PNAS RESEARCH ARTICLE | ECOLOGY

Pollen nutrition structures bee and plant community interactions

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Edited by Anurag Agrawal, Cornell University, Ithaca, NY; received October 9, 2023; accepted November 19, 2023

As bees' main source of protein and lipids, pollen is critical for their development, reproduction, and health. Plant species vary considerably in the macronutrient content of their pollen, and research in bee model systems has established that this variation both modulates performance and guides floral choice. Yet, how variation in pollen chemistry shapes interactions between plants and bees in natural communities is an open question, essential for both understanding the nutritional dynamics of plant–pollinator mutualisms and informing their conservation. To fill this gap, we asked how pollen nutrition (relative protein and lipid content) sampled from 109 co-flowering plant species structured visitation patterns observed among 75 subgenera of pollen-collecting bees in the Great Basin/Eastern Sierra region (USA). We found that the degree of similarity in co-flowering plant species' pollen nutrition predicted similarity among their visitor communities, even after accounting for floral morphology and phylogeny. Consideration of pollen nutrition also shed light on the structure of this interaction network: Bee subgenera and plant genera were arranged into distinct, interconnected groups, delineated by differences in pollen macronutrient values, revealing potential nutritional niches. Importantly, variation in pollen nutrition alone (high in protein, high in lipid, or balanced) did not predict the diversity of bee visitors, indicating that plant species offering complementary pollen nutrition may be equally valuable in supporting bee diversity. Nutritional diversity should thus be a key consideration when selecting plants for habitat restoration, and a nutritionally explicit perspective is needed when considering reward systems involved in the community ecology of pollination.

plant–pollinator networks | nutritional ecology | floral rewards | Great Basin/Eastern Sierra

Significance

Nutrition is widely recognized as a key factor in addressing pollinator declines, and across the tree of life, plants vary in the protein and lipid content of their pollens offered to bees. However, within natural communities, we know surprisingly little about the nutritional value of plants to wild bees, and pollen nutrition has not previously been a priority when selecting plants for restoration efforts. We show that consideration of pollen macronutrient content can help explain patterns of interactions among wild bees visiting wildflowers to collect pollen, which sheds light on the nutritional basis of plant–bee mutualisms, and can help inform plans to restore bee habitat, conserve plant species, and design supplemental plantings for bees in agricultural and urban areas.

Nutrition is at the heart of the mutualism between bees and plants, as most flowers offer food rewards in exchange for the transfer of pollen. Yet although plant–pollinator community dynamics have received longstanding attention in relation to floral display phenotypes (1, 2), floral nutrition is rarely considered on its own merits as a driver of these relationships. This is surprising because dietary macronutrients are known to shape foraging behavior across insect taxa (3, 4), and bees' morphological and behavioral adaptations to collect pollen and nectar for consumption are fundamental to our understanding of foraging economics (5) and the evolution of diet choice (6, 7). Indeed, floral rewards provide the complete source of nutrition for most bee species (8–11) with pollen serving as bees' primary source of protein and lipids. The amount and concentration of these pollen macronutrients vary substantially among plant species sampled opportunistically across the tree of life (11–13), and research on model bee systems shows foragers are sensitive to variation in pollen resources. For example, bumble bees (*Bombus*) prefer plant species offering pollen characterized by high ratios of protein to lipids (pollen P:L ratios), with consequences for individual and colony performance (14–19). Recent research indicates that other model bee genera such as *Apis* and *Osmia* have different nutritional requirements in laboratory settings (20), which may also be reflected in the nutritional content of pollens they collect (11). Other studies have focused on pollen chemical defenses as a mechanism driving specialization in focal systems (21, 22), but the role that variation in pollen macronutrient content plays in interactions between wild bee and plant communities in natural areas has not been examined. There are practical implications of this knowledge gap: Bee declines are linked to habitat loss, compounded by disease, climate change, and pesticides (23–27). Given major initiatives to restore foraging habitat in agricultural, urban, and natural landscapes (28–31), moving beyond consideration of only floral abundance remains a challenge requiring input from nutritional ecology to help define and address the quality of floral resources sought by consumers within ecological communities (10, 11, 32–34) and thus better inform how we restore pollinator habitat.

The Geometric Framework (GF) is a well-established model in the field of nutritional ecology (3, 4) that, given its usefulness in explaining diet choice in model bee systems

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Author contributions: A.D.V., L.A.D., and A.S.L. designed research; A.D.V. performed research; A.D.V. and L.A.D. analyzed data; and A.D.V., L.A.D., and A.S.L. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2317228120/-/DCSupplemental.

Published January 8, 2024.

(14, 15, 35), offers a starting point to frame questions about how pollen macronutrients might structure bee–plant interactions (Fig. 1). We first assume that pollen-collecting bees have taxon-specific foraging targets (i.e., a particular ratio of nutrients that maximizes fitness; see the targets in Fig. 1) (4, 36). We can then visualize pollen macronutrient content (i.e., P:L ratios) of co-flowering plant species, the "nutritional landscape," as "rails" (lines in Fig. 1), which pollen-foraging bees can "travel along" as they visit plants to collect pollen in pursuit of a target P:L ratio (arrows in Fig. 1). Using a GF approach to visualize the relationship between bee nutritional needs and the composition of available resources suggests that while some bees might exclusively visit plants whose pollen composition aligns with their target (Fig. 1, bee #1), others might combine visits to unbalanced yet complementary pollen sources (bees #2 and #3). This dietary mixing could manifest as bees combining visits to plants that hold similar positions in nutritional space (i.e., rails with similar slopes: bee #2), or somewhat counter-intuitively, combining visits to plants with very different nutritional values (bee #3). Given that the nutritional landscape of a co-flowering plant community has not previously been characterized, how different wild bee species might structure their foraging for pollen protein and lipids among available floral resources is an open question. With nutritional geometry as an organizing perspective, we thus analyzed visitation patterns of pollen-collecting bee subgenera and plant pollen nutrition across multiple sites in the Great Basin/Eastern Sierra Sagebrush Steppe habitat. Considering that multiple floral traits may covary, we analyzed the role of pollen nutrition in explaining visitation patterns alongside floral morphology and plant phylogeny (12, 13, 37–40). We used this dataset to explore three related questions about the role of pollen macronutrient composition in community interactions: 1) How likely are plants with nutritionally similar pollens to be visited by similar bee communities? 2) What role does pollen nutrition play in structuring broad patterns of bee–flower interaction networks? 3) Do plants with different pollen nutritional profiles differ in their levels of specialization or generalization within interaction networks?

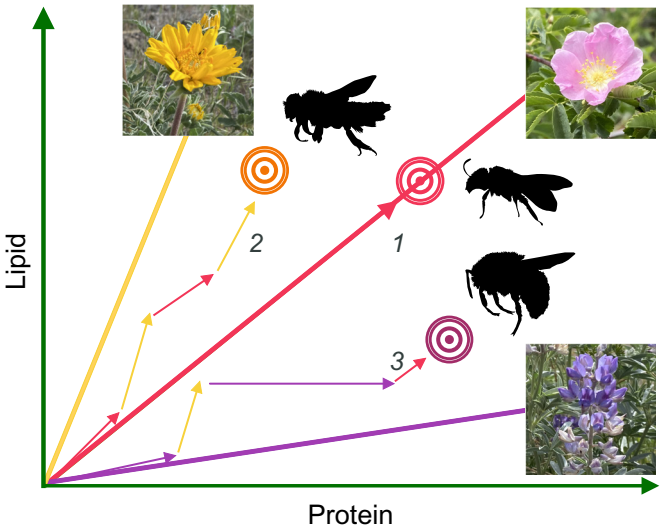

Fig. 1. Conceptual framework for considering bee nutritional niches and pollen foraging behavior. Plants' positions in space represent their pollen protein and lipid concentrations and lines connecting them to the origin represent their protein:lipid (P:L) ratios. Target symbols represent hypothetical nutritional intake targets for different bee species. If groups of bees occupy similar targets, these may be considered nutritional niches. Direction and color of arrows illustrate how bees might use different foraging strategies while sharing similar resources to balance their diet to reach different nutritional intake targets: 1) foraging from a single plant species offering rewards close to the intake target, 2) foraging equally from nutritionally complementary resources close to an intake target, 3) foraging among all plants in the nutritional landscape at varying frequencies to balance their diet to reach a target.

Question 1: How likely are plant species with nutritionally similar pollen to be visited by similarly composed communities of pollen-foraging bees? If most bees tend to forage for pollen relatively narrowly in line with their intake target (Fig. 1, bees #1 and #2), then we expect that plant species offering pollens of similar composition will share visitor communities, and plant species with dissimilar pollen nutrition will be visited by dissimilar bee communities. This signal would be lost however if bees combine visits to plants dispersed widely across nutritional space, if other floral traits more strongly influence pollen foraging behavior, or if bees simply visit the most abundant plants regardless of pollen nutrition.

Question 2: What role does pollen nutrition play in structuring broad patterns of pollen visitation networks? Here, we expected that bee and plant genera that occupy similar nutritional space and more frequently interact may represent nutritional niches (i.e., multiple bee subgenera might share similar intake targets in Fig. 1, and therefore share nutritionally similar host plants across space and time) (36, 41–44). Characterizing our interaction network into aggregated groups of frequently interacting pollen-collecting bees and plants [i.e., modules (44, 45)], we asked whether these modules were also composed of plant species that share similar nutritional values. If nutritional niches did not exist, we expected to find either no modules in the network, or variation in pollen nutrition equally distributed among modules.

Question 3: Do plant species with different pollen nutritional profiles differ in their levels of specialization or generalization within interaction networks? Generalist species can provide resilience in ecological interactions, making them key to consider for pollinator habitat restoration efforts (46–48). We evaluated individual plant species' visitation network–derived metrics of strength and specialization/generalization (e.g., strength, D', effective partners, centrality), in relation to the nutritional value of their pollen. If generally, bees prioritize proteinaceous diets [as in bumble bees (15, 19, 49)], then we expected plants with higher P:L ratios would be visited more frequently by a higher taxonomic diversity of bees; or if bees prioritize lipids given their dietary importance (50–53), then plants with low P:L values may be more generalist. Alternatively, plants with intermediate "balanced" P:L values may attract the highest bee diversity and abundance. A lack of any relationship might suggest that plant species across the spectrum of pollen nutrition are equally important for supporting bees occupying different nutritional niches.

Results

The Pollen Nutritional Landscape. Great Basin/Eastern Sierra (*SI Appendix*, Fig. S1) plant species pollen nutrition was characterized by high variability, and our analysis expands the range of protein and lipid values obtained in previous studies (11) (Fig. 2, *SI Appendix*, Fig. S3, and Dataset S1*C*). Due to an updated lipid analysis, we obtained P:L values higher than previously reported (11). The distribution of pollen protein and lipid concentrations, and P:L values, did not differ between sites (repeated measures mixed model with plant genus as a random effect; protein: $F_{7,166} = 0.38$, $P = 0.91$; lipid $F_{7,166} = 0.45$, $P = 0.87$; P:L: $F_{7,173} = 0.16$, $P = 0.99$; *SI Appendix*, Fig. S2 and Table S1) indicating that bee communities had similar foraging options across habitats even as plant species turned over. We note that our method of lipid analysis, the sulfo-phospho-vanillin assay (SPV), may be biased toward unsaturated fatty acids and thus

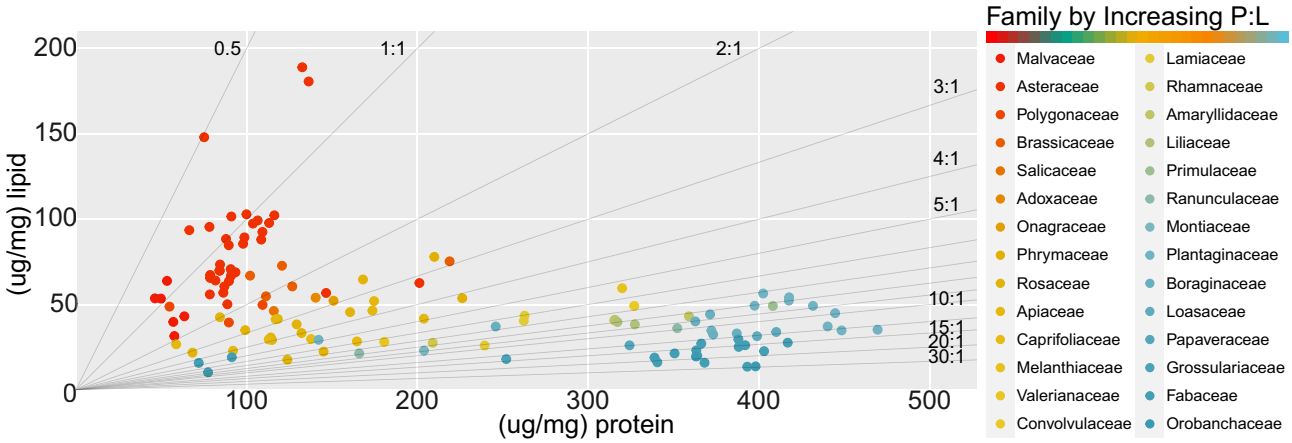

Fig. 2. Pollen nutritional landscape of the Great Basin/Eastern Sierra flora. Pollen protein and lipid concentrations (μg/mg) are arranged in two-dimensional nutritional space. Each marker represents an individual plant species, colored by plant family along a gradient from low to high pollen P:L (see Dataset S1*C* for individual species protein, lipid, and P:L values). Gray lines represent different P:L values.

underestimate the total lipid content of pollen (54). Nonetheless, digestible unsaturated fatty acids are important for bee health and perception (51–53) and thus comparative values across plant species have direct relevance to analyses of behavior and physiology.

We used factor analysis to provide estimates of pollen nutrition and morphology as latent variables based on measured pollen nutritional traits (protein μg/mg, lipid μg/mg, and P:L ratios) and morphological traits (floral symmetry, morphology, depth, and width) (*SI Appendix*, Table S2). Among our pollen nutrition metrics, P:L was the most strongly correlated with the pollen nutrition latent variable (factor loading: 1.0, *SI Appendix*, Table S2) indicating that P:L ratios are a strong predictor variable for evaluating pollen nutrition from both protein and lipid concentrations. Likewise, floral symmetry and open vs. tubular/complex flowers were the strongest metrics associated with floral morphology (factor loadings: 0.94 and 0.88, respectively) while depth or width were not as correlated with these other morphological factors (*SI Appendix*, Table S2).

Further testing the relationship between pollen nutrition and floral morphology, we found that pollen P:L ratio and protein concentration increased, and lipid concentration decreased, from radially to bilaterally symmetrical flowers (repeated measures mixed model with plant genus as a random effect; protein: $F_{1,75} = 25.82$, $P < 0.01$; lipid: $F_{1,75} = 9.87$, $P < 0.01$; P:L: $F_{1,75} = 36.07$, $P < 0.01$), and from open, to tubular, to complex morphologies (protein: $F_{2,75} = 12.65$, $P < 0.01$; lipid: $F_{2,75} = 5.98$, $P < 0.01$; P:L: $F_{2,75} = 22.63$, $P < 0.01$), meaning that complex flower morphology was generally associated with higher pollen P:L values (*SI Appendix*, Fig. S4 and Table S3).

Pollen nutritional profiles exhibited a phylogenetic signal among closely related plant species, yet these profiles (high or low P:L for instance) arose multiple times throughout the plant phylogeny (Fig. 3 and *SI Appendix*, Fig. S5; protein: K = 0.59, λ = 0.98; lipid: K = 0.34, λ = 0.98; P:L: K = 0.08, λ = 0.83).

Question 1. We asked how interspecific variation in pollen nutrition among plant species (protein and lipid content and P:L) contributed to the subgenera composition of bee communities we observed visiting plants to collect pollen, while accounting for floral morphology and phylogenetic covariance of these traits (*SI Appendix*, Fig. S6). We summarized bee communities associated with each plant species using principal components analysis (PCA). Pollen nutrition and floral morphology were considered to be latent variables and were estimated by factor analysis (*SI Appendix*, Fig. S6). We also conducted the analysis of bee community composition directly with the P:L ratio as a fixed effect stratified by floral symmetry.

PCA plant scores closer in space along PC1 (22% variation explained) or PC2 (14%) axes shared similar bee communities in identity and visitation frequency. The most abundant bee subgenera, *Dialictus* and *Melanosmia*, were on the negative and positive ends of the PC1 axis respectively, while they both occupied the most negative values of PC2. Pollen nutrition was linearly related to plant scores along PC1 in both total effect [posterior distribution of slope mean (upper, lower 90% CI): P:L = 0.52 (0.39, 0.62), Nutrition factor = 0.54 (0.41, 0.66)] and while analyzing by morphology and phylogenetic covariance [P:L[radial] = 0.59 (0.08, 1.09), P:L[bilateral] = 0.63 (0.48, 0.78); Nutrition factor = 0.65 (0.50, 0.80)] indicating that the majority of variance in ordination was predicted by pollen nutrition (Fig. 4*A* and *SI Appendix*, Table S4). Likewise, PC2 scores were linearly related to pollen nutrition in total effect [P:L = −0.22 (−0.37, −0.07), Nutrition factor = −0.23 (−0.38, −0.07)] and especially after accounting for morphology and phylogenetic covariance [P:L[radial] = 0.10 (−0.56, 0.77), P:L[bilateral] = −0.58 (−0.73, −0.43); Nutrition factor = −0.58 (−0.74, −0.43)], yet for PC2 the relationship between variation in pollen nutrition and bee community composition was mainly within bilaterally symmetric flowers (*SI Appendix*, Table S4). That is, as pollen nutritional content differed among plant species, so did the visiting community of bees. Floral morphology also contributed to differences in bee communities as radial and bilateral flowers had different intercepts, yet this difference was dampened by including phylogenetic distances and the counterfactual effect of nutrition on morphology (nutrition-morphology = 0.70 (0.58, 0.82); Fig. 4*B* and *SI Appendix*, Table S4). Clearly, there was high phylogenetic covariance in plant nutritional values and morphologies (Ornstein–Uhlenbeck posterior $\eta^2 = 2.6$ vs. prior $\eta^2 = 1$, Fig. 4*C* and *SI Appendix*, Table S4); but including this variance in our models strengthened the association between floral nutrition and bee community likely because bee communities were more associated with plants whose pollen had a specific nutritional value regardless of plants' (familial) relatedness.

Question 2. The visitation network that we estimated from observations of pollen-collecting bees was partitioned into a handful of major modules (Fig. 5*A*), which represent bee subgenera and plant genera more likely to interact with each other than with

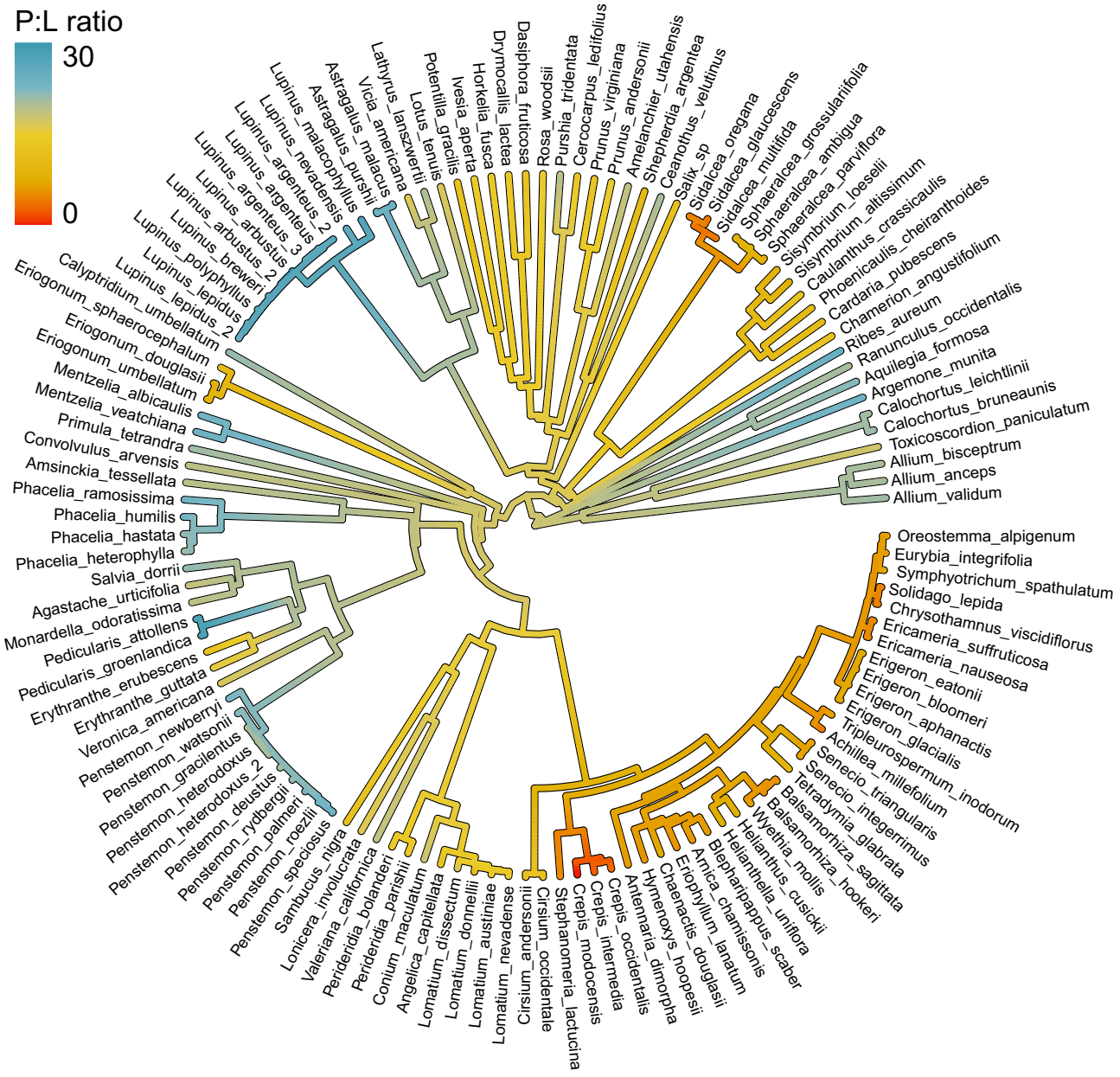

Fig. 3. Phylogenetic tree of plant species colored by their associated pollen P:L ratio. For some species, distinct populations analyzed separately are represented by different numbers.

members outside their group. The average pollen P:L of plant genera within modules differed between modules (Fig. 5 and *SI Appendix*, Table S5). These results held true when we manipulated the data in two ways: 1) Treating all plant genera in each module equally and taking the module average; or 2) weighing each plant genus by bee visitation frequency because some genera were more frequently visited for pollen than others, and thus more influential in the visitation network and likely to contribute more to bees' nutrient intake (Fig. 5*C* and *SI Appendix*, Table S5; see bee #3 in Fig. 1). The module with the highest average P:L had the widest distribution of P:L values, while the module with the lowest average P:L had a very narrow distribution of pollen P:L values collected by bees (Fig. 5*B*). Other modules exhibited intermediate yet decreasing distributions of P:L values from the high to low P:L modules. Bayesian predicted P:L distributions between modules were much narrower than observed values and clearly distinct between modules. Modules therefore may be used to delineate nutritional niches and predict potential intake targets for bees. These results were also corroborated by repeating the analysis such that the major modules remained consistent across iterations (*SI Appendix*, Table S5).

Question 3. We analyzed whether plant species' pollen nutrition was related to their network strength and degree of generalization/specialization in the pollen visitation interaction network, including the following species-level network metrics: strength, effective partners, nested rank, D', betweenness centrality, and closeness centrality. The data did not support the hypotheses that plants with differing nutritional values would be visited by a higher diversity and frequency of bee taxa (Fig. 6 and *SI Appendix*, Fig. S7 and Tables S6 and S7). Contrarily, there was a trend that increased P:L ratios values were associated with increased specialization mainly within bilaterally symmetric flowers (e.g., fewer effective partners, higher nested rank, and lower strength; Fig. 6 and *SI Appendix*, Fig. S7 and Tables S6 and S7). But posterior distributions of these slopes crossed 0, and the indices for D', betweenness centrality, weighted betweenness, and weighted

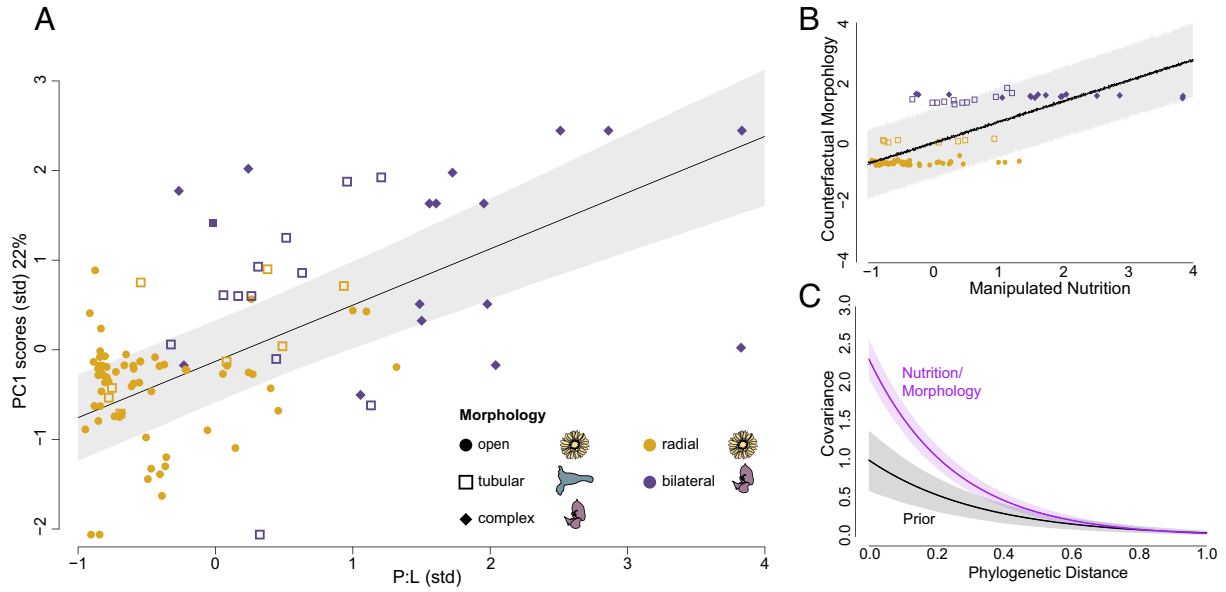

Fig. 4. The influence of pollen nutrition on bee community visitation, representing three processes analyzed in our model (see model 6 in *SI Appendix, SI 3*). (*A*) Standard scores of nutrition factors regressed against PC1. Each marker represents a different plant species, and associated visiting bee community, where distance between markers on the *Y* axis represents differences in bee visitors. Plant species markers are colored and shaped by their floral symmetry and morphology respectively. The trend line and shade represent the predicted slope and 90% credible interval of the effect of plant species' pollen nutrition on bee community (*SI Appendix*, Table S4). (*B*) Counterfactual effect of nutrition on floral morphology representing the relationship between nutrition and morphology by manipulating pollen nutrition and predicting morphology. Markers represent individual plant species. As floral morphological complexity increases, so does its associated nutritional value. (*C*) Posterior distributions of phylogenetic signal against priors via Ornstein–Uhlenbeck covariance process. Highly related species share high covariance in pollen nutrition and morphology yet as distance increases, covariance in traits drops rapidly (Fig. 3). Legume image credit: Alexander Schmidt-Lebuhn, https://creativecommons.org/licenses/by-nc-sa/3.0/.

closeness showed no trend (Fig. 6 and *SI Appendix*, Fig. S7 and Tables S6 and S7). Likewise, there was no indication that plants whose pollens had intermediate P:L nutritional values were more generalist, exhibiting very wide posterior distributions (Fig. 6 and *SI Appendix*, Fig. S7 and Tables S6 and S7). These results indicate that generally, plants with different pollen nutritional values were equally important and complementary in attracting diverse bee communities, and continuity within the nutritional landscape

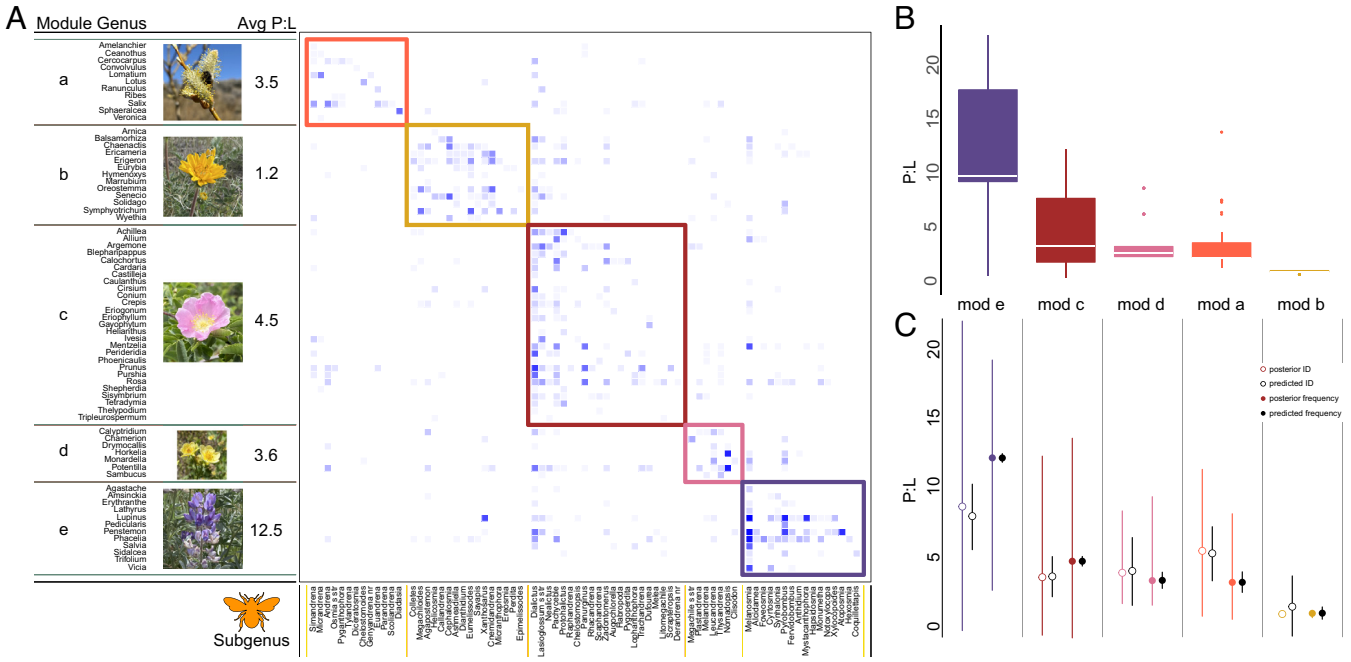

Fig. 5. Modules of Great Basin/Eastern Sierra bee–flower interactions representing potential nutritional niches. (*A*) Matrix of interactions where each blue square represents an observed interaction between a plant genus and bee subgenus, and the darkness of the square represents the frequency of the interaction. Data are standardized such that rows (i.e., plant genera) range from light to dark to compare relative visitation frequencies. Each module is outlined and labelled for plants and bees. (*B*) The raw distribution of P:L of each module weighted by visitation frequencies. (*C*) Bayesian posterior predictions of P:L associated with each module for analysis by both plant identity (each plant weighted equally) or weighed by visitation frequency. These data may be used as predictions of nutritional niches of bee–flower community interactions in the Great Basin/Eastern Sierra habitat.

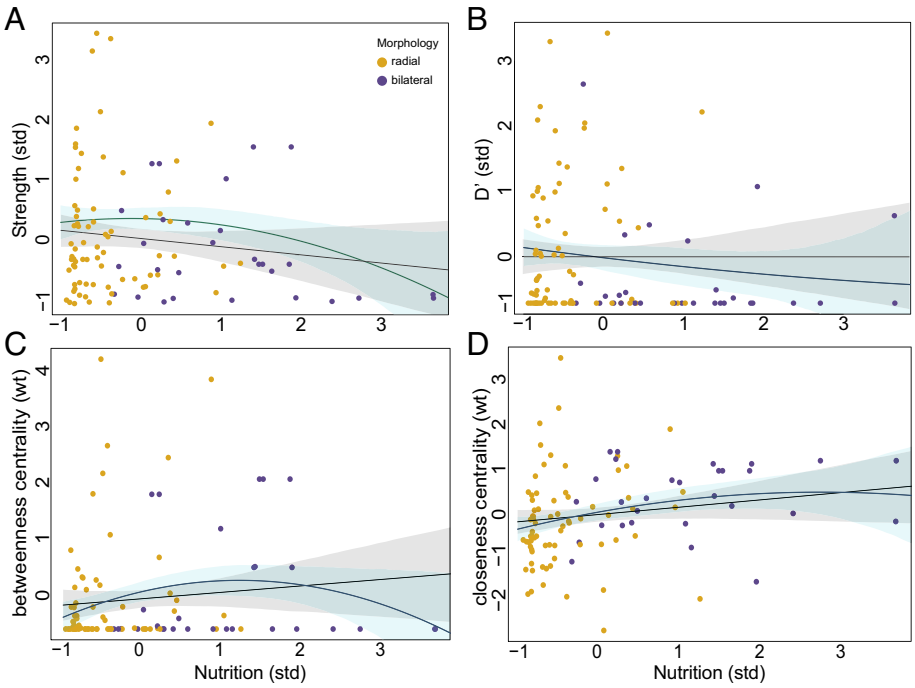

Fig. 6. The relationship of plant species' network indices for strength and specialization regressed against their pollen nutritional value. Trend lines and shade represent the Bayesian predicted slope and 90% credible interval of the effect of plant species' nutrition on each network index. Black lines and gray shade represent predicted distributions of the linear relationship, and blue lines and shade represent the quadratic relationship. Note that in each case, predicted distributions of the slopes crossed 0, the value at which there is no observable relationship between plant species pollen nutritional value and its role in the pollen interaction network (*SI Appendix*, Table S7). (*A*) Plant species strength, (*B*) D′, (*C*) weighted betweenness centrality, and (*D*) weighted closeness centrality.

may allow bees competing for resources to find alternative hosts with relatively comparable nutritional values.

Discussion

The nutritional threads that connect plants and pollinators within a community are impossible to see, challenging to study, and critically important for both understanding plant–pollinator mutualisms and informing their conservation. Although taxonomic patterns of pollen host plant specialization are a canonical theme in bee natural history (55), the role of pollen nutrition in explaining broad patterns of interactions has only recently received attention (10, 11, 32, 33, 49, 50), and has been often limited by the concept that a single dimension of pollen chemistry (largely, protein content) equates to quality. Yet, a parallel literature in nutritional ecology has long demonstrated that variation in multiple dimensions of macronutrient content is a primary driver of animal foraging behavior and trophic interactions more generally (3, 4). Understanding bee–host plant relationships may thus depend upon a nutritionally explicit consideration of reward composition, rather than plant taxonomic identity. A significant implication of our study is that generalist bees that visit unrelated plant species may indeed be cryptic nutritional specialists if those plants have chemically similar pollen. Likewise, we reveal that the natural distribution of nutritional diversity likely supports entire bee communities, and without this consideration of floral nutritional diversity, species-diverse restoration plantings could function as monocultures.

A key first step toward understanding floral nutrition's relevance to bee community ecology is to characterize its general patterns within plant communities. Rather than opportunistically sampling pollens across the tree of life, from plants used for pollinator habitat supplementation, or in agriculture (11–13, 56, 57), we sought to gain a nutritional snapshot of co-flowering plants within an ecological community. This allowed us to ask in real time whether pollen nutrition, on its own and in concert with other floral traits, explained broad patterns of wild bee pollen foraging. We found that, despite phenological and elevational turnover between sites, and independent of plant species richness at any given site, bee-visited plant communities shared similar distributions of pollen lipid and protein content, covering the aggregated distribution of observed values (Fig. 2 and *SI Appendix*, Fig. S2). This is significant in that natural areas had a "nutritionally complete" and diverse suite of pollen protein and lipid nutrients available to the bee community. After generating a visitation interaction network to specifically focus on pollen nutrition and pollen collection (and limiting the influence of nectar collection on visitation), we demonstrated that: 1) Pollen nutritional content and floral morphology are often correlated and both affect bee–flower associations, but nutritional content predicts bee communities when controlling for morphology (Fig. 4). 2) The most frequently interacting groups of bees and plants (i.e., modules of the interaction network) represent nutritional niches characterized by plants differing in average pollen P:L ratios (Fig. 5). 3) On its own, pollen macronutrient content does not predict floral generalization or strength in connecting the community (58, 59) (Fig. 6 and *SI Appendix*, Fig. S7). Thus, across its measured distribution, variation in pollen lipid and protein content is equally valuable in supporting a diverse bee community.

The Nutritional Landscape, Floral Morphology, and Patterns in Wild Bee Visitation. Reward nutrition does not function in isolation, and bee foraging patterns within a plant community are often associated with suites of covarying floral traits (39), many of which may be also predicted by relatedness. In line with previous studies (e.g., protein content: refs. 12 and 13), we found that more closely related plant species had pollens with

similar protein content, lipid content, and P:L ratios (Fig. 3 and *SI Appendix*, Fig. S5). Nutritional diversity at each site and across sites was thus maintained by abundant, species rich, and ubiquitous plant taxa that demonstrated consistent P:L values within their clade, yet differed between clades (e.g., Asteraceae with low P:L, Rosaceae and Apiaceae with intermediate P:L, and *Penstemon* (Plantaginaceae) or *Lupinus* (Fabaceae) with high P:L values). Our analysis also yielded an association between pollen nutrition and floral morphology, where higher complexity floral phenotypes tended to have higher pollen P:L ratios on average, as did bilaterally symmetric as compared to radially symmetric flowers (*SI Appendix*, Fig. S4). There were exceptions to this trend: Some complex flower morphologies such as *Lotus* and *Vicia* (Fabaceae) had lower P:L ratios than other legumes; and some simpler morphologies such as *Cirsium* (Asteraceae) or *Purshia* (Rosaceae) exhibited higher P:L ratios relative to their sister taxa (Fig. 3 and *SI Appendix*, Fig. S3).

Floral morphology and pollen chemistry have a complex functional interplay: complex morphology such as poricidal anthers and keel petals may restrict reward access to more behaviorally specialized bees (37, 40), and broad patterns of protein content correlate with these restrictive mechanisms (13, 60). The premise that complex flower morphology, here associated with higher P:L values, would lead to visitation by a less diverse community of bees (37, 38, 58), was only marginally supported by our data (Fig. 6 and *SI Appendix*, Fig. S7 and Table S6). For example, *Pedicularis* which has extremely high P:L values associated with poricidal anthers, was solely visited by bumble bees (*Bombus spp.*), yet other flowers with complex morphologies attracted a diversity of subgenera.

Even after accounting for the fact that closely related plant species often share similar pollen nutrition and floral morphology, variation in pollen macronutrient content explained variation in bee community composition, i.e., plants with similar pollen P:L ratios were frequently visited by bee communities comprised of similar subgenera (Figs. 4 and 5). For example, Rosaceae (with open radial flowers) and Brassicaceae (with more tubular radial flowers and fewer lines of symmetry) are not close relatives; yet these two groups nonetheless have similar P:L ratios and were visited by similar communities of pollen-collecting bees. Similarly, tubular radially symmetric flowers (e.g. *Phacelia*) and bilaterally symmetric keel flowers (e.g. *Lupinus*) with high P:L ratios shared similar communities of pollen-collecting bees. By the same token, plants with different pollen nutrition with similar morphologies were visited by disparate communities of bee subgenera. For example, among similarly shaped and highly related flowers, such as members of Asteraceae, *Cirsium* exhibited a higher P:L ratio than its relatives and was associated with a distinct community of bee visitors. Likewise, within Fabaceae, all of which have highly complex (keel petal) morphology, *Lotus* had very different P:L ratios than its relatives and was host to a different community of pollen-foraging visitors.

Nutritional Niches and Network Structure. Bees must navigate a variable environment in search of an appropriate diet that has direct fitness consequences (16, 50, 61). We know from manipulative experiments that pollen macronutrient content plays a key role in multiple dimensions of bee performance: For example, pollen protein and lipid content shape ovary activation and egg weight, larval weight and survival, learning and memory, adult immune function and survival, and colony reproduction (reviewed in ref. 11). Given this, we asked what role the pollen nutritional landscape found in natural communities played in structuring interactions with wild bees and found that explicit consideration of pollen macronutrient content shed light on bee–flower interaction networks in three ways.

First (*Question 1*), we asked how likely nutritionally similar plants are to be visited by similar bee communities. Our analysis revealed a diversity of strategies in *how* bees may achieve their macronutrient targets, via differing mechanisms of nutrient balancing. Namely, some similar bee communities (i.e., points near each other on PC1) are associated with plants that offer a range of pollen nutritional values (Figs. 4 and 5), indicating that some bees forage widely around their nutritional targets (if bees only foraged close to their nutritional target, we would expect to see the plant species' PC scores to lie close to the line of regression), perhaps even exhibiting a particular level of nutritional tolerance (33) (e.g., Halictidae genera *Lasioglossum* and *Halictus*, Fig. 5). In these cases, it may be that no single plant species' pollen aligns with bees' nutritional needs. Consistent with this pattern, we show that even some bee species classically considered to specialize on pollen from a restricted number of host plants (i.e., those considered oligolectic) do not forage from taxa strictly close to a single macronutrient ratio (e.g., *O. cornifrons* exhibits preferences for Fabaceae and Rosaceae which differ in P:L values (62), or *Megachile* here visiting Fabaceae and Asteraceae at opposite ends of the P:L spectrum).

Second (*Question 2*), we asked what role pollen nutrition plays in structuring broad patterns of bee–flower interaction networks. By assigning the most frequently interacting groups of bees and plants to modules and determining that these modules differ in pollen P:L ratios, we demonstrate that, even with environmental and community variation across our sites, the broad structure of the interaction network is comprised of nutritional niches (44, 63) (Fig. 5), providing an estimate of bees' nutritional intake targets and foraging strategies to obtain them. At a community level, bee nutritional niches may be established by bees sharing resources in a landscape yet occupying distinct nutritional space by collecting different macronutrient ratios based on collection frequencies or quantities from pollen hosts (36); e.g., compare *Bombus* and *Melanosmia* to *Dialictus* and *Lasioglossum* in Fig. 5. For example, bees and plants associated with the module characterized by the largest mean P:L value had the widest distribution of plants' P:L values, yet this module housed many of the most morphologically complex flowers (Fig. 5). Perhaps bees in this module, while requiring high protein pollen, still need to obtain lipids from plants to balance their high protein diet, resulting in visitation to a wider distribution of nutritional values. On the opposite end, we see a high level of nutritional specialization associated with the lowest P:L value module. This module was dominated by the family Asteraceae, and the bees foraged very narrowly within this group (64, 65). Finally, the modules with the highest numbers of plant and bee subgenera occupied intermediate P:L values and housed a spectrum of bees with both locally observed generalist and specialist foraging patterns. Supporting previous research, bumble bees (*Bombus spp.*) occupied the highest P:L module confirming they were assigned the niche shown in laboratory-based experiments to support their developmental needs (14–16, 18, 19). Interestingly, we found that related bee subgenera frequently differed in their assigned modules and potential intake targets (e.g., *Andrena*, *Perdita, Osmia*, *Anthophora*, etc. Fig. 5) indicating a potential mechanism of dietary adaptive radiation.

Finally (*Question 3*), we found that differences in pollen nutrition did not predict the strength or generalization of plants' roles in the network (Fig. 6 and *SI Appendix*, Fig. S7): Plants from any nutritional niche can be specialist or generalist, be of equal strength within an interaction network, and support diverse bee

communities. Further, the hypothesis that the most intermediate P:L values could support most bees by overlapping with most intake targets, and therefore create resilience in the network, was not supported here, nor was the hypothesis that high protein or high lipid content would drive preferences of most bee species (based on the presumption that a single macronutrient's concentration equates to quality).

Although these analyses suggest pollen macronutrients help structure bee–plant interactions, it is likely that additional ecological factors and reward traits operate alongside pollen to shape visitation patterns. For instance, competition among communities of floral visitors can influence which plants are accessible at any given time (66). Our network thus represents the realized, rather than fundamental, diet choices of bees; from a metanetwork perspective, differing levels and patterns of competition across sites could explain some of the intraspecific variation in floral visitation we observed. Like other foragers who must cope with suboptimal dietary prospects (for many reasons, including competition), bees might choose alternative yet still complementary hosts in pursuit of their nutritional target, as predicted by nutritional geometry theory (3, 36). A second important consideration relates to the chemical complexity of floral resources. While we focused here on pollen protein and lipids due to the evidence of their functional relevance to bee reproduction and floral choice (11), pollen micronutrients, such as essential fatty acids (51–53), amino acids (17, 35, 56), and sterols (50), as well as microbial symbionts (67), and specialized metabolites (21, 22), may also guide foraging preferences, but were not analyzed here. The degree to which chemical or physical pollen defenses covary with macronutrient content within an ecological community is an obvious but, to our knowledge, completely open question worthy of future consideration. More broadly, while we limited our observations to pollen-collecting bees, nectar collection often occurs alongside that of pollen, potentially adding some degree of noise to the visitation dataset as nectar traits can influence floral choice and response to pollen chemistry (68). Analysis of individual bee pollen loads to determine the mix of collected pollens would help refine our estimates of bee species-specific nutritional values (32) (*SI Appendix, SI 4*).

Potential Applications. The nutritional insights our study reveals may improve our ability to predict plant–pollinator interactions in altered landscapes, design habitat restoration protocols, and inform conservation efforts. A major concern in addressing wild bee population declines is the simple question, what plants to plant for bees? There are many factors to consider (10, 31, 69–72), but pollen is a critical nutritional resource for bees that our work shows deserves urgent attention. Beyond its relevance to larval and adult performance, floral nutrition can buffer bees against pathogens, environmental stress, and pesticides (20, 33, 34, 73–78). Here, we found that pollen nutrition across its community distribution attracted a diversity of bee visitors, and thus, pollen nutritional diversity may be critical for supporting bees that occupy different nutritional niches. In short, when it comes to pollen, a single plant species is unlikely to satisfy the nutritional needs of bee communities, even if it attracts the highest species richness, as a single pollen nutritional value may not represent the same quality for all bee species. As nutritional diversity was widely distributed in the natural systems we surveyed in this study, supporting bee functional and phylogenetic diversity in working lands may be in part accomplished through plant lists that represent the span of macronutrient values observed here or measured at baseline conditions specific to a region. The potential for plasticity in these critical dimensions of pollen chemistry and their effects on pollinators is a critical next step of research in the face of climate change.

Conclusions

The biological marketplace is a potent model for species interactions, shaping our understanding of both the evolution of mutualisms (79, 80) and competition among plants for pollination services (81). This microeconomic perspective has guided our understanding of resource selection by bees (82, 83) and has shaped our view of flowers as sensory "billboards," advertising their value via colors, patterns, and scents (2, 84, 85). Traditionally, the marketplace is characterized by a single currency (nectar sugar), and thus, basic questions about how nutritionally complex floral rewards structure community-level interactions have largely escaped study. Insights from the field of nutritional ecology indicate that foraging decisions often are driven by combinations of various nutrients distributed unevenly among food sources that foragers must regulate to achieve a physiological target. Adopting a nutritionally explicit approach toward understanding plant–pollinator interactions, we found that two focal pollen chemical traits (protein and lipid content), known to be highly relevant to bee performance in ecologically simplified model systems, helped explain patterns of association between members of wild bee and plant communities. A view of the pollination marketplace filtered through the lens of nutritional ecology may thus help uncover previously hidden drivers of bee community dynamics and ultimately suggest considerations for effective conservation of plants and pollinators.

Materials and Methods

Sample Collection and Analysis.

Bee observation, collection, and identification. We collected bee–flower visitation data across eight sites in the Great Basin/Eastern Sierra region (1,400 to 2,850 m in elevation; *SI Appendix*, Fig. S1) from April to August 2020 (66 d). On each collection date, we identified focal plant species within flower patches ≥25 m^2 (14 to 42 species per site in total; Dataset S1*A*) by walking 4 to 10 miles along trails, service roads, and open meadows (*SI Appendix*, Fig. S1). Along these routes, and within flower patches, we chose to observe plant species that had at least 10 individual plants in bloom (we recorded GPS waypoints of floral patches for revisiting).

For each plant species on each collection day, we spent approximately 10 min per plant species (in total ~87 h, Dataset S1*D*) collecting all bees observed contacting the anthers of the flowers, focusing on pollen collection behavior (40). We identified bees to the lowest taxonomic level possible (Dataset S1*B*), targeting the subgenus level using keys and nomenclature in refs. 6 and 86, discoverlife.org (87), and references therein (a more comprehensive list of bee identification references used is provided in *SI Appendix, SI 1*). We considered bees at the subgenus level (or genus level in the absence of described subgenera) due to 1) the difficulty in many groups' species identification (including lack of descriptions and keys), and 2) the observation that many bees within subgenera had similar foraging behavior and high species turnover between sites.

To focus on how pollen nutrition affects pollen collection behavior (and reduce the influence of nectar collection behavior on the visitation network), we filtered the bee–flower interaction dataset to include only female bees that were actively collecting pollen during their foraging bout (visually estimated to have scopa ≥10% filled with pollen). We excluded the genus *Hylaeus* because these bees carry pollen in their crop and we could not confirm pollen collection. We also did not collect bumble bee gynes and therefore only workers are included in the analysis. Bee specimens are stored at the University of Nevada, Reno Museum of Natural History (specific specimen collection numbers are provided in Dataset S1*B*).

Plant collection. We observed bee visitation from 138 wildflower plant species (131 native; Dataset S1*C*). We pressed specimens of plant species observed and all were identified to species, except for *Salix spp.* and a *Castilleja sp.*, by A. Tiehm (Herbarium Curator, University of Nevada, Reno Natural History Museum, but not kept due to redundancy). We categorized flowers by floral shape and anther

architecture using categories modified from ref. 88: "open" (open/bowl flowers with anthers fully exposed), "tubular" (tubular flowers with more recessed anthers), and "complex" (keel and poricidal flowers where pollen is not exposed). Finally, we categorized floral symmetry as radial (actinomorphic, ≥2 planes of symmetry) or bilateral (zygomorphic, 1 plane of symmetry). For each species, we measured 5 to 10 individual flowers to estimate floral size, including average width (corolla diameter) and depth (from flower base to anther tip; Dataset S1*C*).

Pollen collection and nutritional analysis. We analyzed a total of 109 species for pollen nutritional content. We harvested at least 10 mg pollen by hand from each plant species using techniques described in ref. 11 that include collecting pollen from flowers directly or extracting pollen from anthers (*SI Appendix, SI 2* and Dataset S1*C*). We determined fresh pollen protein and lipid concentration (μg/mg) and P:L ratios via established protocols slightly modified from ref. 11 (see the step-by-step protocol in *SI Appendix, SI 2*). Briefly, three 1 mg replicates from pooled pollen samples were used for both protein and lipid analysis. Protein concentration was analyzed with the Bradford assay using a NaOH extraction buffer for 24 h (disrupting ~78% of pollen grains; see table in *SI Appendix, SI 2*), and lipid content via SPV using chloroform:methanol:water lipid extraction. SPV lipid analysis is commonly used to estimate total lipid content but may be biased toward unsaturated fatty acids and exclude undigestible pollen lipid components (e.g., sporopollenin of the pollen exine). It may thus underestimate the total lipid content of pollen (54). However, these digestible unsaturated fatty acids (e.g., omega-3, omega-6, omega-9) are deemed important for bee health and perception (51–53), and thus comparative values across plant species have direct relevance to behavior and physiology.

Data analysis.

Question 1.

Principal components of bee–wildflower visitation. The pollen-collecting bee–flower interaction matrix contained 2,261 interactions between 101 plant species and 73 bee subgenera (Dataset S1*D*). We standardized the interaction matrix by dividing the number of bees in each subgenus by the total minutes spent observing each plant species to create a visitation frequency matrix (plant species by number of bees observed per minute observation). We conducted PCA on this interaction frequency matrix using the R package "*vegan*" [function *rda* and with *row total* standardization using the function *decostand* (89)]. Site scores represent individual plant species and their associated community of bee visitors where distance along either PC axis represents similarity in the composition of these communities. We used these scores as response variables in further analyses (Dataset S1*C*).

Factor analysis. The latent variables "nutrition" and "morphology" were estimated via factor analysis in JMP Pro v16 (SAS Institute Inc., Cary, NC). For nutrition, we used standard scores of plant species' pollen protein μg/mg, lipid μg/mg, and P:L ratio. For morphology, we used standard scores of floral width and depth; floral symmetry was scored as 0 for radial or 1 for bilateral; floral shape of open/tubular vs. complex was scored as 0 or 1, and floral shape as open vs. complex/tubular as 0 or 1 (Dataset S1*C*). We first used exploratory factor analysis of two factors including all variables to determine factor loadings and correlations. We then assigned variables to two separate factors associated with nutrition (protein concentration, lipid concentration, and P:L ratio) and morphology (symmetry, morphology, depth, and width), such that the effects of nutrition and morphology could be analyzed independently (*SI Appendix*, Fig. S6). We exported plant species factor scores for both nutrition and morphology to be used in further analysis (Dataset S1*C*).

Plant phylogeny. We tested for phylogenetic signal (Pagel's λ and Blomberg's K) in pollen nutrition using the R packages "*ape*" (90), "*pez*" (91), and "*phytools*" (92). We pruned the plant phylogenetic tree published by Smith and Brown (93) for plant species included in our dataset (Dataset S12). For species not in the tree, we chose closely related plant species in the same genus (only replacing *Eremalche* where *Sidalcea* was unavailable). For plants that we did not identify to species (e.g., *Salix*), we chose a species in the tree that occupied our study region. We created a between-species phylogenetic distance matrix using the *cophenetic* function in base R "stats" package and standardized it by dividing all pairwise distances by the maximum distance.

Phylogenetic multiple regression. We conducted Bayesian analyses using the R package "*rethinking*" (94) which uses "*Stan*" (95) and Hamilton MCMC to determine posterior distributions. We analyzed the effect of nutrition and morphology on the bee communities associated with each plant species (represented by plant species' PC1 or PC2 scores) in two separate ways (*SI Appendix*, Fig. S6 and *SI 3*): 1) nutrition represented by pollen P:L ratios and morphology represented by floral symmetry (models 1 to 3), and 2) nutrition and morphology represented by their factor analysis latent variable scores (models 4 to 6). We formulated three models for each: 1) total effect of floral nutrition on bee community associated with each plant species (models 1 and 4), 2) the stratified or counterfactual effect of floral nutrition and floral morphology on bee community (models 2 and 5), and 3) the stratified or counterfactual effect of floral nutrition and morphology including phylogenetic covariance [(Ornstein–Uhlenbeck process (94) of these factors on bee community (models 3 and 6)]. We used standardized scores of all input and response variables for analysis.

Question 2. We used network module analysis to test the hypothesis that groups of frequently interacting bees and plants represent nutritional niches. Modules represent aggregated sets of interacting bees and plants, where within-module interactions are greater than between modules (44, 45). To approximate nutritional niches, we analyzed the plants at the genus level because we wanted to represent groups of plants and bees over space and time that may have not been associated at a single site due to high levels of species turnover, and because we wanted to account for their similarity in pollen nutrition revealed through phylogenetic analysis. Using the R package "*bipartite*" (96–98) we determined modules using the function *metaComputeModules*, iterating the analysis 1,000 times; this analysis assigns each plant genus and bee subgenus a module identity. We repeated the analysis to verify consistency in module identification. We conducted Bayesian analyses using the R package "*rethinking*" and used adaptive priors to compare the distribution of P:L ratios of plant genera between modules by 1) plant genus identity where each plant genus within their assigned module was given equal weight, and 2) plant genus weighted by frequency of bee visitation within each module such that plants in the module that are more preferred or more visited (and likely contribute more to bees' nutrient balancing) are more accurately represented (Model 7, *SI Appendix, SI 3*).

Question 3. To evaluate whether plant species differ in their level of specialization in interaction networks based on pollen nutrition, we used the package "*bipartite*" and function *specieslevel* (97) to output the following indices for our focal plant species in the visitation frequency matrix: "species strength" (a quantitative measure of a plant's importance in the community via interaction frequency to a diversity of pollinators (99), "effective partners" (a standardized metric of bee diversity visiting each plant), "nested rank" (a metric of plant generalization/specialization as the rank of the plant when the community matrix is arranged for maximum nestedness), "D'" (a metric of species specialization/generalization based on its discrimination from random selection of partners (100), and both weighted and unweighted "betweenness centrality" (the importance of a species as a connector in the network) and "closeness centrality" (the proximity of a species to all other species, or importance to connectedness of the network) (101). These indices were chosen as a diverse set of typical analyses used to measure species-level specialization/generalization from plant–pollinator networks. We then ran Bayesian analysis on the linear effect of pollen nutrition on these indices using either P:L and symmetry, or nutrition and morphology factor scores (see models 2 and 4). To test whether plant species with pollens of intermediate values were more generalist than those with extreme high or low values, we ran Bayesian analysis on the quadratic effect of pollen nutrition on their network indices using either P:L or nutrition factor scores (model 8).

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

ACKNOWLEDGMENTS. We thank Jacob Francis for sharing knowledge of pollination ecology in the region, Sonja Glasser for help with flower collection, Eva Lin for help with pollen extraction, Danielle Salcido for discussions of network analyses, Arnold "Jerry" Tiehm for plant identification, and David Tank for assistance with plant phylogenetic analysis. This research was supported in part by US Department of Agriculture, Forest Service; the findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. This project was supported by funding from NSF grant number NSF IOS–1755096 to A.S.L.

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