

RESEARCH ARTICLE

Intraspecific Variation in Evolution and Ecology

Intraspecific body size variation across distributional moments reveals trait filtering processes

Jacquelyn L. Fitzgerald^{1,2,3}  | Jane E. Ogilvie³  | Paul J. CaraDonna^{1,2,3} ¹Plant Biology and Conservation, Northwestern University, Evanston, Illinois, USA²Negaunee Institute for Plant Conservation Science & Action, Chicago Botanic Garden, Glencoe, Illinois, USA³Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA

Correspondence

Jacquelyn L. Fitzgerald
Email: jfitzgerald@chicagobotanic.org

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Abstract

1. Natural populations are composed of individuals that vary in their morphological traits, timing and interactions. The distribution of a trait can be described by several dimensions, or mathematical moments—mean, variance, skew and kurtosis. Shifts in the distribution of a trait across these moments in response to environmental variation can help to reveal which trait values are gained or lost, and consequently how trait filtering processes are altering populations.
2. To examine the role and drivers of intraspecific variation within a trait filtering framework, we investigate variation in body size among five wild bumblebee species in the Colorado Rocky Mountains. First, we examine the relationships between environmental factors (climate and floral food resources) and body size distributions across bumblebee social castes to identify demographic responses to environmental variation. Next, we examine changes in the moments of trait distributions to reveal potential mechanisms behind intraspecific shifts in body size. Finally, we examine how intraspecific body size variation is related to diet breadth and phenology.
3. We found that climate conditions have a strong effect on observed body size variation across all distributional moments, but the filtering mechanism varies by social caste. For example, with earlier spring snowmelt queens declined in mean size and became negatively skewed and more kurtotic. This suggests a skewed filter admitting a greater frequency of small individuals. With greater availability of floral food resources, queens increased in mean size, but workers and males decreased in size. Observed shifts in body size variation also correspond with variation in diet breadth and phenology. Populations with larger average body size were associated with more generalized foraging in workers of short-tongued species and increased specialization in longer-tongued workers. Altered phenological timing was associated with species- and caste-specific shifts in skew.
4. Across an assemblage of wild bumblebees, we find complex patterns of trait variation that may not have been captured if we had simply considered mean and variance. The four-moment approach we employ here provides holistic insight into

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intraspecific trait variation, which may otherwise be overlooked and reveals potential underlying filtering processes driving such variation within populations.

KEYWORDS

body size, bumblebee, climate responses, diet breadth, environmental filter, intraspecific variation, phenology, trait variation

1 | INTRODUCTION

Intraspecific trait variation is the raw material on which ecological and evolutionary processes act. The distribution of traits in a population can mediate intraspecific responses to biotic and abiotic factors (Levins 1968; Sultan, 2000; Violle et al., 2007), and the traits of individuals in a population can be a result of environmental filtering (Diaz et al., 1998; Messier et al., 2010). Understanding how intraspecific trait variation is influenced by environmental variation, and how it in turn affects species function (e.g. resource use and phenology), can help to advance our mechanistic understanding of ecological and evolutionary processes (Cianciaruso et al., 2009; Lajoie & Vellend, 2015; Niu et al., 2020).

Trait distributions can be described by multiple dimensions, or mathematical moments: mean, variance, skew and kurtosis. Whereas mean and variance reflect the position and scale of a trait distribution, skewness reflects the asymmetry and kurtosis the relative tailed-ness (Box 1). Deviations from the normal bell-shaped curve can be described through these higher moments (skewness and kurtosis). At the intraspecific level, shifts in one or more of these moments with environmental variation can reflect changing filters acting on phenotypic plasticity, local adaptation or a combination of these processes (Albert et al., 2010; Des Roches et al., 2018). In a simple example, with greater resource availability we might observe a straightforward increase in mean trait values, such as larger body size following a reaction norm, without changes in the spread or shape of the distribution. This might suggest a filter towards larger trait values and against smaller values, a process we call directional filtering (Bulmer, 1971; Endler, 1986).

However, larger mean body size may also emerge from an increased frequency of larger individuals without a change in the range of trait values in a population. Such a shift would alter the shape of the trait distribution, making it more asymmetric and suggesting what we refer to as a skewed filter (Box 1). In contrast, a loss of the largest and smallest individuals would reduce variance and increase kurtosis, without necessarily a change in the mean. Such a pattern may indicate stabilizing filtering around a central trait value (Loranger et al., 2018; Rolhauser & Pucheta, 2017). Multiple filtering scenarios may play out concurrently, such as a change in the mean trait value coupled with a loss of extreme individuals reducing variance and increasing kurtosis, suggesting both a directional and stabilizing filter (Gross et al., 2021; Le Bagousse-Pinguet et al., 2017).

Characterizing the correlations of higher moments of a distribution (variance, skewness, and kurtosis) with environmental variation allows us to consider the loss or addition of trait values at the

distributional tails. These functionally rare traits may influence a population's capacity to adapt to future environmental variation and interspecific interaction patterns (Ellers et al., 2012; Levins, 1968). Extreme trait values at the distributional tails may allow those individuals to exploit unique resource or phenological niches as compared to the rest of the population (i.e. the niche variation hypothesis; Bolnick et al., 2007; Van Valen, 1965; Violle et al., 2017). However, under physiologically stressful conditions, such as a hotter climate, rare traits may be lost (Bradshaw & Hardwick, 1989; Hoffmann & Merilä, 1999), especially if they are metabolically demanding to develop or maintain (Kleiber, 1947; Relyea, 2002; Somjee et al., 2018); this would manifest in changes in the skewness and variance of the trait distribution (Cotton et al., 2004; Parsons, 1995). Alternatively, greater trait variation may increase if harsh conditions promote risk-spreading within a population (Badyaev, 2005).

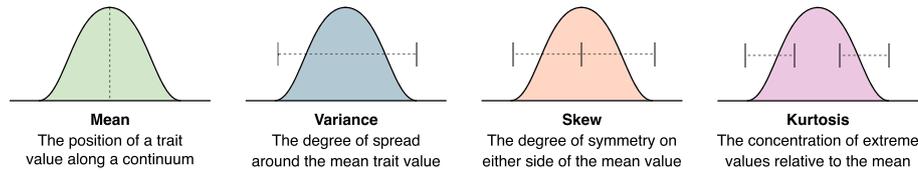
Of an organism's many traits, body size is one of the most fundamental (Calder, 1996; Peters & Peters, 1986). The size of an individual has a strong influence on nearly every aspect of their life history, including diet (Kleiber, 1947), competitive ability (Brooks & Dodson, 1965), and thermoregulation (Stevenson, 1985). In addition, body size itself can be strongly influenced by resources and environmental conditions during development (Schmidt-Nielsen & Knut, 1984; Smith & Lyons, 2013). While all populations are comprised of individuals of varying body sizes, intraspecific size variation is especially striking in social insects, where reproductive and non-reproductive females are largely distinguished by size (Oster & Wilson, 1978). Among some eusocial groups there is also substantial variation within castes, such as in bumblebees, where sister workers may vary in size by an order of magnitude (Fitzgerald et al., 2022; Fletcher & Ross, 1985; Goulson, 2003; Medler, 1962).

In bumblebees, social castes (queens, workers and males) perform distinct functional roles and therefore experience different ecological constraints on body size (Fitzgerald et al., 2022; Free, 1955; Light, 1942). Consequently, the functional role of size variation differs among caste and shifts in the body size distributions within and across caste may reflect demographic responses to variation in the environment (e.g. Ogilvie & CaraDonna, 2022). For example, queens, the central reproductive unit of the colony, may be more likely to exhibit patterns indicative of stabilizing filters to ensure reproductive success (i.e. decreased variance, increased kurtosis), whereas workers, representing colony growth and responsible for most resource acquisition, may be filtered to adapt to shifting resource availability and increase risk spreading (i.e. increased skewness and variance) (Anderson, 1984; Schmid-Hempel & Schmid-Hempel, 1998; Wilson, 1971). Males, as the developmentally cheaper reproductives, may be more likely to

BOX 1

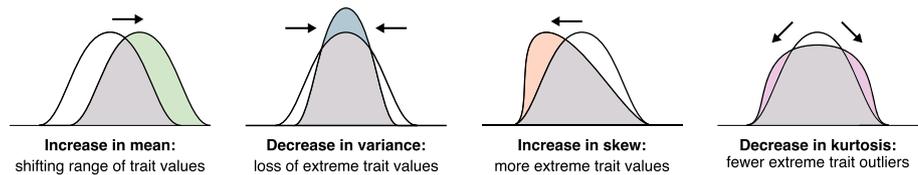
Trait distribution dimensions

The distribution of a trait within a population can be described by multiple dimensions, called moments, including central tendency, the spread of values, the relative symmetry, and the presence and extent of outlier values.



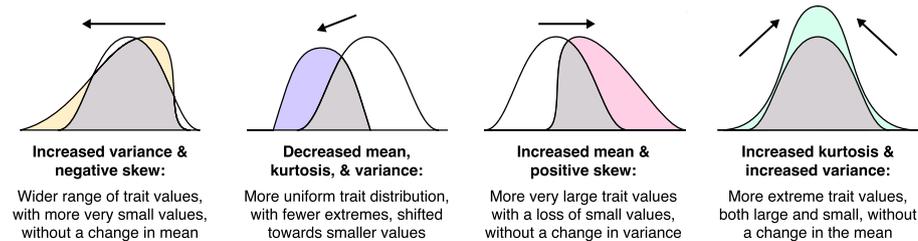
Simple shifts in trait distributions

A shift in a single moment of the trait distribution does not necessarily correspond to shifts in other moments. For example, the mean value can remain stable while changes at the distributional tails alter the trait community.



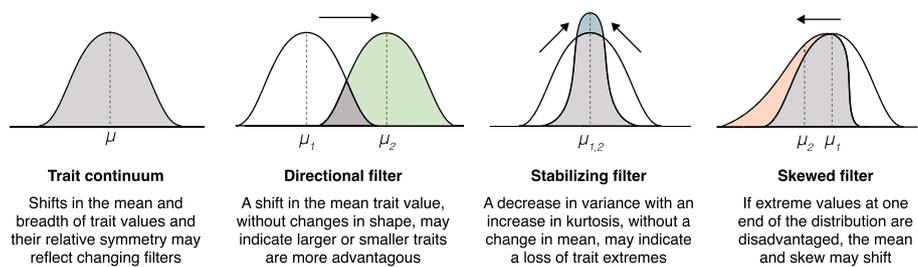
Shifts across multiple trait distribution dimensions

Complex changes in trait distributions involve concurrent alterations in several moments. Understanding how combinations of these moments change can reveal which trait values are gained or lost within a population.



Hypothetical filtering processes shifting trait distributions

The distribution of traits in a population is maintained by both phenotypic plasticity and local adaptation, which filter trait values admitted by changing abiotic and biotic conditions.



The distribution of traits in a population can be described by several measures—mathematical moments—representing its central tendency, variation around the mean, symmetry on either side of the mean and the concentration of extreme values around the mean. Shifts in one or several of these measures can reveal which trait values are gained or lost in a population. Changes in the mean and variance may also be accompanied by changes in the skewness and kurtosis of the trait distribution, which reflect environmental filtering of extreme trait values at the distributional tails. This filtering framework represent ecological analogues of classic evolutionary processes.

exhibit directional filtering to increase mating success (i.e. increased mean) (Amin et al., 2012; Zhao et al., 2021).

To examine how variation in trait distributions correspond to biotic and abiotic variation, and potentially link to trait filtering processes, we investigate the environmental factors and ecological effects associated with intraspecific body size distributions in an assemblage of wild bumblebees in the Colorado Rocky Mountains, USA. We characterize changes in body size distributions across all moments (mean, variance, skew, kurtosis) at the population level and across social castes. Specifically, we ask (1) what is the relationship between body size distributions and climate and floral resource conditions? And, (2) what are the effects of size variation on bumblebee resource use and phenology? We then use these trait distribution patterns to ask how they correspond to trait filtering processes and consider social caste to understand how demography may influence these processes. By examining all distributional moments, we move beyond simple mean trait relationships to consider how environmental processes shape other features of trait distributions including symmetry and extreme trait values. Moreover, our work advances our understanding of intraspecific variation within a trait filtering framework and highlights the usefulness of social species for addressing these questions within and among species.

2 | MATERIALS AND METHODS

2.1 | Study system

We conducted our study of five wild bumblebee species in a series of high-elevation subalpine meadows near the Rocky Mountain Biological Laboratory (RMBL), in Gothic, Colorado, USA (2900 m a.s.l.). The area is highly seasonal, typical of high-elevation and high-latitude regions, with a short growing season beginning with spring snowmelt (April–June) and ending as temperatures cool in the autumn (September–October) (CaraDonna et al., 2014; Cordes et al., 2020). We conducted our study in six established research sites in the East River Valley of the Elk Mountains (for details, see Ogilvie & CaraDonna, 2022). Each site is approximately 500 m in diameter and separated by at least 1 km. This scale reflects typical bumblebee foraging distances in the region (Elliott, 2009; Geib et al., 2015), and we observed no individuals travelling between sites across 3 years of mark-recapture surveys (unpublished data). Our research did not require animal ethics approval. We had permission to conduct field work in the Gunnison National Forest with a US Department of Agriculture Forest Service Special Use Permit GUN1120 and on private land from the RMBL and the Town of Mt. Crested Butte.

2.2 | Quantifying bumblebee body size and size variation

During three growing seasons from 2020 to 2022, we conducted twice-weekly surveys of our study sites (41 weeks and 297 survey

hours in total). We alternated visiting each site in the morning (9:00–12:00 h) and afternoon (13:00–17:00 h) to capture a range of foraging times and daily weather conditions. During each survey, we systematically searched a site for bumblebees and netted individuals for a minimum of 1 h of active sampling effort. For each netted bee we recorded: (1) species identity, (2) caste (i.e. overwintered queen, worker, male) and (3) intertegular distance (ITD), the space between the wing bases (tegulae) and a common and robust proxy for overall bee body size (Cane, 1987; Hagen & Dupont, 2013). We identified bees to species in the field based on distinctive colour patterns following Williams et al. (2014) and against reference specimens in the RMBL Natural History Collection. Before releasing, we marked each bee with a paint pen to avoid remeasuring individuals.

We calculated the four moments of the body size distributions (mean, variance, skew and kurtosis) separately for each species, caste, site and year combination. We only made these calculations for species-caste combinations with sample sizes ≥ 30 . We considered body size variation as the robust coefficient of variation (RCV): the ratio of the interquartile range to the median ($RCV = \frac{IQR}{M}$). This measure of dispersion is less sensitive to outliers than parametric interval estimates, and thus better suited to characterize variance for skewed distributions (Arachchige et al., 2020). We considered skewness as the Fisher-Pearson standardized third moment coefficient:

$$\frac{\frac{\sum_{i=1}^n (x_i - \bar{x})^3}{n}}{\left(\frac{\sum_{i=1}^n (x_i - \bar{x})^2}{n}\right)^{3/2}},$$

where values are unbounded and their sign represents the direction and magnitude of the asymmetry: negative (left skewed), positive (right skewed) or zero (symmetric). We considered kurtosis as Pearson's measure of kurtosis:

$$\frac{n \cdot \sum_{i=1}^n (x_i - \bar{x})^4}{\left(\sum_{i=1}^n (x_i - \bar{x})^2\right)^2},$$

where excess kurtosis greater than zero represents a heavier-tailed distribution (leptokurtosis), less than zero represents lighter tails (platykurtosis) and equal to zero a normal distribution (mesokurtosis). To calculate skewness and kurtosis, we used functions from the R package *moments* (Komsta & Novomestky, 2019). Skewness and kurtosis are related through the inequality $K \geq \beta S^2 + \alpha$, such that an increase in skewness (i.e. greater trait asymmetry) will be accompanied by an increase in kurtosis (i.e. greater trait evenness) (Cullen & Frey, 1999). In our data, skewness and kurtosis were only weakly correlated (adjusted $R^2 = 0.02$, Pearson correlation coefficient = 0.159; Figure S1; Table S1).

2.3 | Quantifying variation in climate

We selected two climate variables known to influence bumblebee populations in our study system (Ogilvie & CaraDonna, 2022):

(1) the timing of spring snowmelt for overwintered queens and (2), the ratio of summer temperature to rainfall for workers and males. Queen emergence in the spring is correlated with snowmelt timing (unpublished data). For overwintered queens, the timing of snowmelt affects the duration that individuals spend in winter diapause. Earlier snowmelt is hypothesized to be favourable for winter survival, as shorter winters allow queens to spend less time in diapause depleting energy stores (Beekman et al., 1998), thus increasing their abundance in the spring (Ogilvie & CaraDonna, 2022). Here, we defined snowmelt timing as the first day of bare ground. Using three HOBO pendant temperature/light loggers (Onset, part no. UA-002-64; Bourne, Massachusetts, USA) deployed year-round at each site, we detected bare ground as the average first day of year with air temperature >5°C and light >10,000 lux, a robust and common measure of spring onset in this snow-dominant subalpine system (e.g. Forrest & Thomson, 2011).

For workers and males, summer climates are hypothesized to affect the activity and abundance of bees (Iserbyt & Rasmont, 2012; Ogilvie & CaraDonna, 2022; Zaragoza-Trello et al., 2021). Here, we use a ratio of mean daily maximum temperature to cumulative rainfall to account for the effect of precipitation (Ogilvie et al., 2017) in a single measure for greater interpretability (similar to Ogilvie & CaraDonna, 2022). We measured temperature with the HOBO data loggers at each of our sites, and rainfall was measured daily at one central site with a standard US National Weather Service rain gauge by local RMBL resident billy barr. This ratio of temperature to rainfall represents a measure of climate variability between sites normalized by precipitation experienced at the level of valley. For workers, we used weather conditions in June and July, and for males we used conditions in July and August, a division that reflects the seasonal activity period of each caste. Higher ratios indicate hotter and drier conditions, which may be favourable to development if these conditions are within tolerable limits (Ogilvie & CaraDonna, 2022; Zaragoza-Trello et al., 2021). However, exceptionally hot and dry conditions may negatively impact bee foraging and survival (Oyen et al., 2016, 2021). In addition, bumblebees exhibit temperature-mediated body sized variation consistent with the temperature-size rule (Guiraud et al., 2021; Kelemen & Dornhaus, 2018), where higher temperatures shorten the larval developmental period leading to smaller adults (Atkinson, 1994; Kingsolver & Huey, 2008).

2.4 | Quantifying variation in floral resources

We conducted weekly surveys of floral abundance at each site, counting the abundance of flowers of plant species visited by bumblebees in 15 permanent 20×0.5m belt transects distributed throughout each site (Ogilvie & CaraDonna, 2022). For our analyses here, we summed floral abundance across transects and year at each site.

We then scaled floral abundance by their visitation rank, represented as the sum of scaled floral abundance:

$$\sum S_i = N_i \left(\frac{V_i}{V_{\max}} \right),$$

where S_i =scaled abundance of species i , N_i =abundance of species i , V_i =number of visits to species i and V_{\max} =number of visits to the most visited species. We used visitation data from the long-term bumblebee monitoring at our focal sites during our 2020–2022 study period (see Ogilvie & CaraDonna, 2022). This scaling approach allowed us to prevent rarely visited but abundant floral species from representing an inappropriate share of the resource environment.

From these rescaled flower counts, we estimated the floral resources during the developmental period of bumblebee caste. For queens, which are born the previous year and overwinter as adults, we considered total floral resources in the prior year ($t - 1$). For workers and males, which develop and are active within a single season, we considered floral resources in the current year from the start of the season through the end of their activity period (August and September, respectively). For improved model convergence, we then standardized these counts by subtracting the mean and dividing by the standard deviation.

2.5 | Quantifying bumblebee resource use

To assess the effects of body size variation on bumblebee resource use, we uniquely calculated diet breadth for each species from our long-term records for each caste, site, and year combination. We use standardized Hurlbert's niche breadth as our measure of diet breadth, which allowed us to account for, and scale variation in, resource availability (Hurlbert, 1978). Hurlbert's niche breadth (B') is defined as

$$B' = \frac{1}{\sum \left(\frac{p_j^2}{a_j} \right)},$$

where p_j =proportion of individuals using resource j and $\sum p_j = 1$, and a_j =the proportion of resource j to total resources ($\sum a_j = 1$). To standardize B' , we use $B'_a = \frac{B' - a_{\min}}{1 - a_{\min}}$, where B'_a =standardized Hurlbert's niche breadth and a_{\min} =the smallest observed proportion of all resources ($\min a_j$). Values closer to one represent more generalized foraging, while values closer to 0 represent more specialized foraging.

2.6 | Quantifying bumblebee phenology

To assess the effects of body size variation on bumblebee timing, we calculated two metrics of phenology for each species and caste: (1) emergence date and (2) activity period. Using weekly bumblebee census data from long-term monitoring in our sites (Ogilvie & CaraDonna, 2022), we constructed kernel density estimates of daily abundance for every species and caste combination at each site in each year. From each density estimate, we

considered emergence date as the day of year on which 2.5% of the population had emerged and activity period as the number of days between emergence date and the date on which 50% of the population of each caste had emerged. We chose to represent emergence as the 2.5% mark as this measure is less sensitive to sample size than first sighting (CaraDonna et al., 2014) and activity period as the length of time between emergence and when half of the population is active as this metric captures peak activity of the bees in this system.

2.7 | Data analysis

We conducted all our analyses in R version 4.2.2 (R core team, 2019), using a series of Bayesian mixed effects models with the package *brms* (Bürkner, 2017). For environmental drivers of body size variation, we used Bayesian mixed effects models to estimate the fixed effects of climatic and floral resource conditions. We included species as a random effect to estimate species-specific intercepts and slopes, and modelled each caste (queen, worker, male) independently, as we hypothesized each caste would be most strongly affected by different climatic predictors and floral resources (see above). For the effects of body size variation, we analysed the fixed effects of each body size distribution moments on diet breadth, emergence timing and activity period, modelling each caste separately using Bayesian mixed effects models as described above, with species as a random effect.

We modelled each moment (mean, variance, skew and kurtosis) independently, each moment with their own weakly informative priors. For the mean, we defined the prior as a gamma distribution with a lower bound of zero and specified k and θ to 2; for variance, we used a beta distribution bounded between 0 and 1 with $\alpha = 2$ and $\beta = 5$; for skewness and kurtosis, we used a normal distribution centered at zero with $\sigma = 1$. For effects on the moments, we defined the priors as the intercept, and for effects of the moments, we defined the priors as the slope. We employed three Markov chains, each run for 4000 cycles with a 2000-iteration warmup phase. To avoid divergent transitions after warmup, we adjusted the adapt_delta parameter to 0.99 to improve smoother sampling behaviour and convergence of the Markov chains. We assessed model convergence using the Gelman-Rubin statistic \hat{R} —all \hat{R} values were below 1.01. We evaluated the evidence for both global (average across all species) and conditional (species-specific) effects considering the 75th, 85th and 95th credible intervals (CI). Higher moments (variance, skew, and kurtosis) are emergent properties of the population and therefore have a lower sample size than the mean ($N = 18$), which we modelled from individual data. We chose to accept a more stringent degree of evidence for the first moment (mean) to account for the difference in sample size across moments. We consider strong evidence of a species-level effect if the posteriors do not cross zero at the 95th CI for the first moment (mean) and at the 85th CI for the higher moments (variance, skew and kurtosis).

3 | RESULTS

Over 3 years (2020, 2021 and 2022), we measured the body size of 2456 individual bees from the five most common *Bombus* species in the area: *Bombus appositus* ($N = 500$, 20.4% of individuals), *B. bifarius* ($N = 688$, 28.0%), *B. flavifrons* ($N = 750$, 30.5%), *B. insularis* ($N = 164$, 6.7%) and *B. rufocinctus* ($N = 354$, 14.4%) (Figure 1). During the study period, there was considerable variation in climate conditions spatially and temporally: across years, site-level snowmelt timing varied by nearly 3 weeks, spanning from 19 April to 8 May. Across years and sites, mean maximum daily summer temperatures ranged from 23.8 to 35.4°C. Across years, total precipitation ranged from 27.68 to 98.04 mm. The ratio of these maximum temperatures to precipitation varied nearly 2-fold (0.38–0.71°C:mm rainfall). Variation in floral resource abundance spanned nearly 10-fold across site and year, ranging from 30 to 291 flowers/m² (summed across each year).

3.1 | How does size variation differ among castes and species?

Within species, bumblebees exhibited a characteristic bimodal size distribution (Figure 1). Queens were, on average, 41.0% larger than workers and 35.6% larger than males. The distribution of male body size was generally a subset of worker size. Within a caste, bumblebee body size was normally distributed with light tails (platykurtic) (Figure 1; Figure S1). The RCR in body size ranged from 9.8% (*B. bifarius* males) to 18.7% (*B. flavifrons* workers), with workers exhibiting a higher degree of body size variation than the other castes. When considered in aggregate across space and time, body size distributions within species and caste were not strongly skewed. When considering how body size distributions varied between years and sites, distributions became more complex, often showing a high degree of skewness (both positive and negative) and variation in the degree of kurtosis (Figure S2).

3.2 | How does variation in climate and floral resources effect body size distributions?

Climatic variation had strong and consistent conditional effects on mean bumblebee body size across caste and species, but with mixed effects on other moments (Figure 2). With earlier snowmelt, queens declined in mean size across species (Figure 3). This was accompanied with negative skewness and increased kurtosis (Table S2), suggesting that a decline in mean size was driven by an increasing frequency of small-bodied queens. For workers, hotter and drier mid-summer conditions were associated with larger mean worker body size across all species (Table S3). Variation in worker size declined under hotter and drier conditions, as well as kurtosis (Table S2). Under hotter and drier conditions, male body size increased, without strong effects on higher moments (Tables S2 and S3).

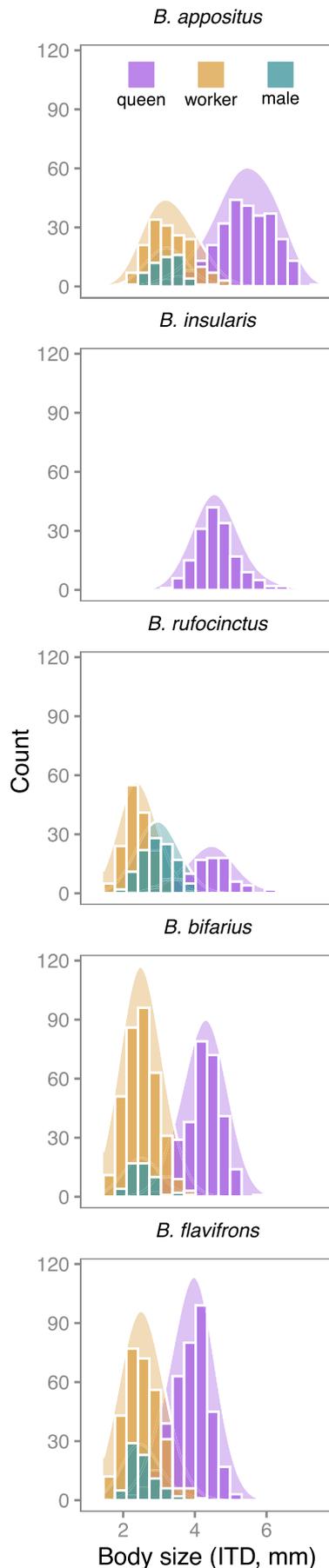


FIGURE 1 Histogram of the spread of bumblebee body sizes among castes and across species, highlighting the characteristic bimodal distribution of larger queens and smaller workers, with males as a subset of worker sizes. On average, workers are more variable in size than queens, followed by males. Species are ordered by descending queen size; ITD, intertegular distance.

The abundance of floral food resources did not have consistent effects on body size across caste and species. For queens at the global level, greater floral abundance in the prior year was weakly associated with larger body size and increased variance, without evidence of an effect on higher moments (Figures 2 and 3; Table S4). At the conditional level, there were mixed effects across all moments and species. For example, *B. appositus* showed strong shifts across all moments with increasing floral resources, while *B. flavifrons* only showed a decrease in kurtosis (Figure 4). For workers, an increase in floral resources in the current year was strongly associated with smaller mean size and increased variance across all species, without evidence of an effect on variance and skewness across species, except for increased kurtosis in *B. flavifrons* (Tables S4 and S5). For males, increasing floral abundance was strongly associated with declining mean size and increased variance at the global and conditional levels, without changes in the other dimensions of the body size distributions (Tables S4 and S5).

3.3 | Is body size variation related to resource use and phenology?

Shifts in mean body size were associated with variable changes in resource use across caste at the global level (Table S6). For queens, larger body size and higher variance was correlated with increased diet breadth in queens at the global level, without effects of skewness or kurtosis on resource use (Table S6). At the species level (Figure 5), there were strong positive effects (i.e. increased generalization) of mean size on diet breadth in *B. insularis* and strong positive effects of body size variance in *B. appositus*, *B. insularis* and *B. bifarius* (Table S7). In workers and males, larger body size and higher variance were strongly correlated with greater diet breadth at the global level (Table S6). At the conditional level, there were mixed and inconsistent effects across species and moments (Table S7). There is strong evidence that *Bombus rufocinctus* workers and males foraged more generally with increasing mean body size, while *B. appositus* workers became more specialized. For *B. bifarius* and *B. flavifrons* workers, greater body size variation was correlated with more generalized foraging, as was higher kurtosis in *B. rufocinctus* and *B. bifarius*.

Mean body size and size variance were positively associated with changes in phenology at the global level across caste (Figure 2; Tables S8 and S10). Earlier emergence and shorter activity periods were associated with smaller bees and less variable body size. For queens, there were species-specific (Figure 5) correlations between phenology and the skewness of body size distributions (Tables S9

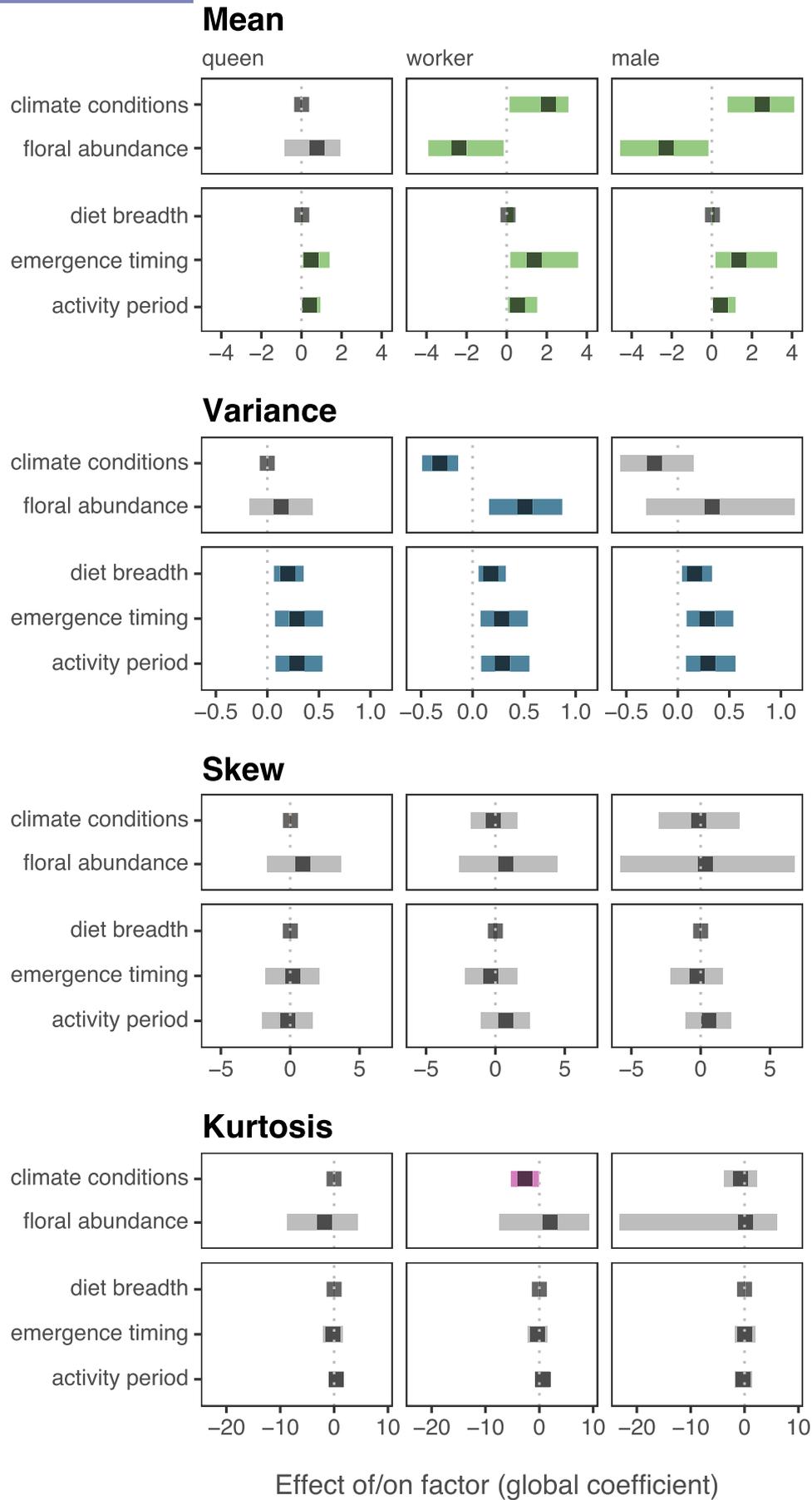


FIGURE 2 Legend on next page

FIGURE 2 The global effects of climate conditions and floral abundance on bumblebee body size distributional moments, and the effects of body size distributions on bumblebee diet breadth and two measures of phenology: Emergence timing and activity period. Points represent the median estimate (i.e. the effect size) of the posterior distribution of the model, error bars represent the 95th credible interval (CI) of the estimate for mean size and 85th CI for higher moments. Coloured points and bars indicate evidence of a strong non-zero effect. For queens, the effect of climate conditions represents a degree change in a body size distributional moment per day change in spring snowmelt, and for floral abundance, the effect size is change per 10 flowers in the previous year. For workers and males, climate conditions represent the ratio of temperature to precipitation during their seasonal activity window and floral abundance the change per 10 flowers during their developmental period in the current year. Diet breadth is measured as standardized Hurlbert's niche breadth, emergence timing is the day of year by which 5% of the population has emerged, and activity period is the number of days between emergence and peak activity. There were strong but mixed global effects on and of mean and variance across caste, with no strong evidence of an effect on or of skew, whereas the kurtosis (i.e. evenness) of worker body size was strongly influenced by climate.

and S11). In *B. appositus*, *B. insularis* and *B. flavifrons*, earlier emergence was associated with negative skewness, suggesting more small-bodied individuals. In these same species, a longer phenological window was also associated with negative skewness.

4 | DISCUSSION

As the biotic and abiotic environment changes, the mean and spread of trait values admitted by environmental filters may shift, as well as the relative symmetry of those trait distributions and the extent of extreme values (Acevedo-Trejos et al., 2015; Hulme & Bernard-Verdier, 2018; Le Bagousse-Pinguet et al., 2017). By considering the four distributional moments—mean, variance, skew, and kurtosis—we can better identify which trait values are gained or lost with abiotic and biotic variation. In our examination of intraspecific trait variation within an assemblage of wild bumblebee species, we find evidence of shifts in body size across all distributional moments, but these responses vary across species and bumblebee social caste. We not only corroborate past evidence of shifts in mean bumblebee body size with variation in climate and floral food resources (Fitzgerald et al., 2022; Gérard et al., 2020; Schmid-Hempel & Schmid-Hempel, 1998; Sutcliffe & Plowright, 1988; Zaragoza-Trello et al., 2021), but also show strong effects of climate on higher moments consistent with trait filtering hypotheses (Box 1). When considering the consequences of trait variation, the most conspicuous patterns were that increases in the degree of size variation was strongly associated with dietary generalization, and that changes in phenological activity were correlated with skewed body size distributions in queens. Together, these patterns suggest underlying filtering processes altering trait compositions of these populations, and variation across social castes suggest different demographic forces guiding these trait shifts. Moreover, without considering higher moments of the trait distributions, these patterns would have been obscured.

We find evidence of multiple trait filtering scenarios in response to climate variation (Box 1). In queens, we find that early snowmelt conditions decreased mean body size while negatively skewing the size distribution and increasing kurtosis (Figure 3). In other words, earlier snowmelt, and therefore shorter winters, leads to a higher frequency of small-bodied queens with an increase in extremely small individuals. In this scenario, these smaller individual queens

may not have survived diapause in a longer winter due to reduced energy stores, but under earlier snowmelt are able to successfully emerge (Holm, 1972; Schultz & Conover, 1999; Vesterlund et al., 2014). For workers, hotter and drier mid-summer conditions were related to increased mean body size, along with decreased variance and kurtosis (Figure 4). This pattern suggests the body size distribution of workers becomes both narrower and more evenly distributed, that is a more homogenized trait community (Gross et al., 2021; Le Bagousse-Pinguet et al., 2017). Thus, when conditions are hot and dry, the body size distribution of workers shifts and concentrates around larger individuals. Finally, under hotter and drier late-summer conditions, males increased in mean size and decreased in variance without strong changes in higher moments. While it is possible that summer conditions during our study period were sufficiently mild as to not induce developmental or physiological stress (Kenna et al., 2021; Oyen & Dillon, 2018), these findings suggest such that larger males are more advantageous, perhaps due to selective pressures related to reproduction (Amin et al., 2012; Zhao et al., 2021). As the abundance of workers and males for the species we examined mostly do not seem to be strongly correlated with temperature:precipitation ratios in our study system (Ogilvie & CaraDonna, 2022), these patterns suggest that hot and dry climate conditions appear to be favourable for larger individuals but the filtering mechanism driving these shifts varies across castes.

Floral resource availability shifted mean size with caste-specific effects on higher moments. Among queens, greater floral abundance was weakly associated with larger individuals at the global level, with no effects on higher moments. Conditional effects varied across species, with *Bombus appositus* showing strong shifts in all four moments (Figure 3). For *B. appositus*, the largest species, greater floral resource availability corresponded with increased body size, increased variance, positive skewness and reduced kurtosis. In other words, higher resource abundance during the developmental period appears to shift the body size distribution towards large queens by increasing the frequency of larger individuals with a loss of and concentration in the frequency of smaller individuals. For workers and males, higher floral abundance was associated with declining mean body size and increased variance without strong global effects on skewness or kurtosis (Figure 2). In our system, floral abundance does not consistently predict the abundance of overwintered queens in spring, but is positively correlated with male and worker abundance

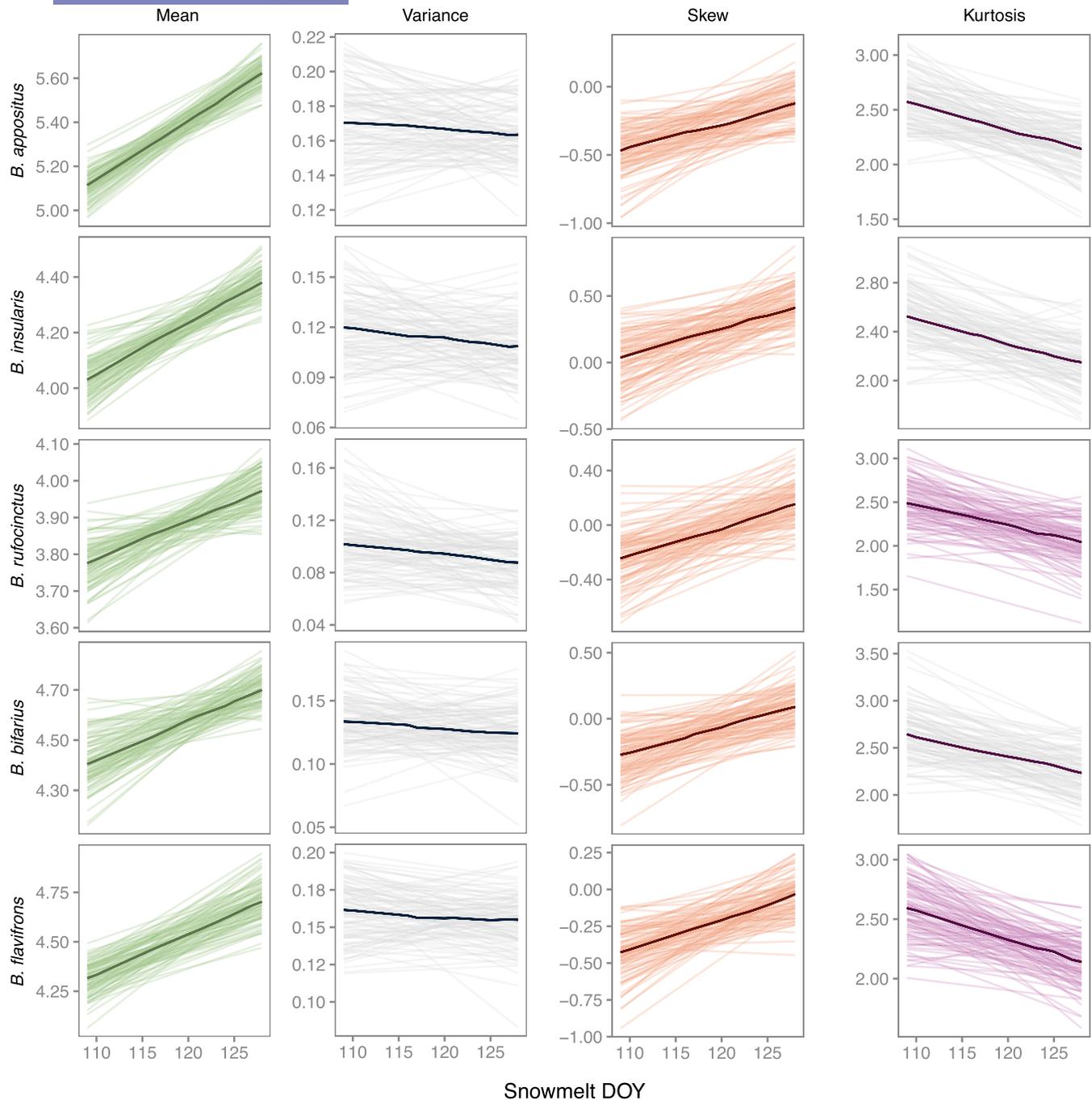


FIGURE 3 Conditional effects of snowmelt timing day of year (DOY) on the body size distributional moments of queens across species. With earlier snowmelt, queens across all species declined in mean size and exhibited negative skew, with two species showing increased kurtosis. In other words, earlier snowmelt led to a higher frequency of small-bodied queens with an increase in extremely small individuals. Model fit lines represent 100 draws from the posterior distribution of a Bayesian linear mixed effect model for each distributional moment, with species as a random effect. Coloured lines indicate evidence of an effect from the full model at the 95th credible interval (CI) for mean size and 85th CI for higher moments. Species are ordered by descending queen size.

(Ogilvie & CaraDonna, 2022). Taken together, these observations are consistent with resource allocation strategies such that with greater floral food resources, bumblebee colonies appear to prioritize producing larger 'high quality' queens that may be more likely to survive winter diapause and establish colonies (Beekman et al., 1998; Fitzgerald et al., 2022), and that producing a greater frequency of

smaller workers and males may be more advantageous for foraging and reproduction (Smith & Fretwell, 1974; Stearns, 1989).

Consistent with the niche variation hypothesis, we find that mean body size and size variation—but not the higher moments—strongly predicted the degree of foraging specialization at the global level across all castes (Figure 4). A greater degree of size variation may

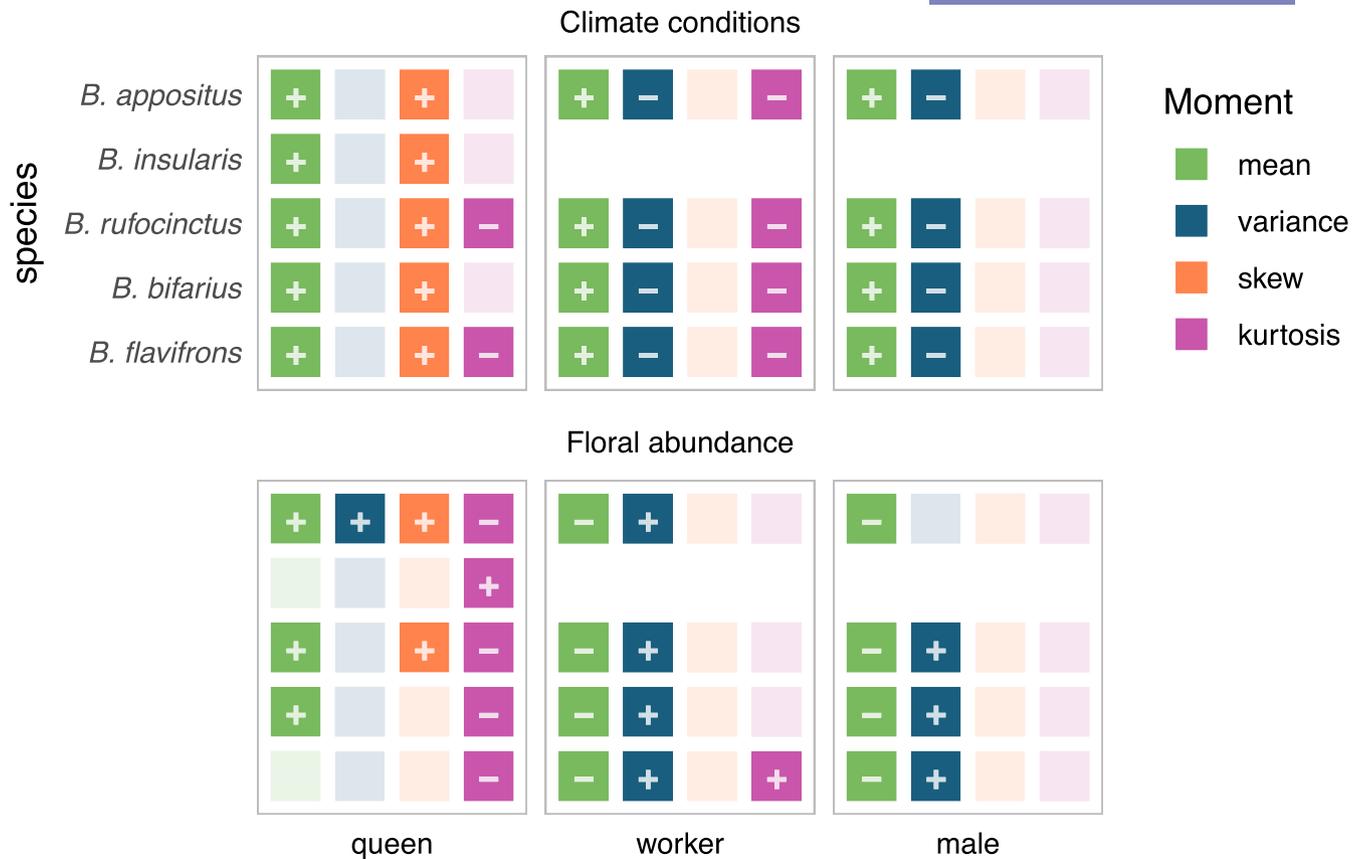


FIGURE 4 Summary of the conditional effects of climate and floral resources on bumblebee body size distributional moments. Each grouped grid represents a set of models (see Figure 3), where any highlighted squares indicate evidence of a correlation at the 95th credible interval (CI) for mean and 85th CI for higher moments, with the direction of the relationship (positive [+] or negative [-]). Each subheading represents a driver of trait variation, each column represents a caste (queen, worker, male) and each row within a group represents a species, ordered by descending queen size. There were strong effects of both climate and floral resources on body size across all distributional moments, with idiosyncratic effects across species and caste. See supplement for full models. Results are absent for *Bombus insularis* workers as this kleptoparasitic species does not produce them and for males as our sample size was less than 30 individuals.

facilitate more generalized foraging within a population because a diverse set of traits may allow individuals to use novel or a broader range of resources (Bolnick et al., 2007; Costa-Pereira et al., 2018; Van Valen, 1965). In workers, species-specific effects suggest that short-tongued species (*B. rufocinctus* and more weakly *B. bifarius*) had more generalized foraging with increasing body size whereas longer-tongued species (*B. appositus* and more weakly *B. flavifrons*) became less generalized. This suggests functional group-specific trait relationships, as the length of the proboscis mediates the depth of the floral corolla an individual is able to extract nectar from and thereby constrains foraging (Inouye, 1980; Ranta, 1984). As longer-tongued species tend to be larger interspecifically, larger worker body size may further constrain the floral morphologies available to them, while for the smaller, shorter-tongued species, larger worker body size expands the possible foraging resources (Wood et al., 2021). Within a population, individuals of different size classes may forage on specific floral morphologies (Heinrich, 1976); changes in the distribution of those sizes classes may alter the identity of the visited plant species without changes in the total richness of diet breadth (CaraDonna et al., 2017; Stang et al., 2009). Thus, there may have been size-related changes

in resource use that we could not capture from a summary measure of diet breadth.

Variation in phenology was caste-dependent and largely correlated with changes in mean size and in the skewness of body size distributions, as individuals at the trait tails shift in frequency (Figure 4). Our two measures of phenology showed inverse patterns, such that changes in activity period are likely a consequence of earlier emergence and reflect changes in the filtering processes that admit individuals at that tail of the phenological distribution. For example, in *B. flavifrons* queens (the smallest-bodied species) a longer activity period and earlier emergence were correlated with negative skewness. This suggests that more small queens are present, which may have otherwise been filtered out, perhaps by later snowmelt timing or other environmental limits to emergences (see above). In contrast, workers showed strong conditional shifts in mean size without strong evidence of changes in other dimensions. This may indicate that when colonies are established earlier in the season, leading to earlier worker emergence, these workers are smaller. In these early season scenarios, it is possible resources are limited for foundress queens, which then go on to produce these

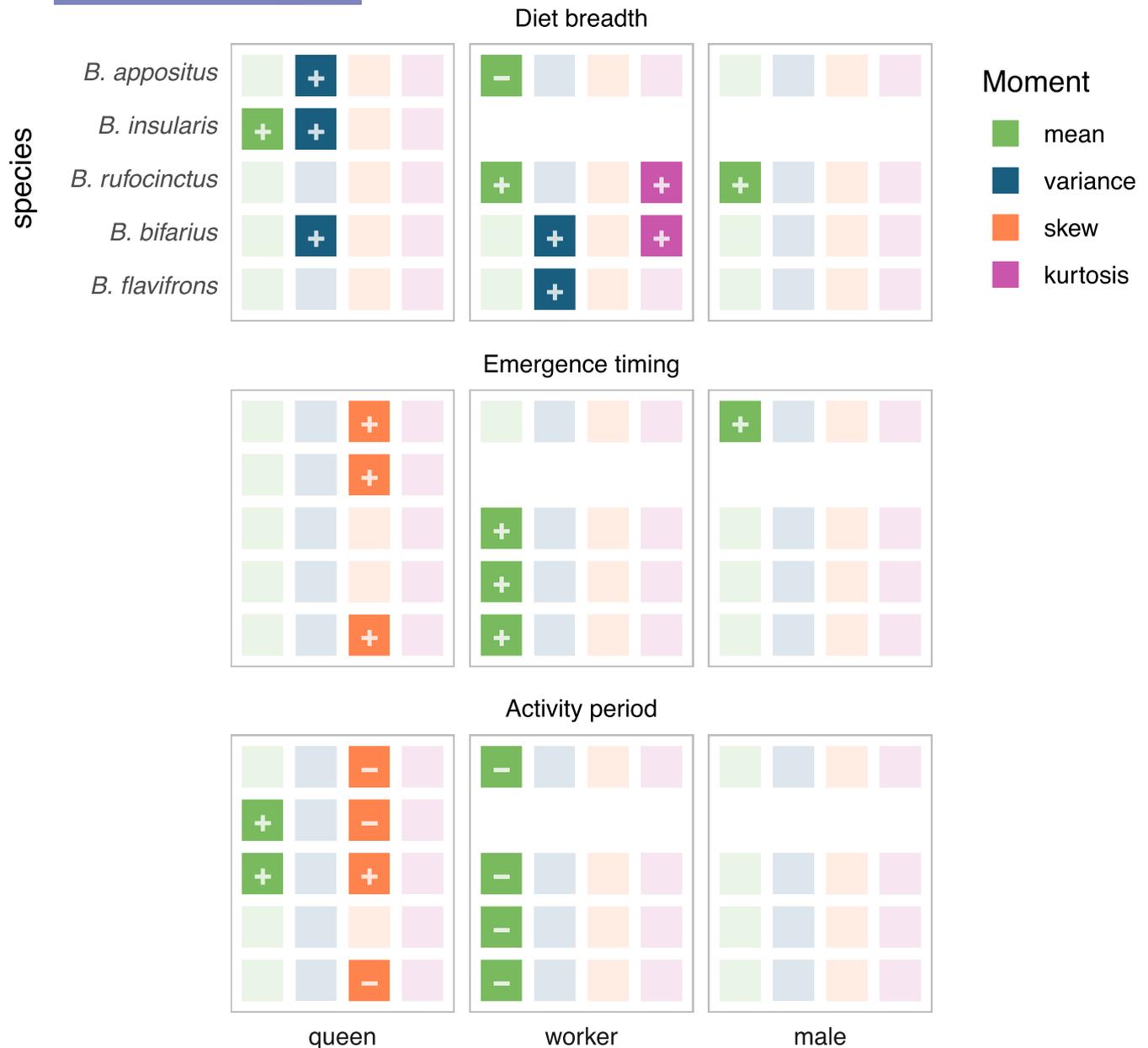


FIGURE 5 Summary of the conditional effects of body size distributions on bumblebee diet breadth and two measures of phenology, emergence timing and activity period. Each grouped grid represents a set of models (see Figure 3), where any highlighted squares indicate evidence of a correlation at the 95th credible interval (CI) for mean and 85th CI for higher moments, with the direction of the relationship (positive [+]) or negative [–]). Each subheading represents an effect of trait variation, each column represents a caste (queen, worker, male) and each row within a group represents a species, ordered by descending queen size. There were strong effects of body size across distributional moments, with idiosyncratic effects across species and caste. See supplement for full models. Results are absent for *Bombus insularis* workers as this kleptoparasitic species does not produce them and for males as our sample size was less than 30 individuals.

smaller workers. The strong conditional correlations between mean size in workers, but less consistent correlation in queens and lack of correlation in males, suggests a demographic link to the role of trait variation. The reproductive role of queens and males may confer a degree of selective stability to their phenology, making them less sensitive to changes in mean size as compared to workers, whose role is more closely tied to colony growth and foraging. Other morphological traits that we did not examine, including body shape, wing length and tongue length, can also influence bumblebees' resource

use and activity in ways that may more strongly explain intraspecific variation in their ecology (Goulson, 2003; Heinrich, 2004; Le Provost et al., 2021).

The four-moment approach we take here with wild bumblebees provides a more mechanistic understanding of how intraspecific variation is driven by trait filtering processes and how this variation correlates to ecological function (Green et al., 2022; Moran et al., 2016). This framework reveals if and how trait values are lost at the distributional tails, and consequently the broader

processes shaping what individuals are present within a population. Looking across multiple species of eusocial bumblebees, we find demographic and functional-group specific patterns of trait variation that may not have been captured if we had simply considered mean and variance. Our findings provide evidence of strong links between bumblebee body size variation and the abiotic and biotic environment across all four moments, and that variation in size has consequences for both foraging and phenology. Ultimately, considering multiple dimensions of the shape, size, and scale of a trait distribution helps advance our understanding of intraspecific variation and the filtering processes maintaining and shaping populations.

AUTHOR CONTRIBUTIONS

Jacquelyn L. Fitzgerald conceptualized the study, collected the morphological data, wrote the initial drafts of the manuscript, analysed the data and designed the figures. Jane E. Ogilvie established the long-term monitoring project and Jane E. Ogilvie, Paul J. CaraDonna and Jacquelyn L. Fitzgerald collected the phenological and interaction data. All authors contributed to interpreting the results and editing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Open Science Framework <https://doi.org/10.17605/OSF.IO/M5KHA> (Fitzgerald et al., 2024).

ORCID

Jacquelyn L. Fitzgerald  <https://orcid.org/0000-0003-1042-1987>

Jane E. Ogilvie  <https://orcid.org/0000-0001-8546-0417>

Paul J. CaraDonna  <https://orcid.org/0000-0003-3517-9090>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. The relationship between skewness and kurtosis of a distribution through the inequality ($K \geq \beta S^2 + \alpha$).

Figure S2. Body size mean, variance, skew, and kurtosis, with standard error, across bumble bee species and caste.

Table S1. Linear model describing the inequality relationship between skew and kurtosis ($K \geq \beta S^2 + \alpha$).

Table S2. Global effects of climate conditions (snowmelt timing, mid-, and late-season temperature:precipitation ratios) on body size distributional mean, variance, skew, and kurtosis for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

Table S3. Conditional effects of climate conditions (snowmelt timing, mid-, and late-season temperature:precipitation ratios) on body size at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

Table S4. Effect of floral resource conditions on body size distributional mean, variance, skew, and kurtosis for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

Table S5. Conditional effects of floral resource abundance on body size at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

Table S6. Global effects of body size distributional mean, variance, skew, and kurtosis on diet breadth for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

Table S7. Conditional effects of body size on diet breadth at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

Table S8. Global effects of body size distributional mean, variance, skew, and kurtosis on emergence timing for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

Table S9. Conditional effects of body size on emergence timing at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

Table S10. Global effects of body size distributional mean, variance, skew, and kurtosis on phenological activity period for queens, workers, and males at the 95th, 85th, and 75th credible intervals.

Table S11. Conditional effects of body size on phenological activity period at the species level for queens, workers, and males at the 95th credible interval for the first moment (mean) and 85th for the higher moments (variance, skew, and kurtosis).

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