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Nutrient niche dynamics among wild pollinators

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Food underpins fitness and ecological interactions, yet how nutrient availability shapes species interactions in natural communities remains poorly understood. Most nutritional ecology research focuses on laboratory or single-species systems, limiting insight into how nutrient use and nutrient niche dynamics occur in complex, multispecies assemblages in the wild. We combined long-term plant–pollinator interaction data with pollen macronutrient analyses to examine how wild bumble bees exploit macronutrients and whether they occupy distinct nutrient niches. Pollen macronutrient composition varied across plant species and over the season, with protein-rich pollen peaking in spring and lipid- and carbohydrate-rich pollen increasing by late summer. Across this nutrient landscape, bumble bee species occupied two distinct macronutrient niches: one high in protein and low in lipid and carbohydrate, and the other lower in protein but moderate in lipid and carbohydrate. Nutrient niche partitioning was associated with differences in feeding morphology and colony life stage (but not phenology). We found little evidence that nutrient niche breadth differed among species or was explained by feeding morphology or colony life stage. Our results extend nutritional ecology to a multispecies context, provide evidence for nutrient niche partitioning among wild pollinators and highlight the need to consider species-specific nutritional requirements in pollinator conservation.

1. Introduction

Food provides the energetic and nutritional basis for fitness and, as such, underpins most ecological interactions [1]. In nature, animals must seek out and compete for resources that fulfil specific nutritional requirements [2–4], particularly for essential macronutrients—proteins, lipids and carbohydrates—that are necessary for growth, metabolism, reproduction and cognition [1]. Despite their fundamental importance, how the availability and distribution of these macronutrients shape species interactions in natural communities remain a critical but understudied dimension of ecology [5].

Nutritional geometry provides a powerful framework to investigate how organisms optimize nutrient acquisition in complex environments [1,6–10]. This approach predicts that species will target specific nutrient compositions, thereby occupying distinct nutrient niches to maximize fitness [10–14]. Laboratory studies demonstrate that even closely related, co-occurring generalists can occupy unique nutritional niches, suggesting that subtle differences in nutrient acquisition may facilitate species coexistence [12]. However, whether these predictions hold in natural communities—where additional ecological constraints influence foraging strategies—remains largely untested [5,6,11] (but [8,13,14]). Therefore, quantifying macronutrient acquisition among co-occurring species in the wild is critical for understanding the ecological and evolutionary processes that shape nutrient niches.

The concept of the multidimensional nutritional niche refines the traditional generalist–specialist continuum by distinguishing species that exploit a broad range of nutrient profiles from those that consistently target specific compositions [9–11]. While nutritional niches are thought to emerge from a combination of species interactions, evolutionary history and physiological constraints, the influence of these factors is poorly resolved [14,15]. Nutrient niches may also shift throughout a species' life cycle owing to ontogenetic changes in dietary needs [1,16–18], although empirical evidence for such flexibility in wild populations is scarce. Additionally, functional traits like feeding morphology and phenological traits (e.g. emergence timing) can shape macronutrient niches by determining resource accessibility [19–23]. Therefore, empirical studies that integrate these factors—quantifying nutrient availability in nature while tracking how traits and life history shape nutrient acquisition—are needed to advance the core predictions of nutritional ecology and clarify mechanisms of species coexistence.

To investigate these ideas in a natural system, we focus on the plant–pollinator mutualism, where the exchange of nutritional resources is directly observable. This system is particularly relevant because the nutritional ecology of wild pollinators is understudied, despite poor nutrition being a key factor implicated in global pollinator declines [24–28]. Bumble bees (*Bombus* spp.) are a compelling model for these questions. Laboratory and semi-natural field studies show that bumble bees can actively regulate their macronutrient intake (e.g. [27,28]) and that dietary nutrient composition directly affects colony health, growth and reproductive success (e.g. [18,27,29–35]). Furthermore, prior work has shown that both evolutionary history (phylogeny) [15] and pollen nutritional quality can influence foraging choices and resource selection among co-occurring bee species [36]. However, it remains unclear how these factors—from innate preferences and evolutionary history to resource availability—interact within a complex community to shape the realized macronutrient niches of diverse, wild pollinator species.

Here, we investigate macronutrient availability and acquisition among eight co-occurring bumble bee species in the Colorado Rocky Mountains, USA. We combine an 8-year dataset of floral availability and bee–plant interactions [37] with a 4-year dataset of pollen macronutrients from 35 plant species to characterize the nutritional landscape and extend the framework of nutritional geometry to a multi-species, community-wide context. Specifically, we ask (i) How does floral macronutrient composition vary across plant species, space and time? (ii) To what extent do wild, co-occurring pollinators exhibit distinct macronutrient niches? (iii) Do nutrient niches shift across bumble bee colony life stages? (iv) How do feeding morphology, emergence phenology and evolutionary history influence macronutrient niches in wild bumble bees? Our results advance our understanding of macronutrient niche formation in ecological communities and underscore the importance of integrating species-specific nutritional ecology into pollinator conservation strategies.

2. Methods

Study system. Our research focused on wild bumble bees (*Bombus* spp.) in a montane ecosystem near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO, USA (38°57.50'N, 106°59.30'W, 2900 m above sea level). This region experiences plant–pollinator activity from spring snowmelt (April–June) to the first autumn freeze (September–October) [37,38]. Bumble bees are abundant and effective pollinators throughout the Northern Hemisphere, with approximately 50 species in the United States and 265 species worldwide [15,39]. These generalist foragers primarily consume pollen and nectar, serving as important pollinators of native plants [39]. Their eusocial life cycle enables bumble bees to pollinate diverse plants throughout the bloom period: queens emerge from diapause in the spring to establish colonies (establishment stage), which then grow throughout the summer by producing workers (colony growth stage) and finally produce new reproductives (gynes and males) at the end of the season (reproduction stage) [37,39,40]. This seasonal progression could mean that bumble bees potentially prioritize different macronutrients at each colony life stage to meet shifting nutritional demands [41].

We monitored plant–pollinator interactions and floral resource availability weekly over eight consecutive growing seasons (2015–2022). Our study targeted eight bumble bee species common to the Colorado Rocky Mountains: *Bombus appositus* (*Subterraneobombus*), *Bombus bifarius* (*Pyrobombus*), *Bombus californicus* (*syn. Bombus fervidus; Thoracobombus*), *Bombus flavifrons* (*Pyrobombus*), *Bombus mixtus* (*Pyrobombus*), *Bombus nevadensis* (*Bombias*), *Bombus occidentalis* (*Bombus*) and *Bombus rufocinctus* (*Pyrobombus*). We characterized macronutrient acquisition across the two pollen-collecting life stages: spring queens (colony establishment) and summer workers (colony growth). To define the nutritional landscape, we focused on 35 plant species from 17 families that accounted for 89.5% of all observed pollen-foraging interactions (i.e. visits where bees were collecting pollen or both pollen and nectar) over the study period.

Bumble bee observations. We monitored plant–bumble bee interactions at six permanent sites distributed across approximately 8 km in the East River Valley near the RMBL (see [37] for detailed site descriptions). Sites were separated by at least 1 km (edge to edge) and had diameters of approximately 500 m, corresponding to typical bumble bee foraging distances in Colorado montane meadows [42,43]. These sites encompassed three habitat types: wet meadows, dry meadows and aspen forest understory. We conducted systematic weekly surveys throughout the bumble bee activity season (16–22 weeks annually), spending 20 min in each habitat type per site (60 min total per site weekly). During surveys, we recorded bumble bee species, caste, plant species visited, foraging behaviour (pollen collection, nectar collection or both) and the presence of pollen loads. Our initial dataset of 45 501 observations was filtered to 18 099 interactions involving foraging queens and workers of the 8 focal species at our study sites. For the macronutrient niche analysis, we used the subset of these interactions where bees were actively collecting pollen ($n = 4716$), thereby excluding nectar-only visits (i.e. pollen-only or pollen-and-nectar visits).

Floral resource monitoring. To quantify floral resource availability, we conducted weekly flower counts along 15 permanent transects (20 m × 0.5 m each) per site. Five transects were systematically distributed within each habitat type (wet meadow, dry meadow and aspen forest understory), resulting in a total survey area of 150 m² per site. For each plant species, we estimated pollen production per flower by measuring mean anther dry mass, sampling anthers from 5 to 15 individual plants. Collected anthers were weighed wet, then dried in an oven for 12 h and re-weighed to determine dry mass. Typically, anthers were weighed in batches of approximately 1.0 mg, unless a single anther exceeded this mass. We calculated per-flower macronutrient quantities by multiplying the mean anther dry mass by the measured nutritional concentration (mass of macronutrients per mg of pollen). Finally, we estimated the total macronutrient availability at each site (e.g. mass of protein per m²) by combining these per-flower values with our floral abundance data.

(a) Quantifying pollen macronutrient content

Field collection of pollen. We collected pollen from 35 focal plant species over 4 growing seasons (2018–2021). To obtain pure samples, pollen was collected directly from flower anthers, either by brushing it into a vial or by extracting whole anthers. When whole anthers were collected, pollen was subsequently isolated by sieving the contents through a steel mesh filter to remove plant debris. To ensure an adequate quantity for analysis, at least 10 mg of pollen was collected for each plant species, with samples pooled within each year. All samples were stored in an ultra-cold freezer (−70°C to −80°C) until analysis.

Pollen macronutrient analysis. We quantified protein, lipid and carbohydrate content of pollen samples following established protocols [44,45]. For each plant species, we prepared three replicate samples (1.00 ± 0.05 mg each) for protein analysis and another three replicates for combined lipid and carbohydrate analyses. Macronutrient contents were expressed as mass per milligram of pollen (mg nutrient / mg pollen), which allowed for the calculation of total macronutrient mass, proportions and ratios for each plant species. Protein was measured using a modified Bradford Assay with a non-animal protein standard (CB Protein Assay, G-Bioscience). Lipids were quantified using a sulfo-phospho-vanillin (SPV) assay, and carbohydrates were measured using an anthrone-sulfuric acid assay [45]. Although the SPV assay may underestimate total lipids due to its bias toward unsaturated fatty acids, these particular fatty acids are known to be important for bee health [46–49]. The validity of these assays for measuring macronutrient content in pollen is well-supported [14,44,50–54]. Finally, total macronutrient quantity per flower was calculated by combining these macronutrient concentration values with the measured anther mass. (For the detailed protocol we used, see electronic supplementary material, appendix 2).

Pollinator traits. To evaluate the influence of key traits on macronutrient niches, we focused on feeding morphology (tongue length) and emergence phenology. We obtained tongue-length measurements for queens and workers of all eight focal species from an existing dataset for this same regional bee community [55]. For one species where worker data were unavailable (*B. rufocinctus*), we estimated worker tongue length from the strong correlation between queen and worker tongue lengths observed in the other seven species (Pearson's $r = 0.99$). We classified tongue length into two categories—short-tongued and long-tongued—based on established thresholds [40] and natural breaks in our dataset.

To evaluate emergence phenology, we used our long-term monitoring data [37] to calculate a mean first observation date for each species and caste. We first identified the day-of-year of the first observation for each species–caste combination in each year, then averaged these values to create a single metric of emergence timing. While our statistical models used this continuous variable, we also created categorical groups ('early' or 'late') for visualization. These categories were assigned based on a median split performed on the emergence dates independently for each caste, such that species whose mean emergence date fell below the caste-specific median were classified as 'early'.

(b) Data analysis

We analysed macronutrient composition and acquisition patterns using Bayesian hierarchical models. Because macronutrient data are inherently compositional (i.e. proportions summing to one), we used Dirichlet regression, a multivariate extension of the Beta distribution well-suited for proportional data [56,57]. All models were implemented in R using Stan via the *CmdStanR* (v. 0.7.1; [58]) and the *brms* packages (v. 2.21.0; [59]). Following a standard Bayesian statistical workflow [60], we assessed model convergence (e.g. *R*-hat values, effective sample sizes) and generated 4000 samples from the joint posterior distribution for each model. All inferences regarding the strength of evidence for our findings were drawn from these posterior distributions, with model parameters estimated using posterior means and 95% credible intervals. From these posterior distributions, we calculated central tendency measures (mean and median) and credible intervals to estimate likely parameter values and associated uncertainty. Narrow credible intervals centred around these estimates indicate stronger evidence and greater certainty for parameter values [60].

(c) Model structure

Plant macronutrient models. We modeled pollen macronutrient composition at two ecological scales: (i) species-level and (ii) community-level. To model the nutritional composition of individual plant species (model i), we included a global intercept (the average composition across all species), random intercepts for each species, floral morphology (corolla tube depth) as a fixed effect and a species-level phylogenetic covariance matrix. To estimate nutrient availability at the community level, we first calculated the total mass of each macronutrient available at each site by multiplying floral abundance, per-flower anther mass and pollen nutritional concentration. These values were then normalized into relative macronutrient abundances for the analysis. The model for these community-level data (model ii) included a global intercept (average site-level composition), fixed effects for season, habitat, and year and a random intercept for each site.

(d) Bumble bee macronutrient acquisition model

Like the plant models, we modelled the realized macronutrient niches of bumble bees using a Bayesian hierarchical Dirichlet regression. The model included a global intercept (average acquisition across all species and castes) and several fixed effects: colony life stage (queen versus worker), mean tongue length and mean emergence date. To account for variation among species and castes, we included random intercepts for each species, with life stage nested within species. Finally, to account for shared evolutionary history, the model also incorporated a species-level phylogenetic covariance matrix [61].

Compositional niche overlap and breadth. To evaluate nutritional specialization and generalization across bumble bee species and plant communities, we quantified compositional niche overlap and breadth [56,62] using posterior samples from the Bayesian models. Compositional niche overlap was used to measure nutritional similarity among our defined groups of interest: (i) between plant species, (ii) across seasons, habitats and years at the community level, and (iii) among bumble bee species and life stages. High overlap values indicate greater nutritional similarity, whereas low values indicate nutritional differentiation.

To quantify compositional niche breadth, we used the ϕ (phi) parameter from the Bayesian models, which represents the concentration of the posterior distribution. We used the reciprocal of this parameter ($1/\phi$) as a measure of dispersion, where higher values indicate broader, more generalized niches and lower values indicate narrower, more specialized niches.

Testing for phylogenetic signal. We constructed phylogenetic trees for both plants and bumble bees to assess the influence of evolutionary history on macronutrient traits. For plants, we pruned a published phylogeny [63] to include only the species in our dataset. In this process, we used *Salix wolfii* as a representative for any unidentified *Salix* species and included *Heliomeris multiflora* under its synonym *Viguiera multiflora*. For bumble bees, we used a published phylogeny [61] without modification.

To quantify phylogenetic signal, we compared variance in posterior predictions from our models with and without including phylogenetic covariance. For each macronutrient, we generated two sets of posterior predictions—one with and one without phylogenetic covariance—and calculated the ratio of their variances (λ) [59]. A λ value greater than 1 indicates that including phylogeny reduced the predicted trait variance, providing evidence for phylogenetic conservatism. Conversely, values near or below 1 suggest minimal phylogenetic influence, with values consistently less than 1 indicating potential phylogenetic overdispersion (electronic supplementary material, S1 and S6). We interpret these results with caution; however, as community phylogenetic analyses based on local subsets of taxa, rather than complete clades, can limit the power to detect strong phylogenetic signals [64,65].

Software. All statistical analyses were conducted in R (v. 4.5.0) [66], and ternary plots were generated using the *ggtern* package (v. 3.5.0) [67].

3. Results

(a) Plant species macronutrient composition

The macronutrient composition of pollen varied substantially among the 35 focal plant species (figure 1a). Protein content ranged from 17.2 to 85.9% (mean 46.9%), lipids from 4.6 to 41.0% (mean 19.5%) and carbohydrates from 5.3 to 65.3% (mean 33.6%) per mg of pollen. Macronutrient ratios displayed considerable variation: protein-to-lipid ratios ranged from 0.6:1 to 16:1 (mean 3:1), protein-to-carbohydrate ratios from 0.3:1 to 14:1 (mean 2:1) and lipid-to-carbohydrate ratios from 0.16:1 to 5:1 (mean 0.8:1; figure 1a, electronic supplementary material, table S1). Floral morphology (corolla tube depth) was not correlated with pollen macronutrient composition (figure 1a). We did not find evidence of a phylogenetic signal ($\lambda \leq 1$) for protein, lipid and carbohydrate content within this plant community (electronic supplementary material, figure S1 and S2).

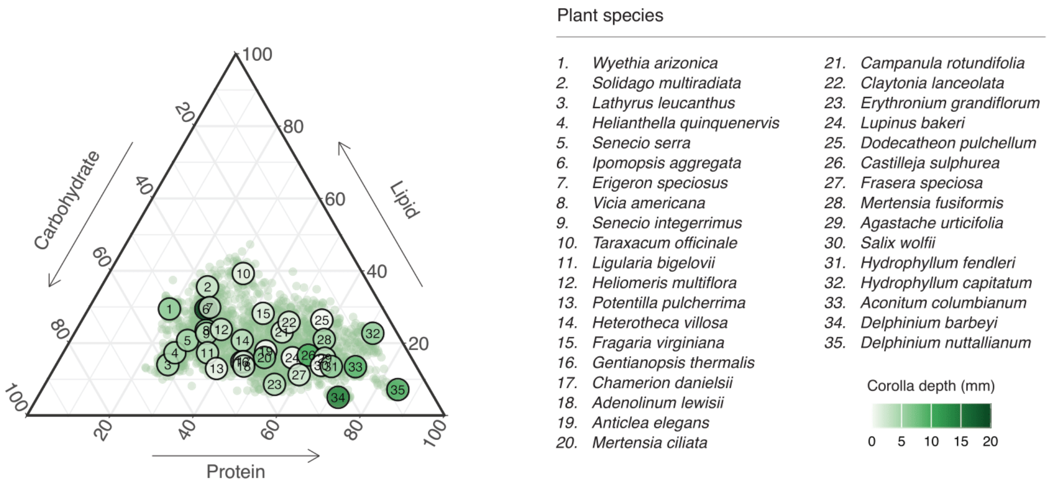
(b) Variation in floral macronutrient availability

Across eight years of floral resource surveys, we recorded a total of 956 894 flowers from the 35 focal plant species. Community-level floral macronutrient composition exhibited strong seasonal shifts, transitioning from being protein-rich in the spring to lipid- and carbohydrate-rich by late summer (figure 1b; electronic supplementary material, tables S2 and S3). Early season landscapes were dominated by high-protein pollen (mean: 60.8% of available macronutrients), driven by species in the Boraginaceae, Fabaceae and Ranunculaceae families. By late summer, the landscape transitioned to lower protein and higher carbohydrate and lipid availability, driven almost entirely by the floral dominance of Asteraceae species (mean floral abundance: 96.8%). In contrast to these strong temporal shifts, we found minimal spatial variation in macronutrient composition among habitats. We also observed minimal interannual variation across the 8-year study period, despite considerable climatic fluctuations affecting floral abundance (electronic supplementary material, tables S2, S3, figures S3, S4).

(c) Bumble bee macronutrient niches and colony life stage variation

Our 8-year dataset of 4716 pollen-foraging interactions revealed distinct macronutrient niche partitioning among the 8 co-occurring bumble bee species (figures 2 and 3; electronic supplementary material, tables S4 and S5, figure S5). One niche, characterized by pollen with higher protein and lower lipid and carbohydrate levels, was occupied by *B. appositus*, *B. californicus*, *B. flavifrons* and *B. nevadensis* (mean P : L = 7.9 : 1; median compositional overlap within group = 94.3%; 95% Bayesian

(a) Community-level floral macronutrient composition



(b) Temporal variation in community-level floral macronutrient composition

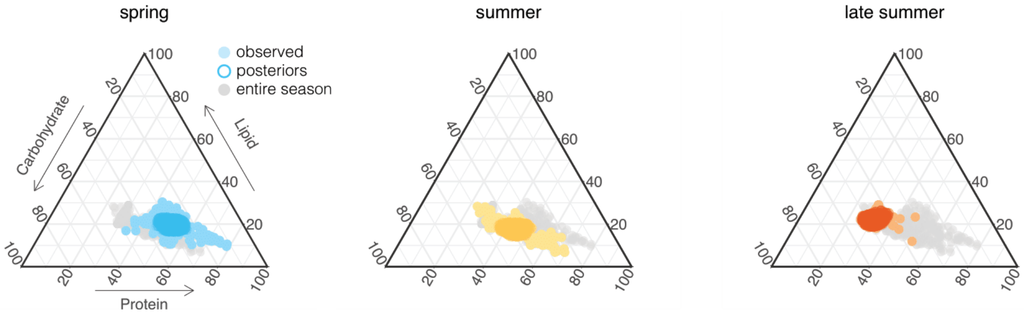


Figure 1. Floral macronutrient landscape and its seasonal dynamics. (a) Macronutrient composition (protein, lipid and carbohydrate) of pollen from 35 plant species in a subalpine ecosystem near the Rocky Mountain Biological Laboratory, Colorado, USA. Each coloured circle represents the observed mean proportion for a species and is shaded by corolla tube depth (mm; legend), while numbers identify species listed in the accompanying legend. The lighter, semi-transparent 'cloud' of points represents 100 posterior draws from the Bayesian model per species, illustrating model uncertainty. (b) Community-level macronutrient composition across the growing season. Each filled circle represents the posterior mean for a unique site × year × season combination (spring, summer, and late summer); lighter background points are corresponding posterior draws; light grey points represent non-focal seasons for comparison. Habitat-specific variation in these seasonal patterns is shown in the electronic supplementary material, figure S3.

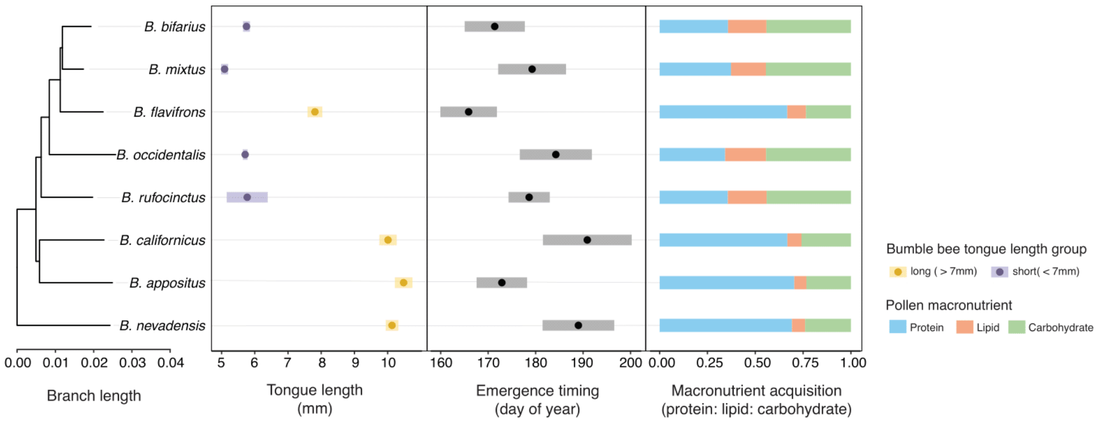


Figure 2. Phylogenetic and trait-based drivers of bumble bee macronutrient acquisition. This figure illustrates the relationship between evolutionary history, functional traits and nutritional niches for eight focal bumble bee species in a subalpine ecosystem near the Rocky Mountain Biological Laboratory, Colorado, USA. From left to right, the panels display: (i) phylogenetic relationships and branch lengths; (ii) mean tongue lengths, categorized into long- (>7 mm; yellow) or short- (<7 mm, grey) tongued groups; (iii) mean (point) and range (bar) of emergence timing (day of year); and (iv) the proportional macronutrient (protein, lipid and carbohydrate) composition of acquired pollen.

credible interval (BCI): [87.8–98.3%]) (figure 3; electronic supplementary material, table S5 and figure S5). The other niche, with lower protein and higher lipid and carbohydrate levels, was occupied by *B. bifarius*, *B. mixtus*, *B. occidentalis* and *B. rufocinctus* (mean P : L = 2.7 : 1; median compositional overlap within group = 98.9%; 95% BCI: [97.1–99.6%]) (figure 3; electronic supplementary material, table S5 and figure S5). The compositional overlap between these two niche groups was low (23.7%;

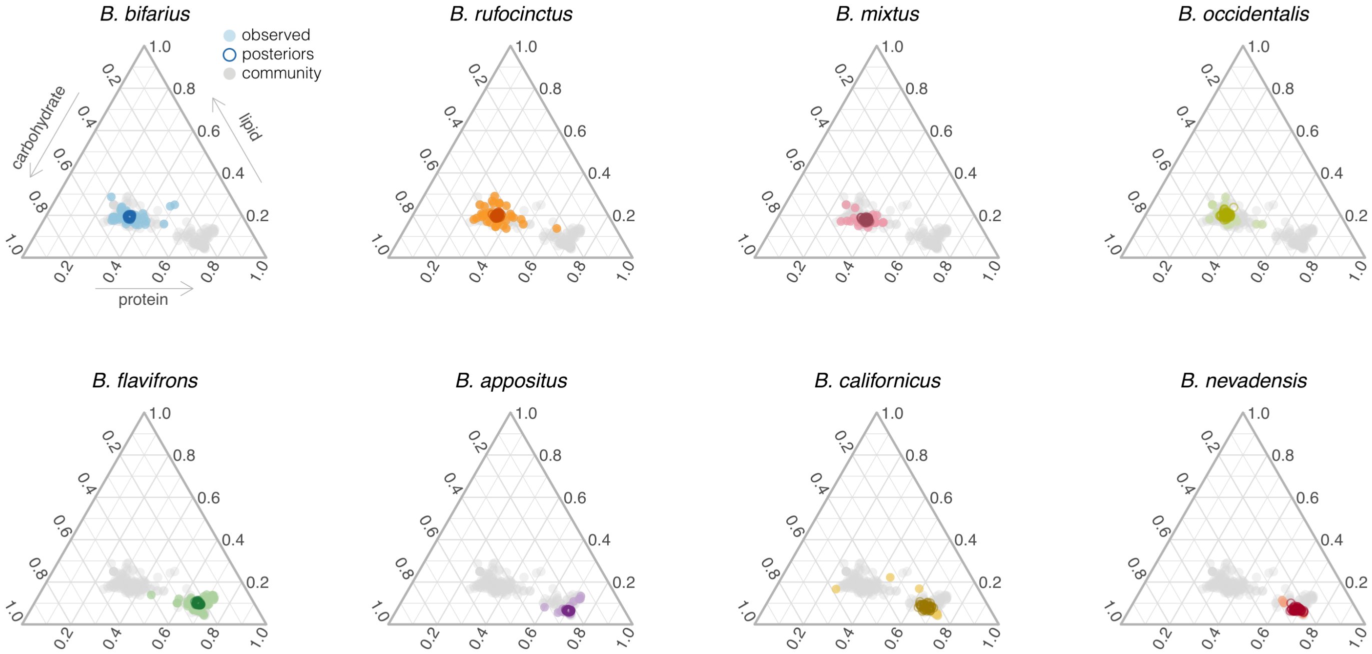


Figure 3. Macronutrient acquisition niches of co-occurring bumble bee species. Ternary plots (protein–lipid–carbohydrate axes) depict the pollen macronutrient acquisition niches for workers of eight bumble bee species in a subalpine ecosystem near the Rocky Mountain Biological Laboratory, Colorado, USA. Within each row, species are arranged left-to-right in descending order of pollen-foraging interaction frequency. Lighter, semi-transparent coloured circles represent the observed macronutrient acquisition for each site × year combination. Darker, open circles show 100 posterior draws for each species, illustrating model uncertainty and the estimated niche. Grey filled circles provide a reference for the macronutrient acquisition niche of the entire bumble bee community.

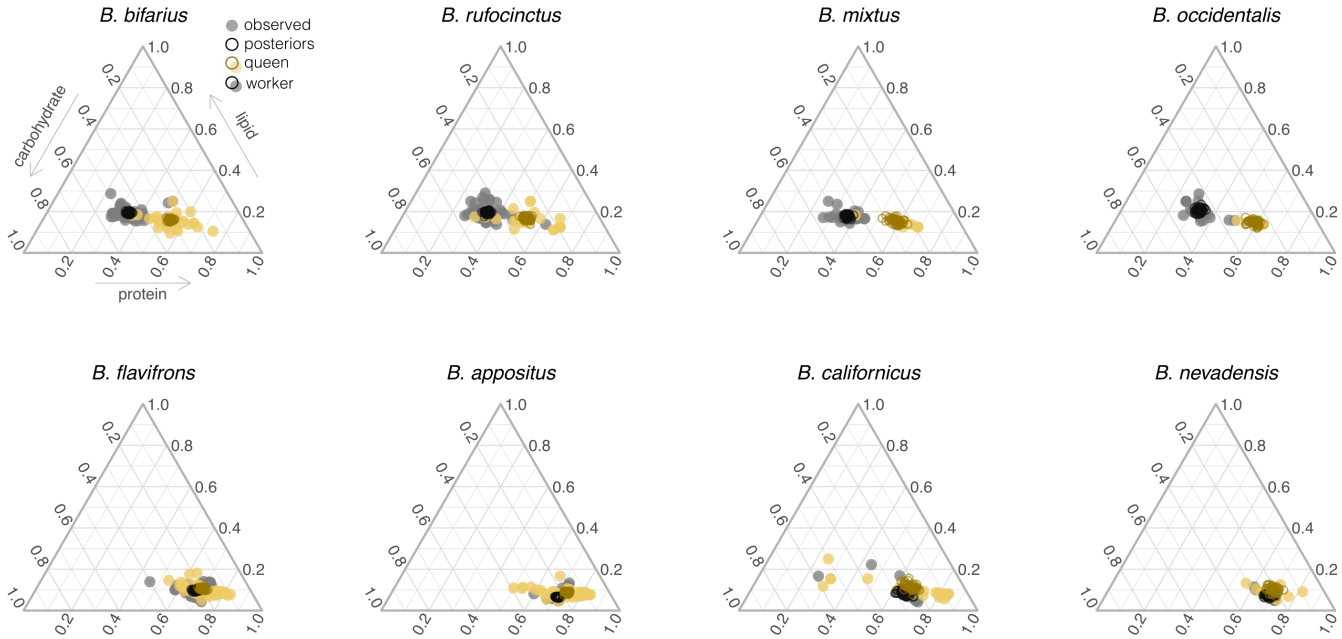
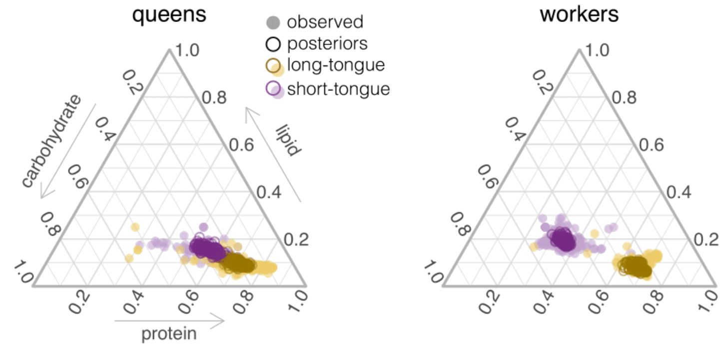


Figure 4. Comparison of macronutrient acquisition niches between bumble bee colony life stages (queens and workers). Ternary plots (protein–lipid–carbohydrate axes) depict the pollen macronutrient acquisition niches for eight bumble bee species in a subalpine ecosystem near the Rocky Mountain Biological Laboratory, Colorado, USA. The plots compare the proportional macronutrient niches for queens (gold) and workers (black) across the eight species. Lighter, semi-transparent filled circles represent the observed macronutrient acquisition for each site × year combination per caste. Darker, open circles show 100 posterior draws from the model, illustrating model uncertainty and the estimated niche for each caste.

95% BCI: [12.1–39.5%]), providing clear evidence for distinct macronutrient acquisition patterns (electronic supplementary material, table S5 and figure S5).

This macronutrient niche partitioning was most pronounced during the worker stage of the colony life cycle (figure 4; electronic supplementary material, table S5 and figure S5). We found strong evidence for a shift in pollen preference for short-tongued species, which moved from higher protein acquisition as queens to lower protein acquisition as workers (median niche overlap between castes = 64.2%; 95% BCI: [39.7%, 75.8%]) (figure 4; electronic supplementary material, table S5 and figure S5). Conversely, long-tongued species maintained relatively consistent nutrient acquisition strategies across their queen and worker stages (median niche overlap between castes = 89.7%; 95% BCI: [73.1%, 98.6%]) (figure 4; electronic supplementary material, table S5 and figure S5).

(a) Tongue length



(b) Phenology

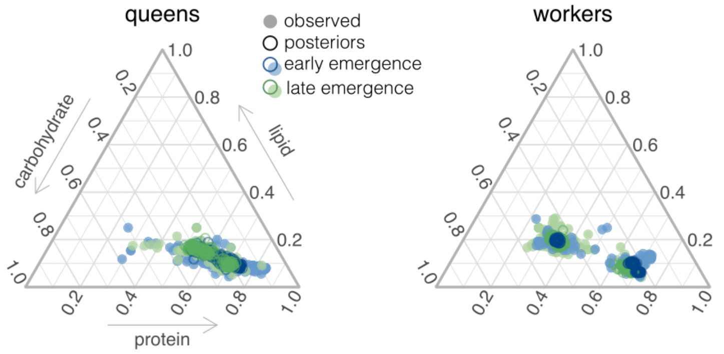


Figure 5. Comparison of the macronutrient acquisition niches of bumble bees by feeding traits and phenology. Ternary plots (protein–lipid–carbohydrate axes) depict the pollen macronutrient acquisition niches of bumble bees in a subalpine ecosystem near the Rocky Mountain Biological Laboratory, Colorado, USA. Plots show niches for queens (left) and workers (right), categorized by (a) tongue length (long versus short) and (b) emergence timing (early versus late). Lighter, semi-transparent filled circles are the observed macronutrient acquisition for each site × year combination. Darker, open circles represent 100 posterior draws from the model, illustrating model uncertainty and the estimated niche for each group.

(d) Ecological drivers of macronutrient niches

We examined how different potential drivers influenced the observed macronutrient niches of bumble bees: feeding morphology (tongue length), phenology (emergence timing) and evolutionary history (phylogeny). Of these drivers, feeding morphology was strongly correlated with macronutrient acquisition patterns. Long-tongued species consistently acquired pollen with higher protein and lower lipid and carbohydrate content, whereas short-tongued species acquired pollen with relatively lower protein and higher lipid and carbohydrate content (figures 2 and 5a; electronic supplementary material, table S5 and figure S5). The mean P : L ratio for long-tongued species was 7.9 : 1, compared with 2.7 : 1 for short-tongued species. In contrast, emergence timing was not related to macronutrient niches (figures 2 and 5b; electronic supplementary material, table S5). We also did not observe clear phylogenetic signal in macronutrient acquisition, as indicated by variance ratio (λ) values close to 1 (electronic supplementary material, figure S6).

(e) Ecological drivers of macronutrient niche breadth

In addition to niche position, we formally investigated factors contributing to niche breadth (i.e. nutritional specialization). While tongue length was a strong predictor of the average nutrients that bees acquired, our analysis showed it did not predict niche breadth (95% CI: [−0.37, 0.39]). Likewise, emergence phenology had no clear influence on niche breadth (95% CI: [−0.07, 0.03]). We also tested for differences in niche breadth between life stages. Although queens exhibited a visually broader macronutrient niche than workers across all eight species (electronic supplementary material, figure S7), we did not find strong evidence that caste had an overall effect on niche breadth, given the high uncertainty in the estimate (estimate = 1.13, 95% CI: [−0.62, 2.81]).

4. Discussion

Understanding how nutrients are distributed in nature and used by co-occurring species is an important, but understudied dimension of species interactions and species persistence [1,5,12]. This empirical knowledge gap is especially important for species of conservation concern, such as wild pollinators, where nutritional stress is a hypothesized mechanism of their declines [28,68]. In the context of our long-term study of plant–pollinator interactions, we find that pollen macronutrient composition varied considerably across plant species (figure 1), with community-level macronutrient availability fluctuating throughout the growing season (figure 1b). Within this nutritional landscape, co-occurring bumble bee species clustered into two distinct macronutrient niches (figure 3; electronic supplementary material, figure S5). These two macronutrient niches correspond to differences in feeding morphology and bumble bee colony life stage: short-tongued species occupied a relatively wide macronutrient niche that was low in protein and higher in lipids and carbohydrates, whereas long-tongued species occupied a narrower niche that was higher in protein but lower in lipids and carbohydrates (figure 5a). We also observed evidence that macronutrient niches can exhibit flexibility (*sensu* ontogenetic niche shifts), at least for some species (figure 4). Together, our findings help to advance our general understanding of how nutrients in nature shape species interactions, especially for wild pollinators.

The pollen available to pollinators in our system constituted a diverse nutritional landscape, with macronutrient ratios varying up to 33-fold among plant species (figure 1; electronic supplementary material, table S1). While prior work suggests that floral morphology and phylogeny could be important drivers of pollen nutrient content [14,50,69,70], our findings did not support a straightforward relationship with either factor. For instance, we found no correlation between floral morphology (corolla tube depth) and macronutrient composition; high-protein pollen occurred in plants with both deep and shallow corollas (figure 1a). The influence of evolutionary history was also more nuanced than expected. Although lipid content showed no phylogenetic pattern, both protein and carbohydrate content exhibited phylogenetic overdispersion ($\lambda < 1$), meaning closely related species were more divergent in these nutrients than expected by chance (electronic supplementary material, figure S2). This species-level divergence, possibly driven by competition, contrasted with broader similarities within major plant families (e.g. protein-rich Ranunculaceae versus carbohydrate-rich Asteraceae), suggesting that evolutionary pressures on pollen nutrients are scale-dependent. Our findings contribute to a broader literature of mixed results [14,69,70], indicating that pollen composition is shaped by multiple, interacting selective pressures beyond evolutionary history alone.

Plant communities naturally vary in their species composition across space and time, yet how this community-level variation translates to the nutritional landscape available to pollinators remains poorly understood. Our study addresses this gap, revealing a temporally dynamic floral macronutrient landscape that shifted from being protein-rich in the early season to lipid- and carbohydrate-rich by late summer (figure 1b). For generalist foragers like bumble bees, this creates a dynamic mosaic of resources, with important implications for their health [28,68,71], as the seasonal loss of high-protein plants could disrupt colony establishment even when other floral resources appear abundant. Despite these pronounced seasonal shifts, the macronutrient landscape was otherwise remarkably stable. We found no evidence of interannual variation over the 8-year study period; community-level macronutrient profiles remained consistent despite considerable fluctuations in climate and floral abundance (electronic supplementary material, figure S4). Furthermore, we found little evidence that macronutrient composition was spatially variable across different habitat types (electronic supplementary material, table S3 and figure S3). This relative spatial homogeneity might occur because, although habitats differ in plant species abundance, they still share many of the same species, which may homogenize the community-wide macronutrient availability.

Our finding that co-occurring bumble bees partitioned the floral macronutrient landscape provides field-based support for a core prediction of nutritional geometry. This framework predicts that co-occurring species should occupy unique nutritional niches, likely to minimize competition and maximize fitness [11,12]. Our analysis revealed two such niche groups: one characterized by high-protein, low-lipid/low-carbohydrate pollen, and another by lower-protein, higher-lipid/higher-carbohydrate pollen (figures 2 and 3; electronic supplementary material, figure S5). The breadth of a species' nutritional niche was not always congruent with its taxonomic diet (i.e. the number of plant species visited), demonstrating that these two axes of specialization are not necessarily equivalent (electronic supplementary material, table S3 and figure S8). While laboratory studies show that bees target specific macronutrient ratios to maximize fitness [44,51], these preferences are inevitably moulded by ecological factors in nature [10]. For example, competition and preference interact to shape macronutrient acquisition, meaning that species must balance nutritional quality and quantity in response to variable resource availability. While our study infers nutrient acquisition from foraging interactions, our findings lay the groundwork for future research. Directly analysing the nutritional content of pollen loads and performing manipulative field experiments represent compelling next steps to test the fitness consequences of occupying different nutritional niches.

For half of the bumble bee species, we observed that macronutrient acquisition shifted across colony life stages (from queens to workers), a pattern likely reflecting the colony's changing nutritional demands from establishment to growth and reproduction [18,39,72]. This divergence was most pronounced in species from the lower-protein nutrient niche, which showed less dietary overlap between queens and workers compared with species in the high-protein niche (figure 4; electronic supplementary material, table S5). We hypothesize that a key mechanism driving these ontogenetic niche shifts is the interplay between feeding morphology and floral access because nectar accessibility often determines initial flower choice [73,74], and differences in tongue length between queens and their workers can alter the pool of available pollen. In short-tongued species particularly, the relatively long tongues of queens grant them access to a wider floral resource pool—and consequently a different pollen macronutrient niche—than is available to their more restricted, short-tongued workers. This hypothesis is consistent with our broader finding that queens generally exhibit broader macronutrient niches than workers (figure 4; electronic supplementary material, figure S8), a strategy potentially reflecting their need for flexibility during the critical colony establishment phase [39,75,76]. Bumble bee workers, by contrast, tended to specialize on more consistent macronutrient sources to meet the particular demands of larval development [18,41]. This overall flexibility in nutrient acquisition likely affects a colony's resilience to environmental change, highlighting how species-specific strategies shape nutrient acquisition across the life cycle [10,28,41].

We found that feeding morphology was an important factor in bumble bee macronutrient niche differentiation. While pollinator tongue length is traditionally associated with nectar foraging [73,74,77,78], our study reveals a strong relationship between tongue length and pollen macronutrient acquisition: long-tongued species occupied niches higher in protein, whereas short-tongued species occupied niches with lower protein but more lipids and carbohydrates (figure 5). This finding raises a question about the underlying mechanism: does tongue length allow for direct targeting of specific pollen nutrients or does it more indirectly grant access to certain flower types that happen to offer distinct macronutrient profiles? Our results suggest the latter hypothesis. Although tongue length is known to mediate access to flowers based on their morphology (e.g. corolla depth), we found no correlation between corolla depth and pollen macronutrient composition (figure 1a). This suggests that tongue length dictates physical access to a subset of floral resources, and the observed nutrient niche emerges as a consequence of the macronutrient composition of those accessible plants rather than from nutrient-specific selection mediated by tongue length itself. Clarifying the links among feeding morphology, resource accessibility and macronutrient acquisition is a critical step for understanding nutritional niche partitioning in wild animals, including but not limited to pollinators.

Our study found that neither phenology nor phylogeny was a strong predictor of macronutrient niche partitioning among the bumble bee species in our study system. Despite strong seasonal shifts in floral nutrient availability, we observed little influence of emergence timing on the macronutrient niches of bee species (for both queens and workers; figure 5b; electronic supplementary material, table S5). In our study system, the extended, overlapping flight seasons of these bumble bees allow them to forage for resources across the entire growing season, likely dampening any potential effect of initial activity timing. However, for other pollinators with shorter, more discrete activity periods, phenology likely plays a more critical role [19,71,79]. Turning to shared evolutionary history, we did not find strong evidence that phylogeny predicted macronutrient acquisition patterns (electronic supplementary material, figure S6). While some closely related species occupied similar nutrient niches (e.g. *B. bifarius* and *B. mixtus*; electronic supplementary material, figure S6), this pattern was not consistent across the community. This lack of a clear phylogenetic signal is exemplified by *B. flavifrons*: despite belonging to the mostly short-tongued *Pyrobombus* subgenus, it occupied the high-protein niche. This absence of a strong phylogenetic signal for nutrient acquisition—especially when contrasted with prior work showing phylogenetic conservation in the plant families that bees visit [35]—suggests a potential decoupling between a bee's taxonomic diet breadth and nutritional acquisition, highlighting the importance of considering nutritional composition separately from plant taxonomy [15].

A nutritional perspective is needed for pollinator conservation and restoration, as inadequate or imbalanced diets are major hypothesized factors contributing to pollinator declines [24,28,41,68]. Management strategies that focus solely on increasing floral diversity while overlooking nutritional composition may fail to support vulnerable species and fall short of their conservation goals [28,68,80]. Our findings demonstrate that even closely related species can occupy distinct macronutrient niches, reinforcing the need for targeted, species-specific conservation approaches. For example, conservation strategies for at-risk pollinators, such as *B. occidentalis*, whose decline has been linked to habitat loss [81], can prioritize plants that align with its nutritional niche rather than defaulting to resources favoured by more common or agriculturally important bees. The clear niche partitioning we document was likely facilitated by the intact, stable, and diverse floral communities of our study sites; in other systems, such as disturbed, heterogeneous or urban landscapes, nutritional niches may be more constrained, making targeted restoration all the more critical. Incorporating species-specific macronutrient needs into conservation planning can help to mitigate nutritional stress and support pollinator resilience, providing a nutritionally explicit framework to inform ecosystem management in changing environments.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data and scripts for this study are available in the Open Science Framework repository [82].

Supplementary material is available online [83].

Declaration of AI use. We used AI-assisted technologies in a limited capacity to troubleshoot code and revise some text to improve readability. AI did not replace key researcher tasks such as producing the writing, scientific insights, analysing and interpreting data or drawing scientific conclusions.

Authors' contributions. J.B.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, visualization, writing—original draft, writing—review and editing; J.O.: data curation, investigation, methodology, writing—review and editing; W.K.P.: formal analysis, writing—review and editing; P.C.: conceptualization, formal analysis, resources, supervision, validation, visualization, 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.

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