. bifarius* complex). We combined bumble bee netting data from our bee sites and visitation data from near the RMBL to determine heavily visited plant species (J. E. Ogilvie, *unpublished data*). The plant species included in each list together comprised 92–95% of the total flower visits made by each bee species (20–24 plant species were included in the site-specific *B. bifarius* complex, *B. flavifrons* and *B. appositus* lists; Table S3).

We calculated two variables to describe floral resource abundance and timing, referred to hereafter as annual floral sum and the number of floral days. To calculate annual floral sum, using the site- and bee species-specific plant lists, we pooled flower counts across plant species and plots on every sampling date, and calculated the sum of flowers from first flower until 80% of flowers had accumulated. We used this measure because peak bumble bee abundance tended to occur near the date that 80% of a season's flowers accumulated and we wanted the floral resource variables to be defined consistently across years and independently of the bee abundance variable. Number of floral days was the number of days above a low flower threshold (0.75 flowers/m^2 or 3 flowers per 2 × 2 m plot) between the first flower date and the date on which 80% of the season's flowers had accumulated. This variable reflects the time span of floral availability for bumble bees – days of very few flowers are likely of poor foraging value. The relationship between bumble bee abundance and the number of floral days was consistent across a range of low flower thresholds from 0.5 to 1 flower/m^2. The variance inflation factors (VIFs) between floral sum and the number of floral days for all three bee species over both time periods (2009–2016, 1974–2016) were 1.19–2.5 indicating low collinearity.

Climate dataset

We used two climate variables, date of snowmelt and cumulative precipitation from May through July, because they have been shown to relate strongly to flower abundance and phenology (e.g. Lambert *et al.* 2010; Iler *et al.* 2013), and could also affect bumble bee populations directly. For queens that hibernate underground, snowmelt signals the potential start of the flight season, while precipitation may govern the time available for foraging. We selected these two variables by first creating a list of *a priori* climate variables, removing those with high VIFs (indicating multicollinearity), and finally removing those with strong one-way correlations with others. We considered temperature variables, though temperature measurements from the RMBL of accumulated degree-days above 0°C in June and July were negatively correlated with snowmelt date and May–July precipitation, respectively (Pearson $r = -0.67$ and -0.54, $P < 0.05$). Annual snowmelt dates were the day of year that a permanent 5 × 5 m plot was bare of snow, recorded 1975–2016 at the RMBL. Daily precipitation, including both snow and rain, was measured in cm water content, and then summed over the period May through July. Precipitation over 2009–2016 was measured at the RMBL, while data over 1975–2016 are from the Crested Butte National Oceanic and Atmosphere Administration weather station (*ca.* 9 km south of the RMBL), because monthly summer precipitation data for the RMBL do not extend as far. 2000–2016 precipitation data from the RMBL and Crested Butte were highly correlated (Pearson $r = 0.78$, $P < 0.001$). Climate measurements at the RMBL were taken by long-time resident, billy barr.

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Direct and indirect climate effects on bees

To disentangle the direct and indirect effects of climate on interannual bumble bee abundance over 8 recent years, we combined the datasets on bees, flowers and climate and used piecewise SEMs (Lefcheck 2015). Piecewise SEMs are conceptually similar to classical path analysis, but rather than use global estimation from a single variance–covariance matrix, piecewise SEMs solve each component model separately. Thus, piecewise SEM allows for models with their own sampling distributions and can operate with smaller sample sizes (Lefcheck 2015). For each bee species, we statistically compared a set of SEMs to determine the key direct and/or indirect climate effects that drive bee abundance. To do so, we first constructed a full causal path model with all hypothesized relationships among our variables using knowledge of the study system (Fig. 1; Grace *et al*. 2012). We then fit the three component models (response variables: number of floral days, annual floral sum and bee abundance) as linear (LMs) or generalized linear models (GLMs) each with their appropriate distributions (negative binomial or Poisson). From the full causal model, we then removed paths to bee abundance to create a set of SEMs with every possible combination of paths that were biologically plausible (16 SEMs, including the full model). In the series of SEMs, each component model had site (three levels) as a predictor to account for variation among sites, and the two floral variable models always had direct climate effects (as in Fig. 1), given well-known effects of climate on flowering. The response variable for the bee abundance model was the number of bees caught on the peak sampling day, with the sampling effort (in hours) included as an offset term to account for different sampling durations.

To assess the overall fit of each SEM, we used Shipley's test of d-separation (Shipley 2009, 2013), which tests whether model fit would be improved by the inclusion of identified missing paths. The d-separation test generates a Fisher's C test statistic, which can be used to assess overall fit of the SEM and to calculate Akaike's information criterion corrected for small sample sizes (AICc) for model selection (Shipley 2009, 2013). For each bee species, we, therefore, used a two-part selection process, in which we first only considered SEMs with *P*-values derived from Fisher's C of > 0.05. Of the SEMs with no significant missing paths, we then selected the SEM with the lowest AICc value by a difference of at least two points. For each best-fit SEM, we extracted all coefficients to determine the strength of paths. We used the Benjamini-Hochberg procedure to correct *P*-values for multiple comparisons (Smith & Cribbie 2013). All statistical analyses were conducted in R version 3.3.2 (R Core Team 2016). Tests of d-separation and extraction of coefficients were done using the R package 'piecewiseSEM' (Lefcheck 2015) and component negative binomial GLMs using 'MASS' (Venables & Ripley 2002).

Long-term climate and flower trends

To test whether climate (snowmelt date and May–July precipitation) and the assemblage of flowers visited by bumble bees (annual floral sum and the number of floral days) have changed directionally over time, we examined the long-term climate and flower datasets. For the flower dataset spanning 1974–2016, we excluded the years 1976–1978, 1990 and 1994 due to missed sampling ($N = 38$ years; 23 2×2 m plots/year). For the climate dataset spanning 1975–2016, precipitation data from 1978 and 1979 were excluded because of missing data ($N = 40$ and 42 years for precipitation and snowmelt date, respectively). To examine how the climate and floral variables have changed over four decades, we used simple linear models for each response variable.

RESULTS

Direct and indirect climate effects on bees

Over 8 years, 2009–2016, there was substantial variation in peak abundance of the three bumble bee species (*B. bifarius*: 0–17, *B. flavifrons*: 0.17–13 and *B. appositus*: 0–8, bees caught/hour). The assemblage of flowers visited by the three bee species also varied over the same time period, both in annual floral sum, an estimate of cumulative floral abundance (*B. bifarius*: 60.7–897.4; *B. flavifrons*: 36.7–850.5 and *B. appositus*: 26.3–810.8 flowers/m^2 accumulated to 80% of the season total) and in the number of floral days, an estimate of the season time span of available floral resources (*B. bifarius*: 14–47, *B. flavifrons*: 20–40 and *B. appositus*: 14–34, days above the flower threshold of 0.75/m^2). Likewise, there was also substantial variation in the climate variables, snowmelt date (April 23 to June 7) and May–July precipitation (11.00–33.63 cm).

For each bumble bee species, we compared a series of piecewise SEMs that varied in the presence of direct and indirect paths of climate variables to bee abundance. Each comparison yielded a single best-fitting SEM (Fig. 2a–c; Table S4). In the best-fitting model for each of the three species, bee abundance was driven most strongly by the indirect effects of precipitation and snowmelt date on the number of floral days (Fig. 2a–c; Table S4). Bee abundance increased with more floral days (Fig. 3), while the number of floral days increased with greater summer precipitation and later snowmelt dates (Fig. 2a–c; Table S5). Annual floral sum was included but not significant in the model for *B. appositus*, and had a weak negative effect on *B. bifarius* abundance (Table S5). There were no significant directional trends through time in peak bee abundance, number of floral days, and annual floral sum for all three bee species over 2009–2016 (Fig. S6).

Long-term climate and flower trends

Over the 42 years (1975–2016), there was a trend for snow to melt 12.8 ± 7.1 days earlier (LM, $F_{1,40} = 3.3$, $P = 0.0781$; Fig. 4a), while May–July precipitation showed no consistent pattern (LM, $F_{1,38} = 0.2$, $P = 0.671$; Fig. 4b). Over 1974–2016 (43 years), the number of floral days increased for the *B. flavifrons* floral assemblage by 5.9 ± 2.7 days (LM, $F_{1,36} = 5.0$, $P = 0.032$; Fig. 4c), while the number of floral days did not change significantly for the *B. bifarius* and *B. appositus* floral

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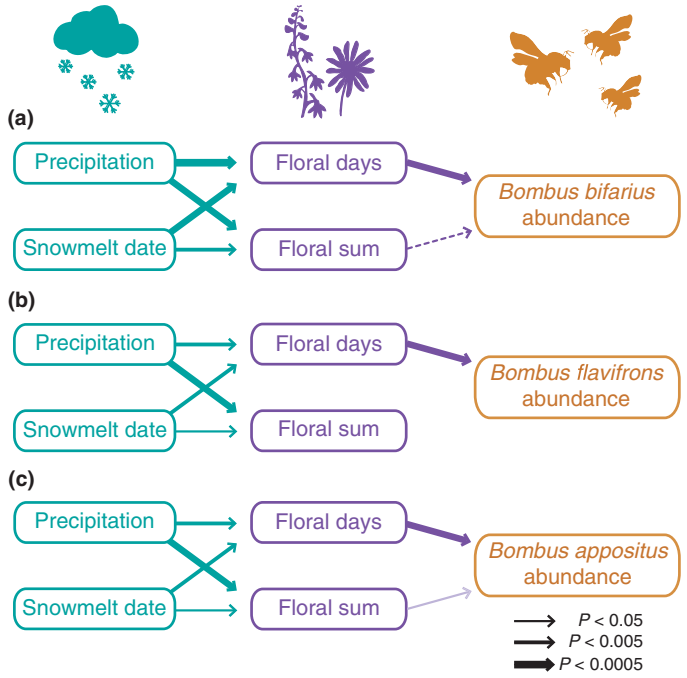

Figure 2 Path diagrams showing the climate and flower variables that govern interannual variation in the peak abundance of (a) *Bombus bifarius*, (b) *B. flavifrons* and (c) *B. appositus*. Paths between variables included in the best-fitting piecewise structural equation models are shown. The faint arrow indicates an insignificant path included in a model; solid and dashed arrows indicate a positive and negative effect of a variable on another, respectively; and the arrow thickness indicates the significance level of the path adjusted for multiple comparisons (thick: $P < 0.0005$, medium: $P < 0.005$, thin: $P < 0.05$). Bee data are from three sites in each of 8 years (2009–2016, $N = 24$); flower and climate data are from a single central site, though the floral variables were created from plant species lists specific to the three bee sampling sites.

assemblages (LMs, *B. bifarius*: $F_{1,36} = 1.1$, $P = 0.31$; and *B. appositus*: $F_{1,36} = 2.7$, $P = 0.11$; Fig. 4c). In addition, the annual floral sum of each bee species' plant assemblage did not change directionally over the four decades (LMs, *B. bifarius*: $F_{1,36} = 0.3$, $P = 0.57$; *B. flavifrons*: $F_{1,36} = 0.03$, $P = 0.85$; and *B. appositus*: $F_{1,36} = 0.8$, $P = 0.37$; Fig. 4d). Additional analyses showed that the total floral season length – which differed from the number of floral days by including all days from first flowers to the date on which 80% of flowers had accumulated – increased over 43 years by 20.9 ± 5.2 and 20.8 ± 5.3 days for the *B. bifarius* and *B. flavifrons* floral assemblages, respectively (LMs with year as the fixed effect; *B. bifarius*: $F_{1,36} = 15.9$, $P = 0.0003$; *B. flavifrons*: $F_{1,36} = 15.6$, $P = 0.0003$) and marginally so for the *B. appositus* floral assemblage by 10.4 ± 5.4 days ($F_{1,36} = 3.6$, $P = 0.064$; Fig. S7). Furthermore, the number of days below the flower threshold (low floral days) significantly increased through time for the *B. bifarius* and *B. flavifrons* floral assemblages by 12.4 ± 3.5 and 8.7 ± 3.1 days, respectively (LMs with year as the fixed effect, *B. bifarius*: $F_{1,36} = 12.7$, $P = 0.001$; *B. flavifrons*: $F_{1,36} = 7.8$, $P = 0.008$), and marginally so for the *B. appositus* flowers by 6.15 ± 3.4 days ($F_{1,36} = 3.2$, $P = 0.081$; Fig. S7). Thus, the trend for earlier snowmelt dates is increasing the length of the floral season; however, those additional days are of low floral abundance for *B. bifarius* and *B. appositus*, while there are days both below and above the flower threshold for *B. flavifrons*. In the 8-year dataset, abundance of all three bee species was negatively affected by the number of low floral days (negative binomial GLMs with number of days ≤ 0.75 flowers/m^2 and site as fixed effects, all three species: $P < 0.0001$, $N = 24$ site-years; Fig. S8), though this effect was only significant with the inclusion of an extreme year with many low floral days.

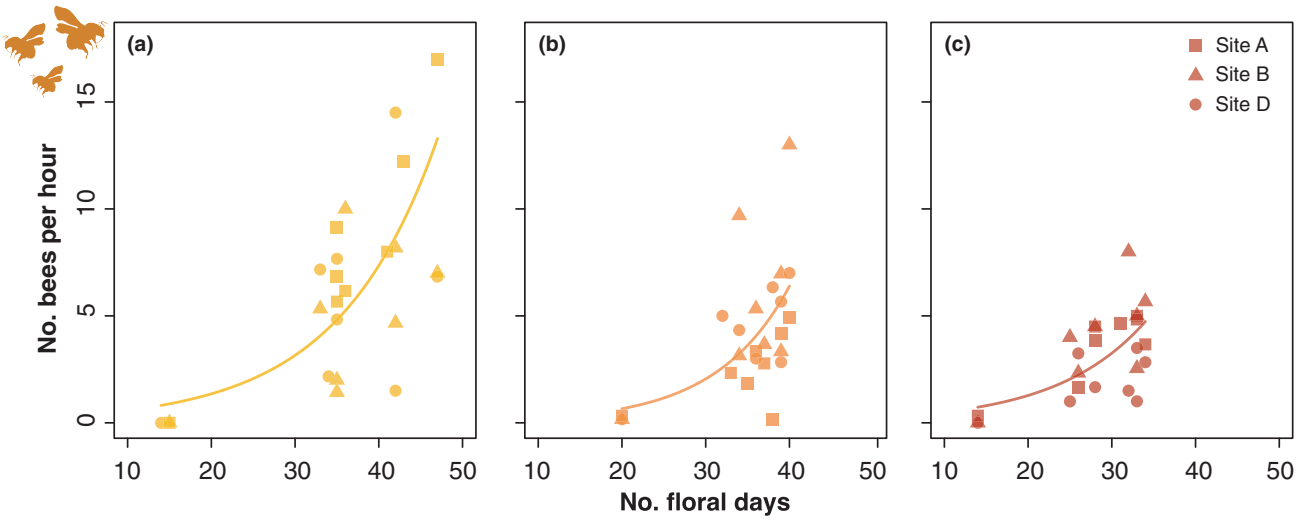

Figure 3 The relationship between annual peak abundance (bees netted/hour) and the number of days above a flower threshold (0.75/m^2) in a season for three bumble bee species, (a) *Bombus bifarius*, (b) *B. flavifrons* and (c) *B. appositus*. The number of floral days was identified as the key driver of bumble bee abundance for all three bee species in our structural equation models (Fig. 2). Bee data are from three sites over 8 years, and floral data are from a central site with plant species lists specific to the three bee sampling sites (2009–2016, $N = 24$). The different shaped points are different sites (squares = site A, triangles = site B, circles = site D).

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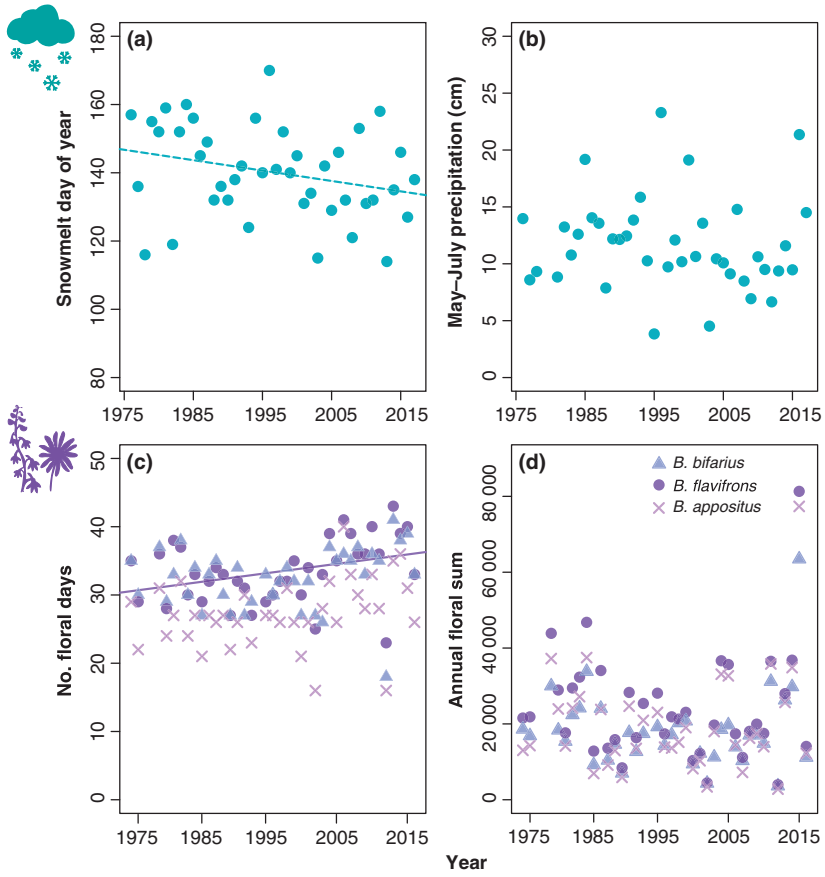

Figure 4 Patterns in (a and b) climate variables and (c and d) the bumble bee-visited floral assemblages spanning 43 years (1974–2016). Long-term climate panels show (a) day of year of snowmelt and (b) cumulative precipitation (rain and snow) from May to July (N = 42 years). The bumble bee floral assemblage panels show (c) the number of days above a flower threshold (0.75/m^2) and (d) the cumulative sum of flowers (to 80% of the season total), in which triangles are *Bombus bifarius*, circles are *B. flavifrons*, and crosses are *B. appositus* (N = 38 years for each species; flower counts made approximately every second day pooled across 23 2 × 2 m plots). The lines are fitted from linear models – marginally significant in (a) (P = 0.0781) and significant in (c) for *B. flavifrons* (P = 0.032).

DISCUSSION

There is evidence that climate change has influenced some bumble bee populations (e.g. Ploquin *et al.* 2013; Kerr *et al.* 2015), but the mechanisms underlying those changes – whether direct or indirect climate effects – remain unclear. We found that interannual abundances of three subalpine bumble bee species were driven by the indirect effects of climate on the temporal distribution of floral resources. In particular, bee abundance was most strongly positively related to the number of days above a low flower threshold. Our study suggests that climate-driven alterations in floral phenology can play a critical role in governing bumble bee population responses to ongoing global change.

Direct and indirect climate effects on bees

Although animal populations can show direct responses to climate variation (e.g. Bale *et al.* 2002; Roland & Matter 2016), there is growing recognition that the indirect effects on species interactions are more common (Ockendon *et al.* 2014). Our results add to these prior studies by demonstrating strong indirect effects of climate on bumble bees, providers of important pollination services. Our SEM approach did not detect any direct climate effects on interannual bumble bee abundances; instead, climate effects were all indirect. Precipitation and temperature (which strongly co-varied with snowmelt date and precipitation) can influence daily bumble bee foraging activity (e.g. Bergman *et al.* 1996) and may cause direct mortality in extreme events (Oyen *et al.* 2016), while snowmelt date contributes to overwintered queen emergence (Kudo & Ida 2013). However, the interannual variation in these climate measures did not directly affect bee abundances in our study. Much more is known about how climate affects plants than how climate affects bees – in part because of a lack of long-term data on bee populations – so it is possible that our climate variables did not capture aspects most important to bumble bees. This may be unlikely, however, because many of the climate variables we considered in preliminary analyses were correlated, so additional variables are likely to provide similar conclusions. Furthermore, bumble bees can tolerate some climate variation: individuals can fly over a broad temperature range (Heinrich 1979), and underground colonies are buffered from temperature and precipitation extremes. This is unlike egg or larval butterflies that may be exposed to and affected by temperature extremes (Boggs &

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Inouye 2012; Roland & Matter 2016). The observed climate variation did, however, strongly affect the abundance and phenology of the floral assemblages, consistent with other studies on single plant species (Iler *et al*. 2013) and the community at our site (CaraDonna *et al*. 2014). Although climate-driven variation in floral resources is known to influence bee abundance (Thomson 2016), we show for the first time that the effects of climate on floral days and floral abundance have a stronger influence on bee abundance than direct climate effects.

Although research has highlighted the positive effect of floral abundance on bee populations (reviewed in Roulston & Goodell 2011), few studies have explicitly considered the effect of within-season temporal resource distribution (floral resource phenology) on bee population size or reproductive output (Crone 2013). Those studies that have considered temporal resource distribution effects find slower or reduced bumble bee brood production with periods of low resources (Schmid-Hempel & Durrer 1991; Kudo 2014). We found that the number of days above a flower threshold – a measure of the time available with sufficient floral resources – had a strong positive effect on the interannual abundance of all three bees, while annual floral sum had a weak effect on only two species. This effect could be weak because our floral abundance measure did not come from the exact sites where bees were sampled. However, the sites at which flowers and bees were sampled contained the same habitats and plant species, and we are confident that the among-year variation in floral abundance is greater than the among-site variation. Future studies of floral resource effects on pollinators need to consider more nuanced ways of deconstructing flowering phenology, as we have done, because temporal resource distribution is multifaceted and the critical components will be organism-specific.

The time available for foraging may limit animal reproductive output more commonly than is appreciated (Rose & Lyon 2013). Subalpine bumble bees have short seasons within which to grow and reproduce: there are typically 10 weeks between queen emergence and the appearance of males at our site (Elliott 2009b), and our study supports suggestions that bumble bees at high altitude may be limited by the time to exploit floral resources (Pyke 1982; Elliott 2009a). The more days with sufficient flowers, the more workers can forage and provision brood and colonies can grow. In a similar vein, with many days below a flower threshold, bee abundances are lower, perhaps because resource gaps cause spring queens to starve or result in insufficient floral resources to maintain colony growth (Kudo 2014). Indeed, bumble bees should be vulnerable to periods of resource shortage because they have limited food storage for withstanding low floral abundance periods (Goulson 2010). Experimental studies that examine how the timing and magnitude of resource gaps affect colony initiation, worker production and reproductive output are needed to understand how global change will influence bumble bees.

Two caveats are important to consider when interpreting our study. First, a single extreme year was important in determining the observed patterns. As extreme weather is predicted to increase with climate change, there is a critical need for continued long-term monitoring of bee populations that allow us to capture these rare but increasing important events. Second, climate variation may have other indirect effects on bee populations that we did not measure. Populations can be limited by top-down instead of bottom-up forces, and this relationship may be modified by climate (Hoekman 2010). For example, with warmer temperatures, the benefit of increased foraging opportunities for mason bees was negated by increases in wasp parasitism (Forrest & Chisholm 2017). Bumble bee populations could also be influenced by predators and intra- and interspecific competition, factors we were unable to capture here.

Long-term trends

Changes in spring snowmelt timing and measures of floral phenology over four decades (see also Aldridge *et al*. 2011; CaraDonna *et al*. 2014) suggest species-specific and potentially conflicting effects on bumble bee populations. First, based simply on long-term trends in floral resources, our results suggest that *B. bifarius* and *B. appositus* populations may have remained consistent over the last four decades given the lack of directional change in the number of floral days of their floral assemblages. In comparison, increases in the number of floral days for *B. flavifrons* floral assemblages suggest the potential for increases in its populations. Thus, the reshaping of flowering communities with climate change (CaraDonna *et al*. 2014) may also indirectly contribute to the reshaping of pollinator communities, alongside climate-induced changes in pollinator distributions (Kerr *et al*. 2015). Second, however, advancing snowmelt dates have lengthened the flowering season, and the number of low floral abundance days have simultaneously increased, perhaps, in part, due to increased incidences of damaging spring frosts (Inouye 2008), or increasing summer temperatures and drought conditions (Aldridge *et al*. 2011). Because resource gaps may negatively affect bumble bee populations, and potentially those of other pollinators that have long foraging seasons (e.g. broad-tailed hummingbirds), continued increases in low resource days may negate any benefits of an extending flowering season. In our system, such low floral resource days occur when bumble bees may be vulnerable to resource deficits: in the spring, when queen bees are initiating nests (Schmid-Hempel & Durrer 1991; Williams *et al*. 2012; Kudo 2014), and in the mid-season before the summer peak of flowers, when colonies are provisioning for reproductive brood. It is unknown which floral resource variable is most important to bumble bee abundance – days above or days below a flower threshold – but given that floral phenology is changing through time, addressing this question should be a priority for future research. We suggest that resource phenology is likely to affect consumer populations more broadly than is appreciated, especially in the context of climate change.

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AUTHORSHIP

DWI and REI designed research; ZJG, SRG, DWI, REI and JEO performed research; JEO, SRG, BDI and NU conducted statistical analyses; JEO and SRG wrote the first draft of the manuscript; all authors provided feedback on analyses and the manuscript.

DATA ACCESSIBILITY STATEMENT

The primary data used in this study are archived at Figshare: http://dx.doi.org/10.6084/m9.figshare.5400796 (Ogilvie et al. 2017).

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