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Life-history traits predict responses of wild bees to climate variation

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Life-history traits, which are physical traits or behaviours that affect growth, survivorship and reproduction, could play an important role in how well organisms respond to environmental change. By looking for trait-based responses within groups, we can gain a mechanistic understanding of why environmental change might favour or penalize certain species over others. We monitored the abundance of at least 154 bee species for 8 consecutive years in a subalpine region of the Rocky Mountains to ask whether bees respond differently to changes in abiotic conditions based on their life-history traits. We found that comb-building cavity nesters and larger bodied bees declined in relative abundance with increasing temperatures, while smaller, soil-nesting bees increased. Further, bees with narrower diet breadths increased in relative abundance with decreased rainfall. Finally, reduced snowpack was associated with reduced relative abundance of bees that overwintered as prepupae whereas bees that overwintered as adults increased in relative abundance, suggesting that overwintering conditions might affect body size, lipid content and overwintering survival. Taken together, our results show how climate change may reshape bee pollinator communities, with bees with certain traits increasing in abundance and others declining, potentially leading to novel plant–pollinator interactions and changes in plant reproduction.

1. Introduction

Unprecedented global warming is causing species to undergo changes in distribution and abundance [1–3]. These climate change responses can be highly variable among species, even within guilds, with some species performing better under climate change while other species are declining and becoming extirpated [4,5]. Thus, it is difficult to make predictions about how entire communities will shift under a changing climate. However, recent studies suggest that an examination of consistent abundance responses within groups based on life-history traits can help predict how biodiversity will be affected by climate change [6,7]. Further, because life-history traits that predict responses to environmental change can also relate to traits that determine species' functional roles in ecosystems, a trait-based approach may provide insight into how climate change will affect important ecosystem functions and services, such as pollination [8,9].

Bees are dominant pollinators globally [9] and are highly diverse in sociality, dietary breadth, body size and nesting behaviour, and these differences have been shown to affect how bees respond to environmental change [7,10–13]. For example, increased urbanization results in declines of soil-nesting bees due to the loss of pervious surfaces [14], and smaller bodied bees are sensitive to increased agricultural dominance across the landscape because they cannot forage as far from their nests as larger bees [15]. Environmentally induced changes in trait distributions of bee communities can modify flower preference, foraging behaviour and pollination efficiency [16], with potential cascading effects on plant–pollinator interactions, plant reproductive success and plant community composition [17–19]. While many studies have examined the effects of climate change on pollination, most have done so from the plant's perspective [20,21], by examining plant–pollinator interactions [22–24], or by focusing on eusocial bumblebees [5,25]. Few studies explore how the remaining approx. 20 000 species of bees, the majority of which are solitary, are responding to a changing climate [26–29]. This lack of data is concerning given that the abiotic environment plays a pivotal role in bee physiology and foraging activity [30]. Because increased trait diversity helps maximize pollination services and acts as a buffer against human disturbance [18], it is important to understand which groups of bees are most vulnerable to climate change and which groups might be tolerant of or even increase with climate warming.

To understand the effects of climate on bee communities and to assess the degree to which a trait-based approach can predict the response of bees to changing abiotic conditions, we collected bees every two weeks throughout the flowering season over 8 years in a montane region of the Rocky Mountains, USA. Montane systems are advantageous for studying climate change in field settings because changes in weather patterns are happening at a greater rate than in other ecosystems [31]. We hypothesized that climate change will reshape bee pollinator communities, with bees with certain traits increasing in abundance and others declining, which could lead to novel plant–pollinator interactions and changes in pollination services. Based on previous research [32], we predicted that bees would respond differently to increased summer temperatures based on their body size, with larger bees responding more negatively to higher yearly summer temperatures compared to smaller bees. Further, we predicted that bees with narrower diet breadths would be more susceptible to changing patterns in precipitation and temperature compared to bees with broader diet breadths. Finally, due to potential variation in insulation capabilities across nesting substrates [33], we predicted that bees that nest in soil would respond differently to snowpack depth and precipitation than comb-building cavity nesters or bees that nest in pre-existing or constructed holes.

2. Methods

(a) Study system and site selection

This study was conducted in meadows surrounding the Rocky Mountain Biological Laboratory (RMBL) in Gothic, Colorado, USA (elevation 2950 m). The RMBL is located in a sub-alpine region hosting over 150 species of bees and a diverse mixture of perennial flowering plants, many of which rely on bees for successful reproduction [34,35]. This area is particularly vulnerable to climate change as spring temperatures have increased by approximately 1.6°C [36], and spring snowmelt has occurred at a rate of 3.5 days earlier per decade over the last 40 years [35]. Despite long-term trends of increased temperature and earlier snowmelt, during the 8 years of data collection for this study (2009–2016), spring and summer weather patterns were highly variable, with some years experiencing earlier snowmelt and dry summers, and other years experiencing later snowmelt and heavy precipitation (electronic supplementary material, table S1). For example, year 2012 had some of the lowest snowfalls and the earliest date of bare ground over a 40-year observation period (b. barr 2020, personal communication). Though year-to-year climate variability is increasing with climate change in many regions globally [37], low snowfall and earlier snowmelt is typical of the growing season we would expect under long-term climate change projections [35,38]. Thus, we are able to use variation over the 8 years of this study to assess how bees might respond to years of higher temperatures, earlier snowmelt and drier conditions based on their life-history traits.

We collected bees from nine sampling sites and grouped them into three blocks based on elevation and proximity. Blocks were separated from each other by at least 1 km and ranged in elevation from 2884 to 3072 m (electronic supplementary material, table S2). Each block contained three sites, located between 200 m and 1 km apart (electronic supplementary material, table S2), with three regionally dominant habitat types represented: dry meadow, *Salix* spp.-dominated wet meadow and *Veratrum tenuipetalum*-dominated wet meadow [34,39].

(b) Bee dataset

Sites were sampled for bees every two weeks throughout the flowering season using the methods outlined by Gezon *et al.* (electronic supplementary material, information S1, [34]). Briefly, during each sampling period, we placed painted bowls of alternating colours (white, fluorescent blue, and florescent yellow and filled with soapy water to attract bees) on the ground every 3 m along two fixed 30 m transects between approximately 09.00 and 17.00 on clear, sunny days. Bee bowls collect predominately small- to medium-sized bees [34], so we also used a non-lethal method of collecting larger bees (in our case primarily bumblebees) by netting for 2 h at each site (1 h each in the morning and afternoon every day that bowls were out at a site). Bumblebees were captured with a net, transferred to a clear vial, identified based on pile colours using identification guides [40], marked with a non-toxic paint pen to avoid re-capturing, and then released back into the site. Because the bee bowls varied in how many hours they were out due to changing weather conditions and the growing season length, we standardized bee abundance across years by taking the weighted arithmetic mean of both male and female bees caught per hour of sampling (i.e. total individuals of a species/total hours of sampling; [37]). We only considered bees that were identified to species with the aid of 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; and see [41]). In exception to this, we were unable to identify individuals of seven genera down to species level due to the difficulty of species-level identification: *Anthidium*, *Ashmeadiella*, *Epeolus*, *Holcopasites*, *Nomada*, *Sphecodes* and *Triepeolus*. We included individuals from these genera in analyses where the life-history traits were consistent across the genus but excluded them from any analyses where the traits could differ across species within the genus.

(c) Climate variables

Following Lynn *et al.* [42], we used interpolation models to estimate the local climate variables because precise weather data were unavailable at each site. To do this, we constructed linear mixed effects models using historical data from 29 weather stations in Gunnison and Pitkin Counties, CO (including data from Snow Telemetry (SNOTEL), Southwest Climate and ENvironmental Information Collaborative (SCENIC), and RMBL stations as well as Gothic, CO data from b. barr). Models to predict the variables of interest incorporated slope, aspect and elevation as fixed effects, and water year and weather station as random effects. For model selection, we compared AICc scores of variations of the models in which the effects were iteratively removed. For all models except mean annual temperature (where including aspect did not improve model fit), we found that including all available effects produced the best fits. We trained the models on data from 1978 to 2016 and predicted variables for the years of this study. All analyses were done in R v. 3.4.0 [43] . We then compiled data on the following annual climate variables within each block to describe the climate at our sampling sites. Climate variables were chosen based on knowledge of the site as well as the literature on the environmental drivers of montane ecosystems [35,36,39,44]. These variables were average summer (May–September) and winter (October–April) temperatures; average annual rainfall; average annual snowfall (October–April) and average April snowpack (which is strongly correlated with date of bare ground; $F_{1,43} = 177.6$, $p < 0.0001$; electronic supplementary material, figure S1). Because of the annual life cycle of most native bees, their responses to variation in the abiotic environment could be due to changes that occurred in the current year or the previous year, and so we considered both current year and lagged effects. The 10 climate variables (five each from the current year and lagged year) were not strongly correlated with one another ($r < 0.40$ in most cases; electronic supplementary material, table S3) and have been shown to affect bee foraging behaviour, physiology and colony build-up (for social species) in other studies [17,26].

(d) Bee species traits

Using primary sources, we described each bee species based on six life-history traits that have been shown to be affected by changes in abiotic conditions: diet breadth (lecty), nesting substrate, spring emergence date, overwintering developmental state, parasitism (brood parasite status versus not) and body size (electronic supplementary material, table S4). For lecty, we classified species as either polylectic if bees collect pollen from flowers in multiple plant families or oligolectic if bees collect pollen from flowers in just one family [45]. Previous studies have shown that insects with narrower diet breadths are more susceptible to environmental change due to their inability to switch hosts [46,47]; thus, any changes in climate that could also affect the flowering community might affect bees differently based on their diet breadth. We described nesting based on the substrate the females use for nest construction: constructed cells, soil, large comb-building cavity nesters, and pre-existing or constructed holes. These substrates might differ in their insulation and permeability, thus affecting how well bees can acclimate to environmental changes within their nests. Early season bees might be the most susceptible to reduced snowpack and earlier snowmelt under climate change; therefore, we estimated spring emergence by determining the average number of days past date of bare ground in Gothic, CO, from b. barr's weather data that an individual of each species was first recorded across all years of our study. Overwintering state included three phases: emerged adults, unemerged adults, or prepupae/pupae. As bees that overwinter in the prepupae state must undergo additional development before emergence [48], their abundance may change with climate variables that affect bee physiology and probability of successful development [41]. We included parasitic bees in our parasitic trait analysis (brood parasite status versus not) but removed these species from our nesting and diet trait analyses as they do not collect pollen or build their own nests. As there is a severe lack of understanding of social characterization of Western North American halictid bees at high elevation, we only classified *Bombus* as eusocial in our study system. We therefore excluded sociality because this trait was highly correlated with nesting substrate as *Bombus* were also the only bees categorized as large comb-building cavity nesters. We used nesting substrate rather than sociality, as previous studies have shown differences in bee response to climate change based on nesting behaviour [41]. We estimated bee body size by measuring intertegular distance, which is the distance across a bee's thorax between the base of the wings [49], for up to 10 female specimens per species using the software program ImageJ (National Institutes of Health, USA). Previous studies have shown differences in thermal tolerance based on body size [32,50]; thus, this trait might be important in determining bee response to temperature. We ran each trait analysis separately so if life-history information for a species was missing for that specific trait, we removed the species, but included it in other trait analyses for which the life history was known.

(e) Statistical analyses

We used fourth-corner analysis in the R package ade4 [51] to identify bee life-history traits that are associated with climate variables. In our analysis, the fourth-corner correlation is the Pearson correlation between a climate variable and a trait value (or a binary indicator for a categorical trait value), calculated across individual specimens [51]. It then compares the observed correlation to two different null models, one randomizing climate variables across sites, and one randomizing trait values across species [52]. Randomization tests assume that replicate observations are exchangeable; however, we identified replicate site-years and species as two important sources of non-independence, and accordingly restricted the randomizations to make our tests more conservative. Because our sites are spatially grouped, we restricted randomizations between site-years to only occur within blocks. Because bee species are phylogenetically non-independent, we constrained species randomizations so that trait values were more likely to be exchanged between more closely related species using the methods outlined in Harrison *et al.* [53]. We used 9999 randomizations for each of our permutations, and only interpreted correlations between traits and climate if they were significant in both null model tests. Finally, we re-ran the trait analysis with *Bombus* excluded as they represent a single phylogenetically related group and comprised half of the dataset, which could bias the results independent of traits.

To visualize a significant fourth-corner correlation, we fit an abundance-weighted linear regression between site-years' community weighted mean trait value and the climate variable. This regression slope is directly proportional to the fourth-corner correlation coefficient (rescaled by the ratio of the abundance-weighted standard deviations of the trait and climate variable; [52,53]).

3. Results

Overall, we sampled 22 160 bees comprising five families, 29 genera and representing at least 154 species. The number of species collected each year ranged from 44 to 96 species. The five most common genera collected across all 8 years were *Bombus* (48.77%), *Lasioglossum* (25.47%), *Panurginus* (7.71%), *Halictus* (5.70%) and *Hylaeus* (2.68%). We were able to collect life-history traits for all 154 species through direct measurements or congeneric representatives (electronic supplementary material, table S4). We found that of the six life-history traits measured, body size, nesting substrate,

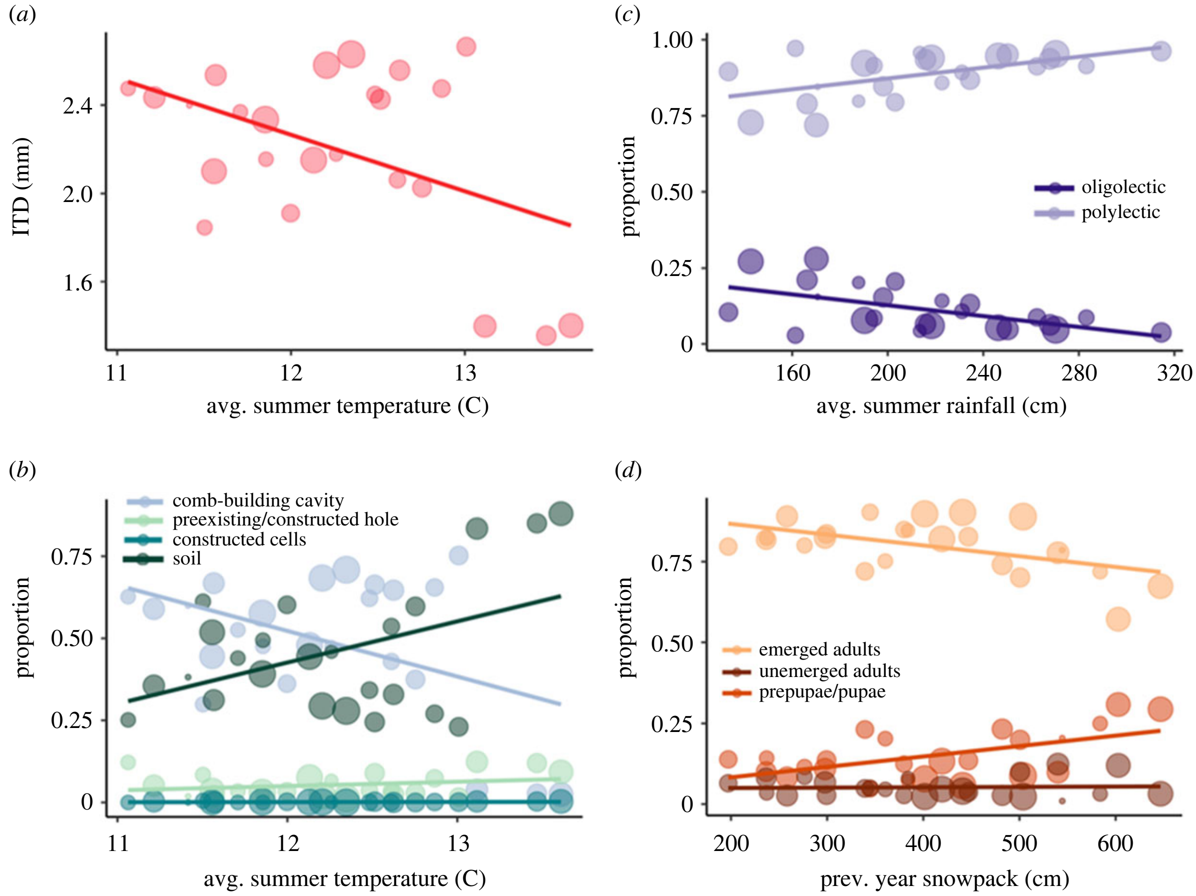

Figure 1. Out of 30 tested fourth-corner correlations between bee species' traits and climate variables, we highlight four results: (*a*) body size (ITD) and summer temperature, (*b*) nesting substrate and summer temperature, (*c*) diet breadth (lecty) and summer rainfall, and (*d*) overwintering state and snowpack from the previous year. Each tested fourth-corner correlation is proportional to the regression slope between the community weighted mean trait value (or equivalently, the proportion of individual bees expressing a categorical trait value) and the environmental variable, weighted by total abundance at each site-year ($n = 24$; larger points represent higher abundances). (Online version in colour.)

lecty, and overwintering state were significantly correlated with at least one of the climate variables (figure 1; electronic supplementary material, table S5). We did not detect any significant correlations for three climate variables (the previous year's summer temperature and the current and previous year's winter temperature), and for two traits (spring emergence date: number of days past bare ground bee was first collected) and parasitism (brood parasite versus not; figure 2).

(a) Body size

Bee body size was negatively correlated with increased temperatures ($r = -0.19$, $p = 0.02$; figure 1*a*) such that smaller bodied bees were more common and larger bodied bees were less common in warmer years. We also found a negative correlation between body size and increased snowfall from the previous year ($r = -0.12$, $p = 0.03$). We did not find any effect of temperature, snowfall or any other climate traits, on body size when *Bombus*, comprising the majority of our large-bodied bees, were excluded from our analyses ($p > 0.10$ in all cases).

(b) Nesting substrate

Bee relative abundance was also associated with temperature based on nesting substrate. We found that the relative abundance of soil-nesting bees increased with increased temperatures ($r = 0.19$, $p = 0.02$; figure 1*b*), whereas the comb-building cavity nesters, comprised only of *Bombus*, decreased in relative abundance with increased temperatures ($r = -0.21$, $p = 0.02$; figure 1*b*). Additionally, soil-nesting bees decreased in relative abundance with reduced snowfall from the previous year ($r = -0.25$, $p = 0.03$), and comb-building cavity nesters increased in relative abundance with reduced snowfall from the previous year ($r = 0.21$, $p = 0.02$). We did not find any effect of climate variables on the relative abundance of bees that nest in pre-existing holes or constructed cells ($r < 0.02$ and $p > 0.11$ in all cases). When we removed *Bombus* from our analysis, we did not find any difference in how bees responded to climate variables based on their nesting behaviour ($p > 0.15$ in all cases).

(c) Lecty

Lecty showed a strong association with precipitation from both the previous and current years. We found that the relative abundance of more specialized oligolectic bees responded positively to reduced summer rainfall (drier conditions) from both the current and previous years, whereas the relative abundance of more generalized polylectic bees responded negatively to reduced summer rainfall (current year rainfall: $r = 0.15$, $p = 0.02$ and previous year rainfall: $r = 0.17$, $p = 0.003$; figure 1*c*). When we removed *Bombus*, oligolectic bees still responded positively to drier conditions for both the current and previous years ($r = 0.17$, $p = 0.05$ and $r = 0.18$, $p = 0.04$, respectively).

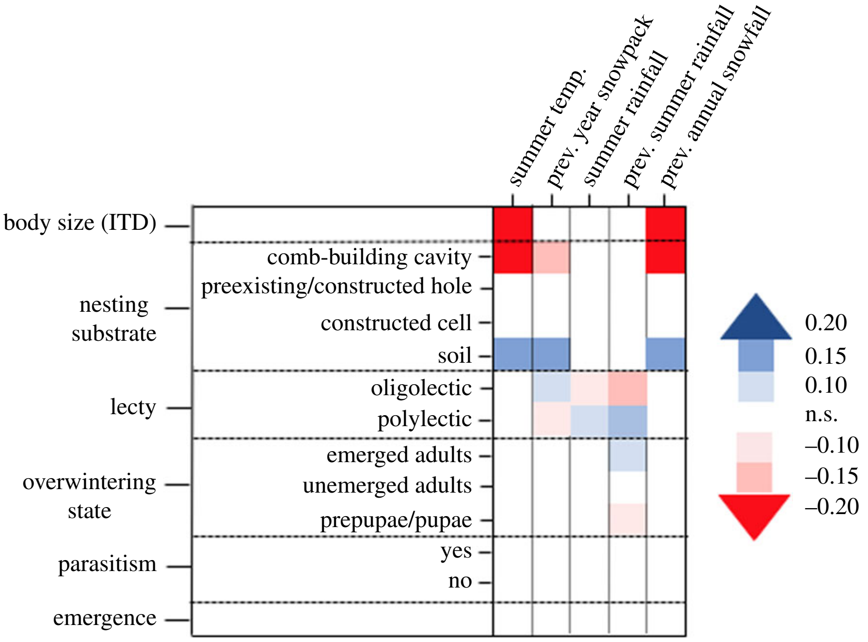

Figure 2. Correlations between six bee species trait frequencies and five environmental variables in bee communities at 24 site-years revealed both positive (blue) and negative (red) trait–climate relationships. Colour saturation indicates correlation strength. Significant correlations were detected by both a block-restricted site-year permutation test and a phylogenetically restricted species permutation test. Five additional climate variables were not significantly correlated with any bee traits (not shown; see main text). (Online version in colour.)

(d) Overwintering state

We found that the relative abundance of bees that overwinter as emerged adults responded negatively to decreased summer rainfall from the previous year ($r = -0.12$, $p = 0.05$), whereas reduced snowpack from the previous year increased the relative abundance of these bees ($r = 0.11$, $p = 0.06$; figure 1*d*). Bees that overwinter as prepupae/pupae responded positively to reduced summer rainfall ($r = 0.13$, $p = 0.01$) and negatively to reduced snowpack from the previous year ($r = -0.11$, $p = 0.07$; figure 1*d*). We found no effect of climate variables on bees that overwinter as unemerged adults ($r < 0.08$ and $p > 0.10$ in all cases; figure 1*d*). When we removed *Bombus* from the analysis, we saw similar but non-significant trends in bee response to precipitation from the previous year (emerged adults: $r = -0.11$, $p = 0.17$; prepupae/pupae: ($r = 0.14$, $p = 0.09$).

4. Discussion

We found that life-history traits predicted bee responses to changes in climate conditions, with bees of some traits likely increasing in relative abundance and others declining in relative abundance under climate change. The reshaping of biodiversity under climate change is becoming a consistent theme across many taxonomic groups, including plants [35], birds [3], butterflies and moths [46,54], and reptiles [55]. By using a trait-based approach, we gained a more mechanistic understanding of why climate change might favour some species over others. Trait–climate relationships were strongest for four traits in our study: body size, nesting substrate, lecty and overwintering state. Given the future climate change projections for this region, under a warmer and drier climate with reduced snowfall and earlier snowmelt timing, we would expect there to be a shift towards smaller and solitary bees, those with more specialized diets, and a decline in relative abundance of some of the larger-bodied and comb-building cavity nesters in our study system. Because comb-building cavity nesters were dominated by *Bombus*, which are also social, it is important to note that we cannot fully separate the effects of traits associated with sociality and nesting substrate in the analyses, and experimental studies will be needed to do so. Moreover, removing *Bombus* from our analysis showed that this group introduces strong variation in the bee community, and it is responding differently to climate change than the smaller and solitary bees. Nonetheless, our results suggest that the higher temperatures and earlier or reduced snowfall expected under climate change in montane systems [38] will likely reshape pollinator communities by favouring bees with certain life-history traits over others, with potential reductions in functional redundancy due to loss of trait diversity.

Based on our findings, increasing summer temperatures in montane systems will likely be associated with a decrease in the relative abundance of larger bodied bees. Body size of insects can have profound effects on their physiologies and thermal heat tolerances [56,57]. Bees have been shown to have species-specific differences in thermal heat tolerances [58–60], and some of this variation can be linked to species traits, such as body size. For example, larger bodied bees have been shown to forage earlier in the day when temperatures are cooler [17,61], and in a 125-year study using museum specimens, the larger bumblebee species showed significant population declines compared to smaller species [62]. This trend of smaller species being able to cope better with increased temperatures has been shown in very different contexts, including in urban systems where city centres tend to be hotter than the surrounding rural areas [53,63], and under different projected temperature scenarios in agricultural systems [17]. Thus, climatic warming might cause shifts towards smaller species on a global scale. Future studies that measure the thermal limits of an entire community of bees and across body size will allow us to determine how body size and thermal limits interact to affect local bee abundance. Because larger surface-to-volume ratios are generally favoured under warmer temperatures, smaller body size may be a common feature of climate warming at population and community levels in terrestrial and aquatic ecosystems [63].

Nesting substrate was also a strong driver of bee response to increased summer temperatures and reduced snowfall. *Bombus*, which nest in large cavities such as abandoned rodent burrows and hollow trees, had lower relative abundances under increased temperatures and reduced snowfall from the previous year. Conversely, bees that nest directly in the soil showed the opposite response. Large cavities used by *Bombus* and small, individual nests that are built directly into the soil might differ in their nesting depth and cell lining materials [33]. These differences could affect insulation, permeability and humidity inside the nest [33], which could explain why we found differences in these nesting substrates based on temperature and snow cover. Further, snowpack moderates soil temperatures; years with lower snowfall and snowpack cause soils to be more exposed to colder air temperatures and undergo higher frequencies of freeze–thaw cycles [64]. As *Bombus* queens hibernate directly in the soil, winters with reduced snowfall could expose queens to harsher conditions during hibernation.

Bee abundance associated with lecty, the diet breadth of a species, responded predominantly to precipitation. We found that the relative abundance of more-specialized oligolectic bees decreased with earlier date of bare ground shown by decreasing snowpack in April from the previous year, but increased in relative abundance with declines in annual rainfall from both the current and previous years. More generalized polylectic bees showed the opposite response. This was an unexpected result as previous studies with butterflies have shown that those with narrower diet breadths are more susceptible to environmental change due to their inability to switch hosts [46,47]. Decreased snowpack and rainfall usually leads to lower floral abundance [39], which should decrease food resources for bees. However, increased rainfall could have several negative effects on bees, and these effects could disproportionately affect oligolectic bees. We highlight that effects could be driven directly by changes in bee physiology or indirectly mediated through flowering host plants. First, rainfall could directly affect pollinators by hindering their foraging ability [65]. Though this could negatively affect all bees regardless of their diet breadth, oligolectic bees usually have shorter foraging phenologies than polylectic bees because their activity period tracks the flowering period of their host plants [66]. Thus, the foraging window for oligolectic bees could be shortened during years with prolonged periods of rain. Second, increased rainfall could cause pollen degradation, nectar dilution, altered volatiles and physical damage to the plants, which could indirectly affect bees through the loss of food resources [65]. These often-overlooked negative effects of increased rainfall could have stronger negative effects on oligoletic bees if their host plant is damaged. However, as polylectic bees can switch plant hosts, it is likely that they are benefiting from increased floral abundance of any plant species due to increased precipitation. Future studies that tease apart the relative importance of direct physiological effects of the abiotic environment versus the indirect effects mediated through floral resources on the entire bee community would yield important ecological insights. One study conducted with bumblebees showed that the indirect effects of climate on floral resources were more important than the direct effects [39]; whether this pattern holds for other bee species and life-history traits awaits further investigation.

Bees that overwinter as emerged adults increased in relative abundance with reduced snowpack from the previous year, but declined in relative abundance with reduced precipitation from the previous year. The abiotic conditions during which a bee hibernates can affect body size, lipid content and overwintering survival [67,68]. Thus, prolonged hibernation due to increased snowpack and later snowmelt timing could affect the survival of bees that overwinter as adults through the depletion of lipid storage. If the depletion of lipids leads to reduced female fitness, this may lead to lower relative abundance of bees the following summer. Experimental studies would be important in testing this hypothesis.

One important caveat to consider in the interpretation of these results is that the patterns we report are correlational, and some trait combinations, such as between larger body size and nesting substrate, were associated with one another. Further, measures of bee abundance and community traits can be affected by sampling method and environmental conditions, and it is unclear how well abundance reflects population size, particularly in social species [69,70]. Additional experimental research will be important in testing the patterns highlighted here, many of which would not have been observable without long-term data. Moreover, similar patterns are starting to emerge in other regions. For example, Hamblin *et al*. [32] found a similar interaction between heat tolerance and nesting substrate in the southeastern USA where bees that nest in pre-existing cavities had lower tolerances to higher temperatures than bees that nest in soil or stems.

Our findings that both larger bodied bees and comb-building cavity nesters are expected to decline in relative abundance with increased temperatures are primarily driven by the genus *Bombus*, thus suggesting that this group is more threatened under climate warming than other bees in our system. The threat of climate change to *Bombus* is a worldwide concern, with other studies showing population declines and range contractions due to increased temperatures [5,71]. Bumblebees are the dominant pollinators in many ecosystems [25]; thus, the loss of this group under climate change could reduce pollination services both in natural and agricultural settings. Previous studies have shown that their decline is associated with lower heat tolerances than other bees, which is why many species have shifted their ranges towards higher latitudes and elevations [72]. Our study suggests that their nesting behaviour and body size could also make them more vulnerable to temperature increases under climate change, though as these traits were highly correlated, future studies are needed to tease apart which trait has a stronger implication for bumblebees under a warming climate.

5. Conclusion

Our research suggests that climate-induced changes in temperature, snowpack and summer precipitation may drastically reshape bee communities. In montane regions that are experiencing increased temperatures and earlier snowmelt, our findings suggest that the bee community will shift towards smaller bodied and solitary bees, those that nest in the soil, and those with narrower diet breadths. We might specifically expect to see a decline in the relative abundance of some of the larger bodied species of *Megachile*, *Osmia*, *Anthophora*, *Melissodes* and *Bombus*. Indeed, many of these genera were shown to be decreasing in abundance in a study that tracked bee responses to environmental change over a 140-year period in the northeastern USA using museum specimens [6], suggesting that declines in large-bodied bees are not restricted to montane ecosystems. Furthermore, as montane systems are expected to become drier over time [38], we may observe shifts towards bees with narrower diet breadths. However, many other regions are expected to increase in precipitation under climate change [73] and our results extended to these other regions would suggest an increase in the ratio of generalist bee species over specialist species. The degree to which these results can be accurately extended to other ecoregions with different climate change projections warrants further investigation.

A reshaping of the bee community under projected climate scenarios could result in novel plant–pollinator interactions and possibly changes in plant reproduction due to shifts in species identities and associations with flowering plants. For example, we could see an increase in pollination by smaller bees, which could act as a buffer against pollination loss from declines in larger bodied bees [6,12]. This prediction assumes that these smaller species can pollinate similar plant species as larger bodied bees and any differences in pollination efficiencies are offset by increases in foraging rates. One potential consequence of the loss of larger bodied bees could be a decline in long-distance pollen transfer as foraging range is positively correlated with body size [74]. Another change in pollination that might occur under climate change is increased specialization among bees due to drier conditions, which could increase conspecific pollen transfer among plants and increase pollination to host plants of oligolectic bees [75,76]. Previous studies have shown that climate change is reshaping plant communities [35,77]. Our study shows that climate change is also reshaping pollinator communities towards smaller bees, ground-nesting bees and bees with more-specialized diets, which could have cascading effects on pollination and ecosystem functioning.

Data accessibility. The data and R codes used in this study are publicly accessible at https://github.com/gpardee/Traits-Paper.git. Further, a fully detailed sampling protocol can be accessed at https://osf.io/kmxyn/.

The data are provided in the electronic supplementary material [78].

Authors' contributions. G.L.P.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, writing—original draft and writing—review and editing; S.R.G.: conceptualization, data curation, formal analysis, methodology, writing—original draft and writing—review and editing; M.S.: data curation, formal analysis, resources, software and writing—review and editing; T.H.: conceptualization, formal analysis, resources, visualization and writing—review and editing; Z.M.P.: methodology, resources, validation and writing—review and editing; M.R.K.: methodology, resources and writing—review and editing; J.S.L.: methodology, resources, writing—review and editing; D.W.I.: conceptualization, funding acquisition and writing—review and editing; R.E.I.: conceptualization, data curation, funding acquisition, supervision and writing—review and editing.

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

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