



Research

Cite this article: Quinlan G, Kazenel MR, Stemkovski M, Irwin RE. 2025 Shorter seasonal snow cover poses a risk to solitary bee populations in a mountainous ecosystem. *Proc. R. Soc. B* **292**: 20251887.

<https://doi.org/10.1098/rspb.2025.1887>

Received: 23 July 2025

Accepted: 5 November 2025

Subject Category:

Ecology

Subject Area:

ecology

Keywords:

pollinator, *Lasioglossum*, *Halictus*, climate change, flower, snowmelt, growing degree days, structural equation model

Author for correspondence:

Gabriela Quinlan

e-mail: gmquinla@ncsu.edu

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.8145750>.

Shorter seasonal snow cover poses a risk to solitary bee populations in a mountainous ecosystem

Gabriela Quinlan¹, Melanie R. Kazenel^{2,3}, Michael Stemkovski^{3,4} and Rebecca E. Irwin^{1,3}

¹North Carolina State University at Raleigh, Raleigh, NC, USA

²Earlham College, Richmond, IN, USA

³The Rocky Mountain Biological Laboratory, Crested Butte, CO, USA

⁴Biology Department and Ecology Center, Utah State University, Logan, UT, USA

GQ, 0000-0002-9814-3936; MRK, 0000-0002-2101-1062; REI, 0000-0002-1394-4946

Climate change poses a threat to organisms globally, but its effects may be particularly pronounced in multi-trophic systems. For example, pollinators are vulnerable to changes in climate, as are flowering plants, but the extent of direct versus floral-mediated indirect effects of climate on pollinators has not been studied for most solitary bee species. We use a long-term dataset (9 years) encompassing a diverse assemblage of bees (13 species) and their flowering plants from a region experiencing rapid effects of climate change (Rocky Mountains, USA). Utilizing piecewise structural equation models, we assess direct and flower-mediated indirect effects of climate variables (snow cover duration and growing degree day accumulation) on each bee species's abundance. For 62% of species, longer snow cover duration had a direct, positive effect on bee abundance the following year and on flower abundance and duration. However, flower abundance and duration in the preceding year did not affect bee abundance the following year. Snow cover provides temperature stabilization for energy-efficient diapausing among bees and frost protection for flowering plants. Given the shift towards earlier snowmelt in this system, our findings raise concern for regional bee community stability and underscore the importance of seasonal snow cover for bees in other systems.

1. Introduction

Global climate change is threatening the distribution, abundance and biodiversity of functionally important organisms [1–3]. Regional shifts in climate are characterized by changes in temperature, precipitation and the frequency and intensity of extreme weather events [4]. The impacts of these shifts can radiate across trophic levels, threatening ecosystem function [5,6]. For example, a meta-analysis of marine systems found that herbivores are more vulnerable to ocean acidification and warming compared with higher trophic levels, possibly contributing to ecosystem destabilization through negative bottom-up effects [7]. In terrestrial plant–insect herbivore interactions, climate change effects can lower the dietary quality of plants (e.g. produce plants with tougher, thicker leaves and more defensive compounds), while directly increasing insect metabolism [6]. Together, these indirect and direct impacts can increase rates of herbivory, as insects attempt to compensate for low-quality food and meet their metabolic needs [6]. Thus, climate change may imperil functionally important relationships through direct impacts on organisms and by affecting the resources upon which they rely [5,6]. Few studies have simultaneously assessed these direct and indirect

effects of climate on organisms, limiting the ability to effectively manage species in the face of climate change.

Pollinators may be affected directly and/or indirectly by climate change [8–10]. Assessments of direct effects of climate change on pollinators reveal changes in emergence timing [11], foraging activity [12], sex ratios [13,14], and overall survival, abundance and/or fecundity [11,15,16]. Pollinators may also be affected indirectly, through climate change effects on flowering plants [17–19]. Climate change can alter the phenology [18,20–22], attractiveness [17,23] and reproductive success [19] of flowering plants. Thus, many studies have raised concerns about indirect consequences of climate change on plant–pollinator dynamics, including phenological mismatch [24] and depressed pollination efficiency [25,26], resulting in overall lower abundance of plants [20,27,28] and pollinators [29,30]. While an increasing number of studies examine effects of climate change on pollinators or flowering plants, very few studies have explicitly considered whether climate change is primarily having direct versus indirect effects on bees (reviewed in [9]). Furthermore, the pollinators used to develop inferences about the effects of climate change are limited in taxonomic scope, focusing mostly, albeit not solely, on pollinating social insects, such as bumblebees [10,31,32].

The degree to which results from social species apply to solitary species is unknown, and the relative importance of direct versus floral-mediated indirect effects of climate could vary by taxa. One study found that floral-mediated indirect effects were more important than direct effects across three bumblebee species [10]. Bumblebees have behavioural adaptations to regulate nest temperatures [33] as well as behavioural and physiological adaptations to regulate their body temperature [33,34] and therefore may be less susceptible to the direct effects of climate change. Bumblebees' larger body size and social nature may also lead to higher nutritional requirements [35,36]. Furthermore, bumblebees have specific foraging behaviours, prioritizing pollen quality over quantity [37], which may make them particularly susceptible to floral-mediated indirect effects of climate change. Bumblebees' climate responses may thus not predict the direct and indirect effects of climate change on bees with other traits, highlighting the importance of examining diverse species separately. However, drawing conclusions on the effects of disturbances—such as climate change—on diverse species assemblages is often limited by the availability of detailed, long-term data [30,38].

Here, we use a long-term dataset from the Rocky Mountains of Colorado, USA, to examine the direct and flower-mediated indirect effects of shifting climate conditions on interannual mean abundance across a diverse assemblage of solitary bees. We hypothesized that we would observe both direct and flower-mediated indirect effects of climate on bee abundances, but that the relative importance of direct versus indirect effects would vary by species.

2. Methods

(a) Study system

To determine the direct and flower-mediated indirect effect of climate on bee abundance, we used long-term datasets on bee and flowering plant assemblages from the Rocky Mountain Biological Laboratory (RMBL) in the Elk Mountains of western Colorado, USA. Like many mountainous systems, the Rocky Mountains are experiencing rapid climate shifts [39]. Over the past four decades, this region has experienced warmer spring and summer temperatures, shifting snowmelt earlier in spring [20,40]. Flowering phenology has likewise shifted earlier and expanded in duration [22], resulting in the expansion of a mid-season floral dearth period [41].

Annually between 2010 and 2018, bee and floral surveys took place at nine core sites, ranging in elevation from 2877 m to 3072 m (electronic supplementary material, table S1). These subalpine sites are characterized as flower-rich meadows with over 680 non-graminoid plant species and over 170 bee species. We sampled bees and flowers in sites representing three dominant vegetation types: rocky dry meadow (three sites), wet meadows dominated by *Veratrum tenuipetalum* (three sites) and wet meadows dominated by *Salix* spp. (three sites).

(b) Bee surveys

Bee sampling took place approximately every two weeks from snowmelt in the spring to the end of the flowering season, typically early to mid-May through early to mid-September. At each site, bees were sampled using bowl traps placed at ground level along two transects at 3 m intervals with alternating bowl colours (fluorescent blue, fluorescent yellow or white). The two transects met approximately in a cross with 15 bowls per transect (30 bowls total per site, 10 per colour). Bowl traps were placed in the field between approximately 09.00 and 15.00 on sunny, clear days and, when needed, were removed early or placed in the field late to avoid precipitation. This resulted in an average sampling effort of 5 h 43 min $\pm$ 1 h 20 min (mean $\pm$ standard deviation) per sampling event. Trapped bees were identified to species either using a key developed for bees around the RMBL or by taxonomists (i.e. *Lasioglossum*: J. Gibbs; *Melissodes*: K. Wright; *Megachile*: J. Neff; *Anthophora*: M. Orr; *Andrena*: C. Sheffield; *Hylaeus*: R. Oram; *Osmia*: T. Griswold and M. Rightmyer; remaining genera: J. Ascher). See Gezon *et al.* [42] for additional sampling details and Stemkovski *et al.* [43] for additional bee identification details.

From these bee data, we selected the most abundant (≥ 100 female individuals) species across all sampling events, excluding *Bombus* species (see [10] for *Bombus*-specific assessment). This resulted in 13 common, solitary species for further study (electronic supplementary material, table S2) across seven genera (five species of *Lasioglossum*, two *Halictus*, two *Panurginus* and one species each of *Dufourea*, *Pseudopanurgus*, *Hoplitis* and *Hylaeus*). Note that while some *Lasioglossum* and *Halictus* species can be weakly eusocial and *Halictus rubicundus* can be social or solitary depending on the environment, nests near RMBL are solitary due to the short season at high elevation [44,45]. To quantify bee abundance, we calculated the mean number of female bees

collected per hour of sampling effort, for each site, in each year, across all sampling rounds. We considered several alternative metrics of bee abundance but consider this to be the most robust approach; all alternative metrics were highly correlated (electronic supplementary material, figure S1).

(c) Flower surveys and bee associations

Flowering data were collected at the same sites, on the same sampling days as bees. At each site, within six 2×2 m plots (three plots each along the two bee-sampling transects at each site), all actively flowering plants (i.e. plants with open blooms, available to be foraged upon) were identified to their lowest possible taxonomic resolution (mostly to species) and all flowers or flowering units (e.g. capitula for Asteraceae) were counted. From these flowering data, we created bee-specific flowering datasets (subsets of the full flowering dataset based on known associations with each of our 13 focal bee species). Bee–flower associations were curated from netting observations from the same study sites [46], Discover Life [47] and a review of the literature and observations from other sites in the RMBL vicinity (J. E. Ogilvie, 2025, unpublished data; electronic supplementary material, table S3).

From these floral surveys and bee–flower association datasets, we calculated two floral variables for each site–year combination—floral abundance and duration. We calculated floral abundance as the daily average number of flowering units associated with each bee species observed per site per year. We calculated floral duration as the number of survey days that had sufficient floral resources for the focal bee species within a site-year. We defined sufficient resources as at least three flowering units per plot (or 0.75 flowers m^{-2}); lower values represent days of low forage availability [10]. In our analyses, similar results were obtained across various low flower thresholds from 0 to 1 flower m^{-2} . Additional justification for floral metrics can be found in electronic supplementary material, file S1.

During the spring and summer, female solitary bees provision their young with floral resources (i.e. pollen and nectar). The number of offspring they can produce is related to resource availability (i.e. floral abundance) as well as the window of time these resources are available (i.e. floral duration) [48]. Offspring typically emerge the following year, creating a time lag in the effects of climate and floral resources on bee abundance. Therefore, in our modelling approach, we related floral metrics to the following year's bee mean abundance.

(d) Climate data

To characterize climate conditions across years and sites, we used temperature and snowmelt timing data from the RMBL Spatial Data Platform [49]. From these data, we calculated growing degree days and snow cover duration to use in our models. These variables were not correlated ($r = -0.12$) based on Pearson's correlation. Growing degree day accumulation from 1 April to 30 September was calculated using the averaging method [50], with a base temperature of 8°C ($(T_{\text{max}} + T_{\text{min}})/2 - 8$). Growing degree day accumulation is a typical temperature metric used to predict the growth and development of plants and insects [51–53]. Higher growing degree day accumulation represents warmer average conditions and is associated with a greater rate of growth for flowering plants and earlier emergence timing for bees [51–53]. Snow cover duration is the number of days from the onset of snow in the autumn (year – 1) to snowmelt the following spring (year). Snow cover duration was highly correlated with alternative climate variables we considered, including spring snowmelt timing ($r = 0.96$) and autumn snow onset ($r = -0.89$) based on Pearson's correlation; for this reason, we did not use these other snow timing variables as predictors. In this system, flower and bee phenology are closely tied to snow cover, which sets an upper and lower bound on the growing and foraging season [43,52,54]. Among potential consequences for bees and plants, early snowmelt in the spring exposes flowering plants to potential frost damage [55], while delayed snow cover in autumn may lead to greater energy expenditure by bees, depleting fat stores and disrupting diapause [56]. Cold temperatures associated with snow cover also provide an essential period of dormancy for many bees [56,57] and a vernalization period for many flowering plants [58].

As with the lagged floral data, we associated climate data with the following year's bee mean abundance data. Note that snow cover duration is tabulated by the preceding water year. So, for example, bees collected in 2010 are associated with snow cover data from autumn 2008 to spring 2009, to reflect conditions influencing maternal bee emergence and foraging.

(e) Statistical methods

To compare the direct and flower-mediated indirect effects of the climate variables (growing degree days and snow cover duration) on bee mean abundance for each species, we used piecewise structural equation models (SEMs), implemented in R v. 4.4.1 [59] using the piecewiseSEM package [60]. Structural equation modelling is a form of path analysis that allows testing of directional relationships among variables, including hypothesized direct and indirect effects [61,62]. Piecewise SEMs build upon this modelling approach by independently estimating each linear equation locally, which allows for more flexibility in model specification (e.g. unique sampling distributions) and theoretically lower sample size requirements [63].

For each bee species, we constructed a set of alternative SEMs—a full SEM composed of all hypothesized paths (figure 1) and 14 subset SEMs, for which we removed paths to assess simplified combinations of direct effects on bee mean abundance. Each of the SEMs, in the full and subset models, included three generalized linear mixed effects models (GLMMs) to assess effects on (i) bee mean abundance, (ii) floral abundance and (iii) floral duration. In all SEMs, the GLMMs for floral abundance and duration had the same predictors—growing degree days and snow cover duration. The SEMs differed only in the predictors used to model bee mean abundance, with the full model including the previous year's floral abundance, floral duration, growing degree

days and snow cover duration. Subset models included all possible combinations of these variables, with 1–4 predictors. All GLMMs, implemented in nlme [64], included a random intercept of site, a first-order autoregressive error structure to account for potential temporal autocorrelation across years, and a log-normal error distribution (floral data and bee abundance data were transformed using $\log(x + 1)$). All predictor and response variables were scaled and centred within each model to assist with convergence and allow for direct comparison of effect sizes among variables.

To assess candidate models for missing connections among variables, we used Shipley's test of directed separation. This test provides a statistic, Fisher's C , which can be used in a chi-square test to determine goodness-of-fit in these alternative SEMs [63]. We used a cutoff of $\alpha = 0.05$ to identify complete SEMs that represented the data well. C can also be used for model selection by calculating Akaike's information criterion corrected for small sample sizes (AICc) [65]. After excluding SEMs with missing paths, we report results from the model with the lowest AICc value. Equally supported models ($\Delta\text{AICc} < 2$) showed comparable results. For the selected SEM(s) for each species, we report path correlation coefficients and p -values, using a more stringent $\alpha = 0.01$ due to the multiple tests performed.

3. Results

Bee mean abundance varied across the 9 year study period (2010–2018; figure 2), as did snow cover duration (figure 2), floral abundance and duration (electronic supplementary material, figures S2 and S3) and growing degree days (electronic supplementary material, figure S4). Across sites and years of the study, snow cover lasted 192 days on average, ranging from 159 to 228 days. The growing degree day accumulation was 468 degree units on average (range: 296–592 degree units).

Climate variables directly predicted mean abundance for 9 of 13 species, as well as floral metrics associated with nine species. However, floral abundance did not, in turn, predict bee abundance, offering poor evidence for indirect effects of climate on bee abundance (figure 3; electronic supplementary material, table S4). In all eight SEMs for which it was predictive, snow cover duration had a strong, direct, positive effect on mean bee abundance the following year (figure 2). Snow cover duration likewise had a consistent, positive effect on the abundance and/or bloom duration of flowering plants associated with four different bee species. Growing degree day accumulation negatively affected bee abundance for one species (*Dufourea harveyi*), while also affecting floral abundance and duration in differing directions across seven SEMs.

Direct climate effects on bee mean abundance and floral abundance/duration varied among bee species. For *Lasioglossum sedi* and *L. tenax*, there was a positive effect of the previous year's snow cover duration on bee abundance and floral duration. Floral communities associated with *L. tenax* further showed a weak positive correlation between floral abundance and snow cover duration and a negative correlation between floral duration and growing degree day accumulation. Similarly, the abundance of *L. ruidosense* was positively related to snow cover duration, while growing degree day accumulation was negatively correlated with floral duration. Both *L. inconditum* and *L. nigrum* also showed a positive correlation between snow cover duration and bee abundance. And for *L. nigrum*, growing degree day accumulation was positively correlated with floral abundance.

Similar to the *Lasioglossum*, snow cover duration had a positive effect on the abundance of *Hoplitis robusta*, *Halictus virgatellus* and *Ha. rubicundus*. The floral duration of plants associated with the *Halictus* species additionally showed a positive correlation with growing degree day accumulation. For *Panurginus cressoniellus*, growing degree day accumulation was positively associated with floral duration and floral abundance, and snow cover duration was positively correlated with floral abundance. Snow cover duration likewise had a weak positive effect on the abundance of flowers associated with *Pseudopanurgus bakeri*. There were no significant paths at $\alpha = 0.01$ associated with *Pa. ineptus*. Finally, growing degree day accumulation was negatively correlated with the abundance of *D. harveyi* and negatively affected the floral duration of plants associated with *Hylaeus annulatus*.

4. Discussion

In multitrophic systems, such as those involving plant–pollinator interactions, climate can affect species directly as well as indirectly via the resources they rely upon [5,6]. Here, we assessed the direct and floral-mediated indirect effects of climate on a diverse assemblage of bee species in the Rocky Mountains of Colorado, USA, an area experiencing rapid rates of climate change [20,40]. We found diverse responses to climate among the 13 solitary bee species we studied, with a notable, positive, direct effect for most species of snow cover duration on both bee abundance in the following year and flowering plant abundance and duration. In contrast, we did not observe significant indirect climate effects on bees via flowers. These findings offer insight into the mechanisms by which climate and ongoing climate change, particularly shorter snow cover duration, may influence wild bee communities now and in the future.

Among most of the species we studied (8 of 13), there was strong evidence for direct effects of snow cover duration on mean bee abundance the following year. Snow cover has a prevailing influence on seasonality—snowmelt signals the beginning of the flowering/foraging season in the spring and places a hard stop on the growing season in autumn. Snow cover is likewise strongly associated with temperature and precipitation [66] and thus serves as a robust indicator of overall climatic variation among the years. Our findings demonstrate that years with prolonged snow cover are associated with higher bee abundance in the subsequent generation. This effect is likely mediated by the importance of snow cover to overwintering by the maternal generation [67]. During the winter in temperate climates, bees go into diapause, a physiological state of arrested development and reduced metabolic activity [68]. Cold temperatures allow for efficient use of energy reserves during diapause, while warm or fluctuating temperatures, often present in autumn and spring, can lead to inefficient energy expenditure, particularly

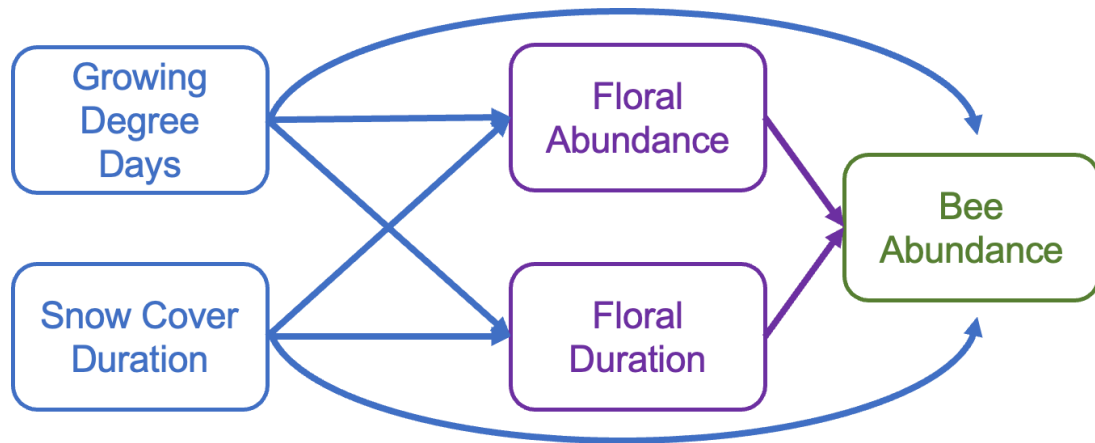


Figure 1. All hypothesized direct and indirect paths included in the structural equation models. From left to right, climate variables are shown in blue, followed by floral variables in purple and bee abundance in green.

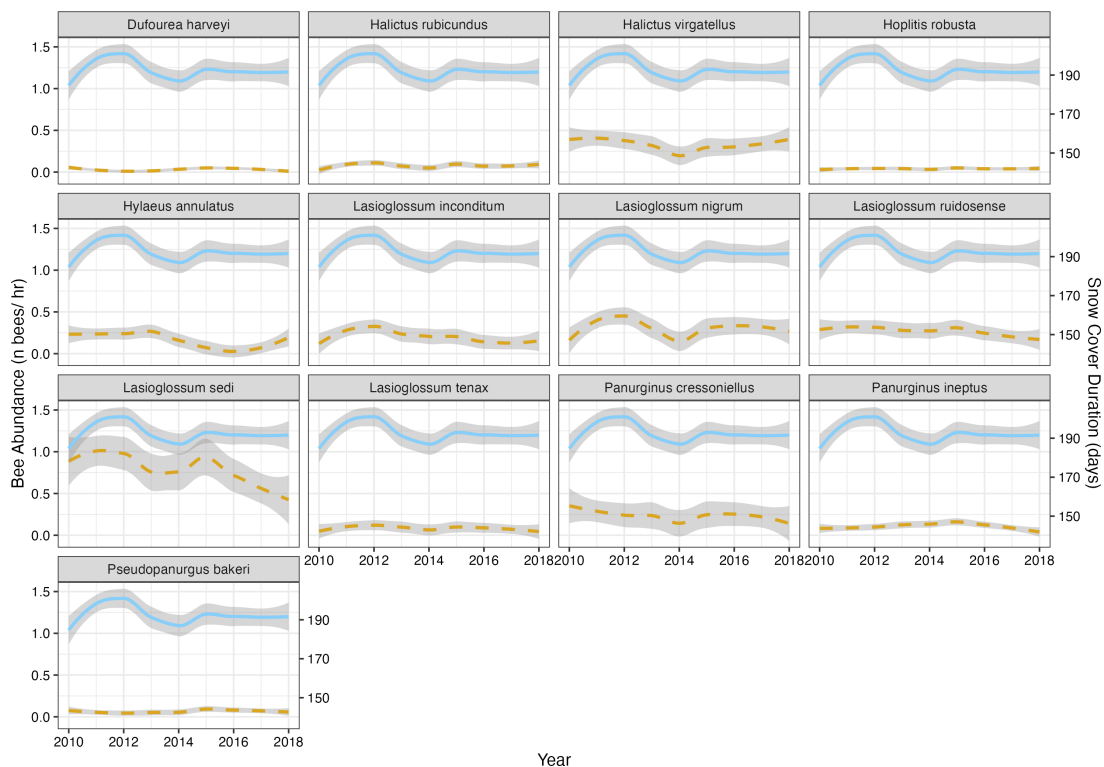


Figure 2. Variation in bee mean abundance (year) and snow cover duration (year – 1) across time, by species. Lines illustrate a generalized additive model smooth across data points, with shaded areas indicating 95% confidence intervals. Snow cover duration (solid blue) and bee mean abundance (dashed gold) are plotted together to illustrate their relationship across time.

in the absence of temperature-stabilizing snow cover [56,69]. Efficient energy use during overwintering can lead to greater overwintering survival, higher fecundity and larger bee population sizes the following year [70,71]. For instance, previous work on *Osmia* showed that delayed diapause leads to greater fat body depletion, decreased winter survival [56], decreased post-emergence longevity, delayed egg maturation and reduced larval provisioning [70], as well as reduced ovary development and fecundity [71]. These mechanistic findings are consistent with the ecological patterns we observed, which demonstrate downstream consequences of shortened snow cover duration on bee abundances the following year for a diversity of bees. Long-term climate data for these sites show that spring snowmelt has shifted earlier by nearly two weeks over the past four decades [10], potentially impacting overwintering stability and reducing bee population sizes.

Snow cover duration may affect bee species differently, depending upon their functional traits such as nesting, overwintering stage and seasonality [70]. Ground-nesting bees may be particularly vulnerable to changes in snow cover duration, due to the moderating effect that snow cover has on soil temperature variability [72]. All but two species (*H. robusta* and *Hy. annulatus*) in our study nest belowground (electronic supplementary material, table S5) [43], which could explain the significant role of snow cover duration in this study. Still, for *H. robusta*, which nests in pithy stems [73], there was a positive relationship between abundance and snow cover duration. Aboveground-nesting bees may be sensitive to air temperature fluctuations, which may correlate with snow duration. While our analysis does not parse effects of snow cover duration from correlated climate variables (e.g. temperature and precipitation), additional climate factors could be explored further in the future. Many of the bees in our study also overwintered as adults (electronic supplementary material, table S5), and all seven species that overwinter as

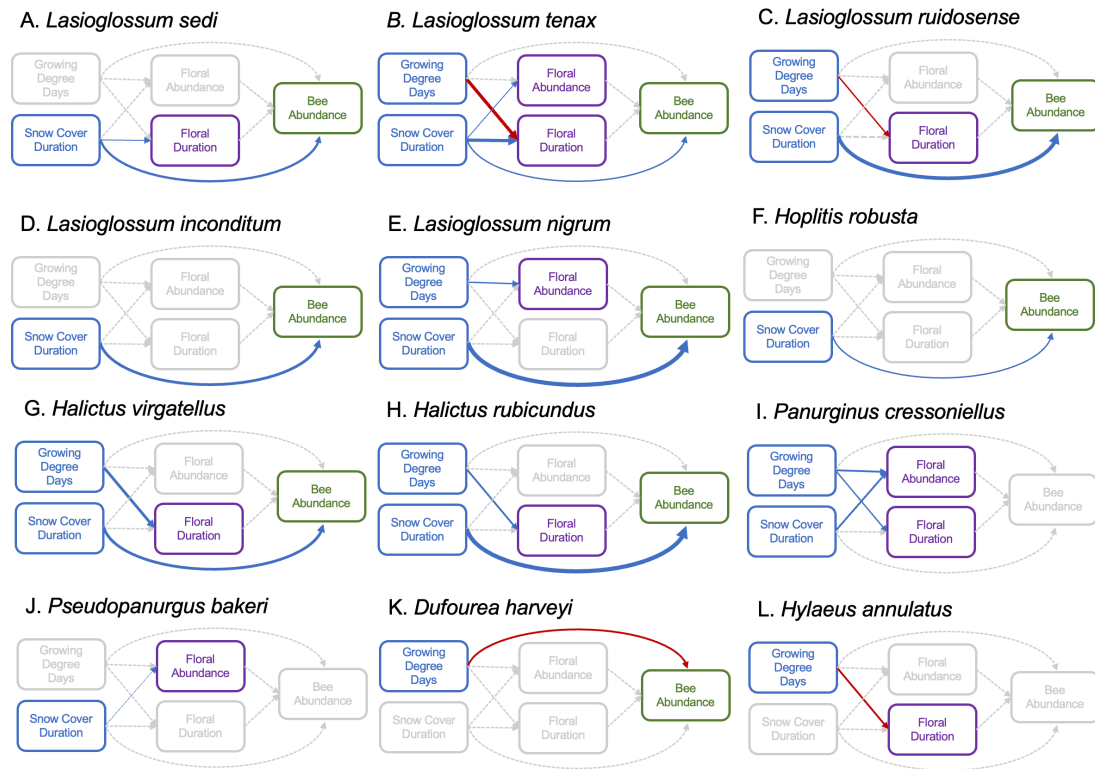


Figure 3. Path diagrams for each bee species illustrating significant direct and indirect relationships between climate variables (blue), floral variables (purple) and bee mean abundance (green). Solid, coloured arrows indicate significant paths, with arrow thickness corresponding to the marginal R^2 value and arrow colour corresponding to effect direction (blue = positive effect, red = negative effect). Non-significant paths are greyed out.

adults showed a significant, positive correlation between snow cover duration and bee abundance. This finding is consistent with Bosch *et al.* [70], who suggest that adult-overwintering bees may be more susceptible to late winter onset because they experience an elevated rate of winter weight loss compared with the prepupal stage. None of the bees that overwinter in the prepupal stage, except *H. robusta*, showed a significant effect of snow cover duration on bee abundance. But, as previously discussed, *H. robusta* may be susceptible to cold temperatures as an aboveground-nesting bee. Each of the bees that showed a positive correlation with snow cover duration tended to be spring bees (electronic supplementary material, figure S5). This is somewhat surprising given that longer snow cover duration is associated with later spring snowmelt, which would theoretically shorten foraging time for spring bees. However, snow cover may also prevent spring bees from emerging too early and risking exposure to cold temperatures in early spring. In our study system, abundant bee species tended to have similar traits (e.g. nesting below ground, overwintering as adults), and sample sizes were too small to statistically examine species with other traits (though see electronic supplementary material, figure S6). In the future, more extensive bee sampling may enable explicit assessment of bees' direct and indirect responses to climate as a function of their functional traits.

Beyond direct effects on bees, climate variables had direct effects on flowering plant communities. Snow cover duration was positively associated with the abundance and/or bloom duration of flowering host plants for 4 of the 13 species studied. These findings are consistent with Ogilvie *et al.* [10], who found that in years with later snowmelt, floral duration increased among flowering plants associated with three different bumblebee species. While earlier snowmelt expands the flowering season, the proportion of low floral abundance days increases, driven by spring frost damage [20] and/or elevated summer temperature and drought [41]. Accumulation of growing degree days was also positively associated with floral abundance for the plants visited by *L. nigrum* and *Pa. cressoniellus*. Conversely, growing degree day accumulation had a variable effect on floral duration, showing a negative effect for three species (*L. tenax*, *L. ruidosense* and *Hy. annulatus*) and a positive effect for three other species (*Ha. virgatellus*, *Ha. rubicundus* and *Pa. cressoniellus*). Previous work in agricultural systems shows that bloom duration depends upon growing degree day accumulation both before and during bloom, expanding bloom duration under certain conditions [74] but shortening it under others [75]. In this system, warming temperatures have led to a more intense mid-season dearth, bifurcating bloom into spring and late summer periods with lower flower abundance in mid-summer [41]. Thus, years with high growing degree accumulation may truncate floral duration in spring or autumn and decrease floral abundance in mid-season. These complex dynamics likely underscore the varied responses we observed among different genera's floral communities in response to growing degree day accumulation.

While growing degree day accumulation can predict insect phenology [52,53], we only detected a significant, direct relationship between bee abundance in the following year and growing degree days for one species (*D. harveyi*). *Dufourea harveyi* is a late-season bee, and accumulation of growing degree days had a negative effect on its abundance the following year. Rapid accumulation of growing degree days early in the season may lead to earlier emergence of this bee [52,76], and as an oligolectic species, this may put it at greater risk of temporal mismatch with its flowering host plants if the host plants do not track growing degree accumulation in the same way [52,77,78]. Indeed, other late-season species such as *Hy. annulatus* and *P. bakeri* showed no correlation with growing degree accumulation but are polylectic. Similar to our findings, a flight-cage study

found that a later-season specialist *Osmia* species had significantly lower fecundity following a short (3 day) temporal mismatch with its host plant, compared with early/mid-season generalist *Osmia* species [79]. Warm days, associated with growing degree day accumulation, may also correlate with the opportunity to forage. Here, the lack of correlation between growing degree day accumulation and bee mean population the following season for most species in our study may suggest that bees had sufficient opportunity to forage across years.

Remarkably, we found poor evidence for floral-mediated indirect effects of climate on bee abundance, with none of the 13 species exhibiting a significant indirect path from any of our climate metrics to flower metrics to bee abundance. This finding contrasts with similar work on three bumblebee species in the same study system, which found primarily indirect effects of climate on bees via floral resources [10]. This discrepancy may stem from differences in body size and sociality among species. Compared with *Bombus*, the species in this study are quite small (electronic supplementary material, table S5) and therefore require fewer floral resources on a per-bee basis [35]. These bees may be able to obtain all the resources they need from relatively few flowering plants without facing resource limitation. *Bombus* are also eusocial and produce large colonies through the foraging effort of a worker population, and colony growth has been connected to the quantity of floral resources in the landscape [80,81]. However, we examined trends for only 13 solitary bee species out of a diverse community with over 100 species. Other solitary species could show different trends and could be examined in the future (see electronic supplementary material, figure S6).

Mountainous ecosystems such as the Rocky Mountains, USA, are experiencing rapid climate change [39], including earlier spring snowmelt. We found that shorter snow cover duration drives lower bee abundance across multiple species of solitary bees. Based on results from our structural equation models, snow cover duration primarily had direct effects on bee abundance in the following year, rather than indirect effects through floral resources. Snow cover may provide temperature stability in the spring and autumn, improving diapause conditions for the maternal generation and leading to higher fecundity and bee population sizes the following year. These findings demonstrate direct, multi-generational effects of climate on multiple bee species and highlight how future climate change may affect bee populations.

Ethics. Invertebrates are exempt from the Institutional Animal Care and Use Committee's (IACUC) oversight. All bee sampling was done in accordance with Standardized Protocol For Collecting Community-level Bee Data [82]. Specimens were collected under the Rocky Mountain Biological Laboratory Special Use Permit, issued by the US Forest Service.

Data accessibility. Code and required data are available on Zenodo [83].

Supplementary material is available online [84].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. G.Q.: data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; M.R.K.: conceptualization, data curation, formal analysis, investigation, methodology, validation, writing—review and editing; M.S.: conceptualization, data curation, formal analysis, investigation, methodology, validation, writing—review and editing; R.E.I.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This work was funded by NSF awards DEB-1354104, DEB-0922080 and DEB-2016749, the USGS Southeast Climate Adaptation Science Center (Cooperative Agreement G23AC00548) and North Carolina State University. Installation, maintenance and publication of data from the RMBL weather stations were supported by NSF award MRI-0821369 and DOE funding as well as ongoing operational support from the RMBL, the Upper Gunnison River Water Conservancy District and the LBNL Science Focus Area 2.0 project. Any opinions, findings, conclusions or recommendations are those of the authors and do not necessarily represent the views of the funding agencies.

Acknowledgements. We thank the many students, research assistants and technicians whose collection of these data made this research possible, including S. Griffin, G. Pardee and R. Dickson, as well as Billy Barr for the collection of the climate data and I. Breckheimer for analysing the climate data. We are also grateful to J. Ogilvie for curating the plant–pollinator association datasets, climate data and piecewise SEM code used in this study, as well as P. CaraDonna, J. Bain and J. Forrest for their contributions to the plant–pollinator association datasets. RMBL Science Director J. Reithel provided access to field sites, and the RMBL Phenology Group (D. Inouye, B. Inouye and N. Underwood) provided intellectual synergy.

References

- Forister ML, Pelton EM, Black SH. 2019 Declines in insect abundance and diversity: we know enough to act now. *Conserv. Sci. Pract.* **1**, e80. (doi:10.1111/csp2.80)
- Brondizio E, Diaz S. Global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. Zenodo. See <https://zenodo.org/doi/10.5281/zenodo.3831673>.
- Wagner DL. 2020 Insect declines in the anthropocene. *Annu. Rev. Entomol.* **65**, 457–480. (doi:10.1146/annurev-ento-011019-025151)
- Intergovernmental Panel on Climate Change. 2023 *Climate change 2023: synthesis report. Contribution of Working Groups I, II and III to the sixth assessment report of the Intergovernmental Panel on Climate Change*. Intergovernmental Panel on Climate Change. See https://www.ipcc.ch/report/ar6/syr/downloads/report/IPCC_AR6_SYR_LongerReport.pdf.
- Harrington R, Woiwod I, Sparks T. 1999 Climate change and trophic interactions. *Trends Ecol. Evol.* **14**, 146–150. (doi:10.1016/S0169-5347(99)01604-3)
- Rosenblatt AE, Schmitz OJ. 2014 Interactive effects of multiple climate change variables on trophic interactions: a meta-analysis. *Clim. Chang. Responses* **1**, 8. (doi:10.1186/s40665-014-0008-y)
- Hu N, Bourdeau PE, Harlos C, Liu Y, Hollander J. 2022 Meta-analysis reveals variance in tolerance to climate change across marine trophic levels. *Sci. Total Environ.* **827**, 154244. (doi:10.1016/j.scitotenv.2022.154244)
- Boggs CL, Inouye DW. 2012 A single climate driver has direct and indirect effects on insect population dynamics. *Ecol. Lett.* **15**, 502–508. (doi:10.1111/j.1461-0248.2012.01766.x)

9. Scaven VL, Rafferty NE. 2013 Physiological effects of climate warming on flowering plants and insect pollinators and potential consequences for their interactions. *Curr. Zool.* **59**, 418–426. (doi:10.1093/czoolo/59.3.418)
10. Ogilvie JE, Griffin SR, Gezon ZJ, Inouye BD, Underwood N, Inouye DW, Irwin RE. 2017 Interannual bumble bee abundance is driven by indirect climate effects on floral resource phenology. *Ecol. Lett.* **20**, 1507–1515. (doi:10.1111/ele.12854)
11. Melone GG, Stuligross C, Williams NM. 2024 Heatwaves increase larval mortality and delay development of a solitary bee. *Ecol. Entomol.* **49**, 433–444. (doi:10.1111/een.13317)
12. Gérard M, Gardelin E, Lehmann P, Roberts KT, Sepúlveda-Rodríguez G, Sisquella C, Baird E. 2024 Experimental elevated temperature affects bumblebee foraging and flight speed. *Proc. R. Soc. B* **291**, 20241598. (doi:10.1098/rspb.2024.1598)
13. Pyke GH, Inouye DW, Thomson JD. 2011 Activity and abundance of bumble bees near Crested Butte, Colorado: diel, seasonal, and elevation effects. *Ecol. Entomol.* **36**, 511–521. (doi:10.1111/j.1365-2311.2011.01295.x)
14. Zaragoza-Trello C, Vilà M, Bartomeus I. 2021 Interaction between warming and landscape foraging resource availability on solitary bee reproduction. *J. Anim. Ecol.* **90**, 2536–2546. (doi:10.1111/1365-2656.13559)
15. Ghisbain G, Thiery W, Massonnet F, Erazo D, Rasmont P, Michez D, Dellicour S. 2024 Projected decline in European bumblebee populations in the twenty-first century. *Nature* **628**, 337–341. (doi:10.1038/s41586-023-06471-0)
16. Walters J, Barlass M, Fisher R, Isaacs R. 2024 Extreme heat exposure of host plants indirectly reduces solitary bee fecundity and survival. *Proc. R. Soc. B* **291**, 20240714. (doi:10.1098/rspb.2024.0714)
17. Descamps C, Jambrek A, Quinet M, Jacquemart AL. 2021 Warm temperatures reduce flower attractiveness and bumblebee foraging. *Insects* **12**, 493. (doi:10.3390/insects12060493)
18. Stemkovski M, Dickson RG, Griffin SR, Inouye BD, Inouye DW, Pardee GL, Underwood N, Irwin RE. 2023 Skewness in bee and flower phenological distributions. *Ecology* **104**, e3890. (doi:10.1002/ecy.3890)
19. Rosenberger NM, Hemberger JA, Williams NM. 2024 Heatwaves exacerbate pollen limitation through reductions in pollen production and pollen vigour. *AoB Plants* **16**, pla045. (doi:10.1093/aobpla/plae045)
20. Inouye DW. 2008 Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* **89**, 353–362. (doi:10.1890/06-2128.1)
21. Johansson J, Bolmgren K, Jonzén N. 2013 Climate change and the optimal flowering time of annual plants in seasonal environments. *Glob. Chang. Biol.* **19**, 197–207. (doi:10.1111/gcb.12006)
22. CaraDonna PJ, Iler AM, Inouye DW. 2014 Shifts in flowering phenology reshape a subalpine plant community. *Proc. Natl Acad. Sci. USA* **111**, 4916–4921. (doi:10.1073/pnas.1323073111)
23. Plos C, Stelbrink N, Römermann C, Knight TM, Hensen I. 2023 Abiotic conditions affect nectar properties and flower visitation in four herbaceous plant species. *Flora* **303**, 152279. (doi:10.1016/j.flora.2023.152279)
24. Renner SS, Zohner CM. 2018 Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annu. Rev. Ecol. Evol. Syst.* **49**, 165–182. (doi:10.1146/annurev-ecolsys-110617-062535)
25. Walters J, Zavalnitskaya J, Isaacs R, Szendrei Z. 2022 Heat of the moment: extreme heat poses a risk to bee–plant interactions and crop yields. *Curr. Opin. Insect Sci.* **52**, 100927. (doi:10.1016/j.cois.2022.100927)
26. Walters J, Isaacs R. 2023 Pollen germination and tube growth in Northern highbush blueberry are inhibited by extreme heat. *HortScience* **58**, 635–642. (doi:10.21273/hortsci17075-23)
27. Saavedra F, Inouye DW, Price MV, Harte J. 2003 Changes in flowering and abundance of *Delphinium nuttallianum* (Ranunculaceae) in response to a subalpine climate warming experiment. *Glob. Chang. Biol.* **9**, 885–894. (doi:10.1046/j.1365-2486.2003.00635.x)
28. Miller-Rushing AJ, Inouye DW. 2009 Variation in the impact of climate change on flowering phenology and abundance: an examination of two pairs of closely related wildflower species. *Am. J. Bot.* **96**, 1821–1829. (doi:10.3732/ajb.0800411)
29. Papanikolaou AD, Kühn I, Frenzel M, Schweiger O. 2017 Landscape heterogeneity enhances stability of wild bee abundance under highly varying temperature, but not under highly varying precipitation. *Landsc. Ecol.* **32**, 581–593. (doi:10.1007/s10980-016-0471-x)
30. Kazenel MR, Wright KW, Griswold T, Whitney KD, Rudgers JA. 2024 Heat and desiccation tolerances predict bee abundance under climate change. *Nature* **628**, 342–348. (doi:10.1038/s41586-024-07241-2)
31. Soroye P, Newbold T, Kerr J. 2020 Climate change contributes to widespread declines among bumble bees across continents. *Science* **367**, 685–688. (doi:10.1126/science.aax8591)
32. Zapata-Hernández G, Gajardo-Rojas M, Calderón-Seguel M, Muñoz AA, Yáñez KP, Requier F, Fontúrbel FE, Ormeño-Arriagada PI, Arrieta H. 2024 Advances and knowledge gaps on climate change impacts on honey bees and beekeeping: a systematic review. *Glob. Chang. Biol.* **30**, e17219. (doi:10.1111/gcb.17219)
33. Maebe K, Hart AF, Marshall L, Vandamme P, Vereecken NJ, Michez D, Smagghe G. 2021 Bumblebee resilience to climate change, through plastic and adaptive responses. *Glob. Chang. Biol.* **27**, 4223–4237. (doi:10.1111/gcb.15751)
34. Heinrich B. 2004 *Bumblebee economics*. Cambridge, MA: Harvard University Press.
35. Müller A, Diener S, Schnyder S, Stutz K, Sedivy C, Dorn S. 2006 Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee–flower relationships. *Biol. Conserv.* **130**, 604–615. (doi:10.1016/j.biocon.2006.01.023)
36. Cane JH, Tepedino VJ. 2017 Gauging the effect of honey bee pollen collection on native bee communities. *Conserv. Lett.* **10**, 205–210. (doi:10.1111/conl.12263)
37. Leonhardt SD, Blüthgen N. 2012 The same, but different: pollen foraging in honeybee and bumblebee colonies. *Apidologie* **43**, 449–464. (doi:10.1007/s13592-011-0112-y)
38. Miller-Struttmann NE. 2024 Climate change predicted to exacerbate declines in bee populations. *Nature* **628**, 270–271. (doi:10.1038/d41586-024-00681-w)
39. Nogués-Bravo D, Araújo MB, Errea MP, Martínez-Rica JP. 2007 Exposure of global mountain systems to climate warming during the 21st Century. *Glob. Environ. Chang.* **17**, 420–428. (doi:10.1016/j.gloenvcha.2006.11.007)
40. Iler AM, Høye TT, Inouye DW, Schmidt NM. 2013 Nonlinear flowering responses to climate: are species approaching their limits of phenological change? *Phil. Trans. R. Soc. B* **368**, 20120489. (doi:10.1098/rstb.2012.0489)
41. Aldridge G, Inouye DW, Forrest JRK, Barr WA, Miller-Rushing AJ. 2011 Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change: seasonal low in montane flowering. *J. Ecol.* **99**, 905–913. (doi:10.1111/j.1365-2745.2011.01826.x)
42. Gezon ZJ, Wyman ES, Ascher JS, Inouye DW, Irwin RE. 2015 The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods Ecol. Evol.* **6**, 1044–1054. (doi:10.1111/2041-210x.12375)
43. Stemkovski M *et al.* 2020 Bee phenology is predicted by climatic variation and functional traits. *Ecol. Lett.* **23**, 1589–1598. (doi:10.1111/ele.13583)
44. Eickwort GC, Eickwort JM, Gordon J, Eickwort MA, Wcislo WT. 1996 Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **38**, 227–233. (doi:10.1007/s002650050236)

45. Soucy SL, Danforth BN. 2002 Nesting biology and socially polymorphic behavior of the sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Ann. Entomol. Soc. Am.* **95**, 57–65. (doi:10.1554/0014-3820(2002)056[0330:potsps]2.0.co;2)
46. Irwin R, Inouye B, Inouye D, Underwood N. 2018 Long-term bee phenology and abundance data at the RMBL, Gothic, Colorado. OSF. (doi:10.17605/OSF.IO/KMXYN)
47. Schuh RT, Hewson-Smith S, Ascher JS. 2010 Specimen databases: a case study in entomology using web-based software. *Am. Entomol.* **56**, 206–216. (doi:10.1093/ae/56.4.206)
48. Roulston TH, Goodell K. 2011 The role of resources and risks in regulating wild bee populations. *Annu. Rev. Entomol.* **56**, 293–312. (doi:10.1146/annurev-ento-120709-144802)
49. Kazenel MR *et al.* Climate and floral availability predict solitary bee sex ratios in a montane ecosystem. *Ecology* In review.
50. Battel B. 2017 *Understanding growing degree-days*. MSU extension. See https://www.canr.msu.edu/news/understanding_growing_degree_days (accessed 17 August 2021).
51. Jackson MT. 1966 Effects of microclimate on spring flowering phenology. *Ecology* **47**, 407–415. (doi:10.2307/1932980)
52. Forrest JRK, Thomson JD. 2011 An examination of synchrony between insect emergence and flowering in Rocky Mountain meadows. *Ecol. Monogr.* **81**, 469–491. (doi:10.1890/10-1885.1)
53. Cane J. 2021 Global warming, advancing bloom and evidence for pollinator plasticity from long-term bee emergence monitoring. *Insects* **12**, 457. (doi:10.3390/insects12050457)
54. Inouye DW, Morales MA, Dodge GJ. 2002 Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. *Oecologia* **130**, 543–550. (doi:10.1007/s00442-001-0835-y)
55. Pardee GL, Jensen IO, Inouye DW, Irwin RE. 2019 The individual and combined effects of snowmelt timing and frost exposure on the reproductive success of montane forbs. *J. Ecol.* **107**, 1970–1981. (doi:10.1111/1365-2745.13152)
56. Sgolastra F, Kemp WP, Buckner JS, Pitts-Singer TL, Maini S, Bosch J. 2011 The long summer: pre-wintering temperatures affect metabolic expenditure and winter survival in a solitary bee. *J. Insect Physiol.* **57**, 1651–1659. (doi:10.1016/j.jinsphys.2011.08.017)
57. Bosch J, Kemp WP. 2003 Effect of wintering duration and temperature on survival and emergence time in males of the orchard pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). *Environ. Entomol.* **32**, 711–716. (doi:10.1603/0046-225x-32.4.711)
58. Henderson IR, Shindo C, Dean C. 2003 The need for winter in the switch to flowering. *Annu. Rev. Genet.* **37**, 371–392. (doi:10.1146/annurev.genet.37.110801.142640)
59. R Core Team. 2024 R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
60. Lefcheck JS. 2016 piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods Ecol. Evol.* **7**, 573–579. (doi:10.1111/2041-210x.12512)
61. Grace JB *et al.* 2007 Does species diversity limit productivity in natural grassland communities? *Ecol. Lett.* **10**, 680–689. (doi:10.1111/j.1461-0248.2007.01058.x)
62. Shipley B. 2016 *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference with R*, 2nd edn. Cambridge, UK: Cambridge University Press.
63. Shipley B. 2000 A new inferential test for path models based on directed acyclic graphs. *Struct. Equ. Model. Multidiscip. J.* **7**, 206–218. (doi:10.1207/S15328007SEM0702_4)
64. Pinheiro J, Bates D, DebRoy S. 2020 nlme: linear and nonlinear mixed effects models. CRAN: Contributed Packages. The R Foundation. (doi:10.32614/cran.package.nlme)
65. Shipley B. 2013 The AIC model selection method applied to path analytic models compared using a d-separation test. *Ecology* **94**, 560–564. (doi:10.1890/12-0976.1)
66. Switanek M, Resch G, Gobiet A, Günther D, Marty C, Schöner W. 2024 Snow depth sensitivity to mean temperature, precipitation, and elevation in the Austrian and Swiss Alps. *Cryosphere* **18**, 6005–6026. (doi:10.5194/tc-18-6005-2024)
67. Bale JS, Hayward SAL. 2010 Insect overwintering in a changing climate. *J. Exp. Biol.* **213**, 980–994. (doi:10.1242/jeb.037911)
68. Denlinger DL. 2022 *Insect diapause*. Cambridge, UK: Cambridge University Press. (doi:10.1017/9781108609364)
69. Williams CM, Marshall KE, MacMillan HA, Dzurisin JDK, Hellmann JJ, Sinclair BJ. 2012 Thermal variability increases the impact of autumnal warming and drives metabolic depression in an overwintering butterfly. *PLoS One* **7**, e34470. (doi:10.1371/journal.pone.0034470)
70. Bosch J, Sgolastra F, Kemp WP. 2010 Timing of eclosion affects diapause development, fat body consumption and longevity in *Osmia lignaria*, a univoltine, adult-wintering solitary bee. *J. Insect Physiol.* **56**, 1949–1957. (doi:10.1016/j.jinsphys.2010.08.017)
71. Fliszkiewicz M, Giejdasz K, Wasielewski O, Krishnan N. 2012 Influence of winter temperature and simulated climate change on body mass and fat body depletion during diapause in adults of the solitary bee, *Osmia rufa* (Hymenoptera: Megachilidae). *Environ. Entomol.* **41**, 1621–1630. (doi:10.1603/en12004)
72. Pauli JN, Zuckerberg B, Whiteman JP, Porter W. 2013 The subnivium: a deteriorating seasonal refugium. *Front. Ecol. Environ.* **11**, 260–267. (doi:10.1890/120222)
73. Gibbs J *et al.* 2023 A checklist of the bees (Hymenoptera: Apoidea) of Manitoba, Canada. *Can. Entomol.* **155**, e3. (doi:10.4039/tce.2022.45)
74. Covert MM. 2011 The influence of chilling and heat accumulation on bloom timing, bloom length and crop yield in almonds (*Prunus dulcis* (Mill.)). Thesis, California Polytechnic State University, San Luis Obispo, CA. (doi:10.15368/theses.2011.222)
75. Abbott DL. 1962 The effect of four controlled winter temperatures on the flowering and fruiting of the apple. *J. Hortic. Sci.* **37**, 272–284. (doi:10.1080/00221589.1962.11514046)
76. Pitts-Singer TL, Bosch J, Kemp WP, Trostle GE. Field use of an incubation box for improved emergence timing of *Osmia lignaria* populations used for orchard pollination. *Apidologie* **39**, 235–246. (doi:10.1051/apido:2007061)
77. Bartomeus I, Ascher JS, Wagner D, Danforth BN, Colla S, Kornbluth S, Winfree R. 2011 Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proc. Natl Acad. Sci. USA* **108**, 20645–20649. (doi:10.1073/pnas.1115559108)
78. Kudo G, Ida TY. 2013 Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* **94**, 2311–2320. (doi:10.1890/12-2003.1)
79. Schenk M, Krauss J, Holzschuh A. 2018 Desynchronizations in bee–plant interactions cause severe fitness losses in solitary bees. *J. Anim. Ecol.* **87**, 139–149. (doi:10.1111/1365-2656.12694)
80. Williams NM, Regetz J, Kremen C. 2012 Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. *Ecology* **93**, 1049–1058. (doi:10.1890/11-1006.1)
81. Quinlan GM, Milbrath MO, Otto CRV, Isaacs R. 2021 Honey bee (*Apis mellifera*) colonies benefit from grassland/ pasture while bumble bee (*Bombus impatiens*) colonies in the same landscapes benefit from non-corn/soybean cropland. *PLoS One* **16**, e0257701. (doi:10.1371/journal.pone.0257701)
82. Levenson H *et al.* Standardized protocol for collecting community-level bee data. *J. Melittol.* **123**, 22649. (doi:10.17161/jom.vi123.22649)
83. Quinlan G, Kazenel M, Stemkovski M, Irwin R. 2025 Data and code for: Shorter seasonal snow cover poses a risk to solitary bee populations in a mountainous ecosystem. Zenodo. See <https://doi.org/10.5281/zenodo.17525714>.
84. Quinlan G, Kazenel MR, Stemkovski M, Irwin RE. 2025 Supplementary material from: Shorter seasonal snow cover poses a risk to solitary bee populations in a mountainous ecosystem. Figshare. (doi:10.6084/m9.figshare.c.8145750)